

Advection-diffusion models of spiny lobster *Palinurus gilchristi* migrations for use in spatial fisheries management

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ABSTRACT: Advection-diffusion models were constructed to simulate migration patterns of juvenile and adult spiny lobsters off southern South Africa. Models based on tag-recapture information collected between 1978 and 2005 (2665 tag recaptures) were used to quantify directional movements and to estimate distances moved along a bathymetric gradient. Sex, length at tagging, tagging area and time at large were the main explanatory variables considered. Empirical tests showed that tagging did not delay the onset of advective movements. Lobsters were advected from west to east, and no return migrations were observed. Advection was strongly size dependent, with juvenile and small mature individuals moving further than larger adults. Advection was also area dependent, decreasing from west to east, and lobsters at the easternmost site were not advected and did not receive immigrants from elsewhere. Juvenile lobsters tagged at a recruitment hotspot at the westernmost site migrated 100 to 250 km onto the Agulhas Bank (90 % probability after 5 yr at large), or continued along the coast to more distant sites (400 to 900 km; 10 % after 5 yr). This effect was stronger in males, but we could not detect a trade-off in growth rate. Two theories are advanced to explain these migration strategies: evolutionary effects of past range expansions and density dependence. A novel approach for quantifying migrations in spiny lobsters is demonstrated, for potential use in spatial fisheries management.

KEY WORDS: Advection · Bathymetric gradient · Fisheries management · Migration models · Tag-recapture

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INTRODUCTION

Quantitative models to describe large scale movements are instrumental for the spatial management of exploited fish populations, because they can be used to predict the effects of a fishery operating in one area on the yield of a fishery operating elsewhere (Sibert et al. 1999, Goethel et al. 2011). In general ecological research, these models are not restricted to adult fishes that can be tagged and recaptured to infer movement patterns, but have also been used to estimate larval dispersal patterns, based on advection-diffusion concepts and oceanographic data (Hill

1990, Chiswell & Booth 1999, Largier 2003, Rudorff et al. 2009). Movement models are also useful for deciding the configuration of marine reserves, where connectivity through larval and/or adult dispersal is sought, particularly in areas with large alongshore advection rates (Stockhausen et al. 2000, Kaplan 2006).

Several general classes of models can be applied to the quantitative analysis of fish movements, as summarized by Sibert et al. (1999) and Goethel et al. (2011). Bulk-transfer (or box-transfer) models, where exchange rates between regions are characterized by transfer coefficients, have been applied to migra-

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tory tuna stocks (Hilborn 1990, Hampton 1991), but they are not continuous in space and therefore cannot predict the changes in population density at an arbitrary point. Diffusion models have a long history in animal ecology (Skellam 1951). These models ultimately produce a uniform distribution of a population at equilibrium, except if directional movements are incorporated by adding 'advective' terms (Okubo 1980). Advection-diffusion models have been applied to estimate movement parameters for yellowfin (Deriso et al. 1991) and skipjack tuna (Kleiber & Hampton 1994, Sibert et al. 1999), based on tag-recapture data. State-space models that may require nonlinear methods to include animal behaviour (i.e. changes between behavioural states) have been described by Jonsen et al. (2003). In the last few decades, tag-integrated stock assessment methods in fisheries have allowed the explicit incorporation of movement among spatially discrete sub-populations (Goethel et al. 2011).

Spiny lobsters exhibit movement patterns that range from dispersal of pelagic larvae by oceanic processes (Cobb 1997) to movements by juveniles or adults on the seafloor to find food, shelter, or reproduce (Herrnkind 1980). The latter movements may be nomadic or homing (periodic excursions from a shelter with subsequent return), or they may be migratory, involving directional movements made by distinct parts of a population over relatively long distances within a confined time period (Herrnkind 1980). Long-distance migrations on the seafloor sometimes occur against prevailing currents (contranant; Meek 1915) to redress downstream dispersal of pelagic larvae, and comprise pre-adult benthic individuals recruiting to adult populations (Moore & MacFarlane 1984, Bell et al. 1987, Booth & Phillips 1994, Booth 1997, Groeneveld & Branch 2002).

The most widely used technique to examine the movement patterns of marine animals is the attachment of external tags, along with instructions for reporting of recaptured animals (Semmens et al. 2007). In lobster research, anchor tags are typically inserted into the abdominal muscle of lobsters, and recaptured individuals are used to evaluate somatic growth, mortality rates or movement patterns. Long-term tagging programmes exist for several commercially important lobster stocks (Phillips 1983, Haakonsen & Anoruo 1994, Groeneveld & Branch 2002, Gardner et al. 2003, Linnane et al. 2005). There are several potential disadvantages to using anchor tags, however, including variable recapture and/or reporting rates (Frusher & Hoenig 2001), tag loss or shedding (Montgomery & Brett 1996), and causing lethal

or sub-lethal injuries (Brouwer et al. 2006). Lobster growth rates may be retarded as a result of physical injuries or physiological stress (Vermeer 1987, Dubula et al. 2005, Haupt et al. 2006). Similarly, tagged lobsters released at the sea surface may be displaced and disoriented by strong currents, which could lead to a delay in the onset of migrations.

Commercial quantities of the spiny lobster *Palinurus gilchristi* were first discovered in 1974, and the species now supports the second largest lobster fishery in South Africa, with landings of approximately 1000 t yr⁻¹ (Groeneveld et al. 2013). Fishing takes place along the southern Cape coast, between Cape Point (18°E) and East London (28°E) on rocky patches between 50 and 200 m depth (see Fig. 1). Given its economic importance, a management strategy for the fishery has been in place since the late 1970s (Pollock & Augustyn 1982), and for this purpose, catch, effort, length-composition and tag-recapture data have been collected regularly and are used in annual resource assessments (Groeneveld et al. 2013).

An extensive tag-recapture database spanning from 1978 to the present has been used to estimate growth rates of *Palinurus gilchristi* (Groeneveld 1997), and also to infer benthic movement patterns (Groeneveld & Branch 2002). Counter-current migrations of pre-adult lobsters of both sexes against the net flow direction of the Agulhas Current, presumably to redress downstream dispersal of drifting larvae, have been demonstrated. In conjunction with the migration pattern, lobster populations along the coast exhibited considerable spatial heterogeneity, with mean size increasing from west (downstream) to east (Groeneveld & Branch 2002). Lobsters at the easternmost site (Port Alfred, at the upstream end of the species distribution) did not migrate, grew slower and had lower fecundity than elsewhere (Groeneveld 1997, 2005). Nevertheless, no genetic population structure could be observed over the geographic distribution range of *P. gilchristi* (Tolley et al. 2005), thus supporting a well-mixed gene pool.

We used tag-recapture data to develop quantitative advection-diffusion models of dispersal for *Palinurus gilchristi*, and to test the effects of tagging on migration rates. The present study extends the work on long-distance migrations of *P. gilchristi* undertaken by Groeneveld & Branch (2002), to refine and quantify migration for use in the development of spatial management strategies. To our knowledge, this is the first attempt to use advection-diffusion concepts to quantify dispersal of benthic marine fauna.

MATERIALS AND METHODS

Field work

The tagging programme was described in detail by Groeneveld & Branch (2002). In brief, scientists stationed on commercial fishing boats tagged lobsters in 5 areas: from west to east these were Cape Agulhas, West and East Agulhas Bank, Mossel Bay to Algoa Bay and Port Alfred (Fig. 1). The areas were geographically distinct, except for West and East Agulhas Bank, which were contiguous, but could be distinguished based on different depths and distinctly different size frequencies of lobsters occurring in each.

Some tagging occurred in 1978 (see Pollock & Augustyn 1982), but the bulk of tagging expeditions were undertaken between 1988 and 2005 (no tagging in 1989, 1991, 1994, 2000 and 2001). Due to the unfeasibility of tagging lobsters in all 5 areas in each year, greatest effort was concentrated at Mossel Bay to Algoa Bay (the largest area; 8 trips), followed by West and East Agulhas Bank (4 trips each), and Port Alfred and Cape Agulhas (2 trips each).

Standard numbered plastic T-bar anchor tags (Hallprint TBA-1) were inserted into the abdominal muscle of each lobster, dorso-laterally between the posterior edge of the carapace and the first abdominal segment, or between the first 2 abdominal segments. Sex, carapace length ($CL \pm 0.1$ mm, measured mid-dorsally from the tip of the rostrum to the posterior edge of the carapace), depth and date of tagging were recorded. After being tagged, lobsters were immediately released at the sea surface, and the geographic position of release recorded.

Tagged lobsters recaptured by the commercial fishery were returned to fisheries inspectors at landing points. A tag-reward system was used as an incentive to encourage the return of tagged lobsters, together with information on the date, location and depth of recapture. These data provided information on the time between release and recapture (time at large, in d), as well as distance, direction and rate of movement for each lobster.

Quality control of data

The full set of observations consisted of 2665 recaptured lobsters out of 40 030 tagged individuals between 1989 and 2005 (6.7% recapture rate). The tagging location, time, depth, sex, and size variables were measured by researchers, and the quality of these observations was therefore considered to be

better than the recapture coordinates, time and depth, which were measured by fishermen, and sometimes coarsely or poorly recorded in logbooks. Certain observations were thus discarded if they clearly indicated unlikely recapture positions.

Movement and distance

The distance between the points of capture and recapture was calculated in 2 ways. The first was the shortest distance between 2 points on the surface of the globe, namely an arc commonly denominated as the great circle (GC) distance. The distribution of the points of capture and recapture (Fig. 1) seemed, however, to indicate convoluted dispersal paths along defined bathymetric lines. A more realistic description of distance was thus calculated using the median depth of captures and recaptures in each fishing area, and assuming an advection pathway along a bathymetric contour connecting these median points. The westernmost point of tagging (Lat.: 34.084° S, Long.: 18.212° E) was defined as the origin (the geodetic datum) of the advection pathway, i.e. km 0. The local perpendicular deviation of each sampling point to the advection pathway, either at tagging or at recapture, was considered to be a measurement of diffusion (Fig. 2). The total distance elapsed was thus considered to be the sum of 2 diffusion segments (A to A' and B' to B) and advection (A' to B'). The advection distance (ADV, km) was measured as the difference between points B' and A' in the datum line.

The calculation of all lobster movements was performed using the ArcMap 9.2 GIS software package. The software features used included 'Topo to Raster' interpolation, surface length 3-dimensional distance calculation, as well as the lines to points and distance between points Hawth's Tools plugins. The data projection used was the World Geodetic System WGS_1984_UTM_Zone_34S. Bathymetry data was obtained from Shuttle Radar Topography Mission (SRTM) SRTM30_Plus, a global 30 arc second grid of depth values, derived from a compilation of single and multibeam echo-soundings (Becker et al. 2009). The first movement calculation method, the straight-line distance, involved evaluating the total distance travelled from point A to point B, using the surface length tool. For the second method, a Digital Elevation Model was first created from SRTM bathymetry lines using the Topo to Raster interpolation tool, and median depths were determined from extracted z-values of all tag and recapture points in each area (Area 4 was split into 4a and 4b). A shapefile contain-

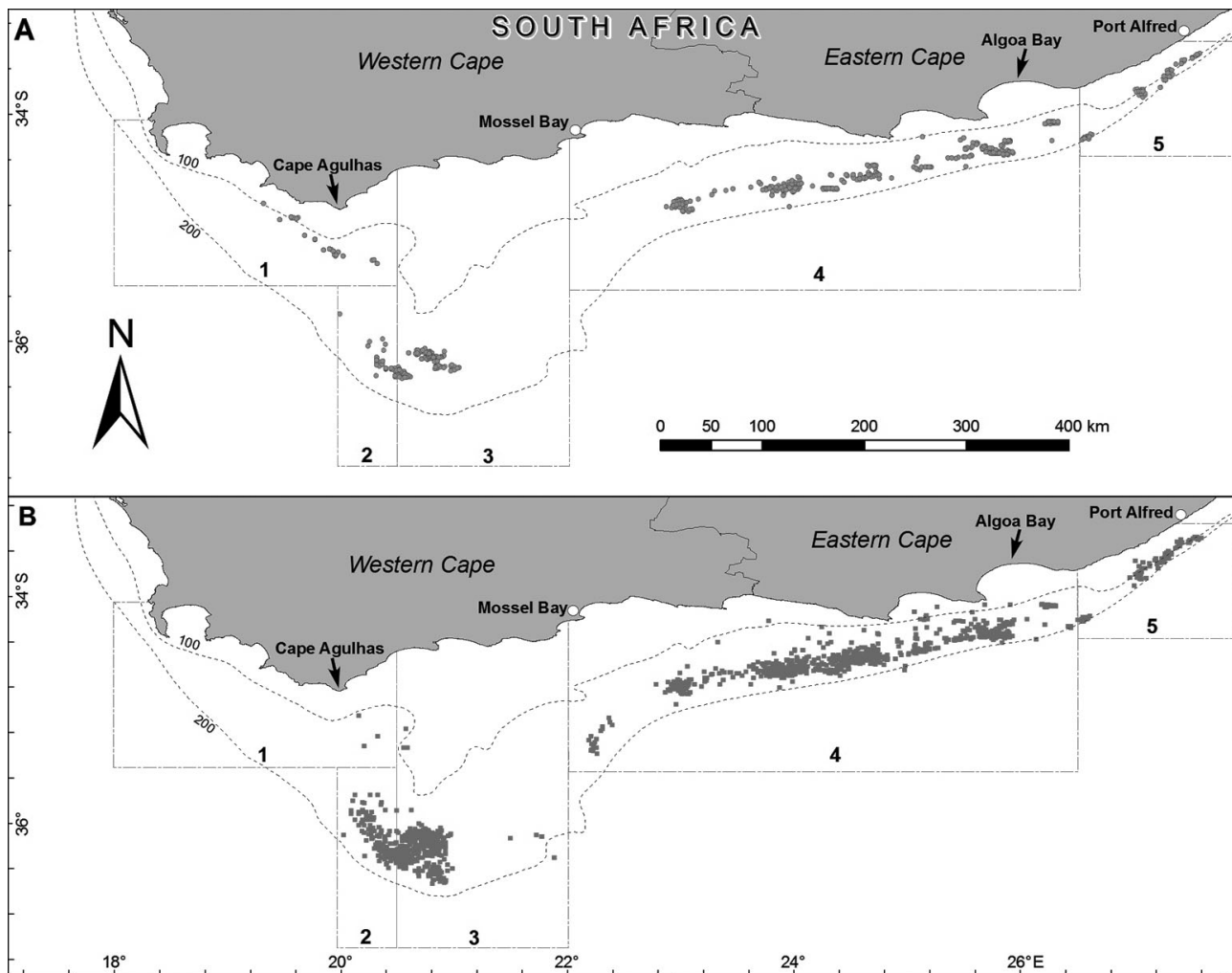


Fig. 1. (Figure continues on next page) Southern coast of South Africa showing the 5 sampling areas, Cape Agulhas (1), West Agulhas Bank (2), East Agulhas Bank (3), Mossel Bay to Algoa Bay (4), and Port Alfred (5). (A) Locations of release of tagged lobsters in batches; (B) individual recapture positions; (C) Straight-line trajectories of lobsters that moved >100 km—all movements of this distance were in an eastwards direction; and (D) the proposed advection gradient. Distances measured at the boundaries of the 5 sampling areas are relative to the geodetic datum (0 km) at the westernmost origin of the migration path

ing numbered points (ADV_s) at 1 km intervals along the unified and smoothed median depth line was then generated using the lines to points Hawth's Tools plugin. Using this shapefile, the 3 distance components (tag points to nearest ADV₁, ADV₁ to ADV₂, and recapture points to nearest ADV₂) were calculated with the distance between points Hawth's Tools plugin.

Data analysis

The movement model comprised 3 probabilistic and independent sub-models: the first was an analysis of the direction of movement; the second was a

quantification of the advection distance along the median depth; and the third was a model of the diffusion distance from the median line. The sum of advection and diffusion to and from the median line is here called the dispersal distance. It is important that the resulting dispersal model be simple and robust to be useful for prediction of individual migration and in population management. Preliminary analyses were performed to test whether tagging itself interfered with lobster movements between areas. The latter analysis investigated whether truncation of the data would remediate bias. Truncation of observations based on increasing time at large could correct for initial retardation of body growth as a result of tagging effects (J. Santos pers. obs.).

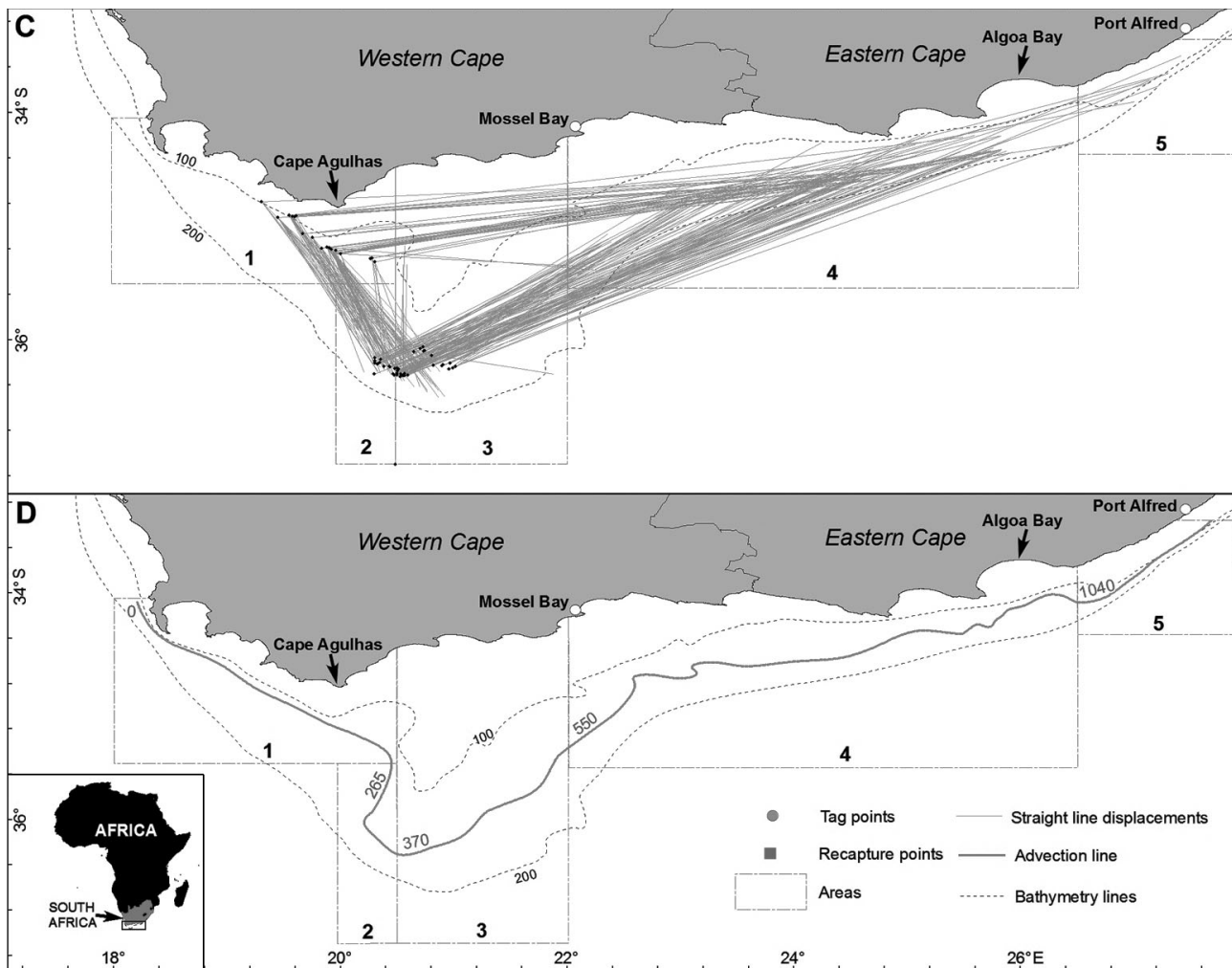


Fig. 1 (continued)

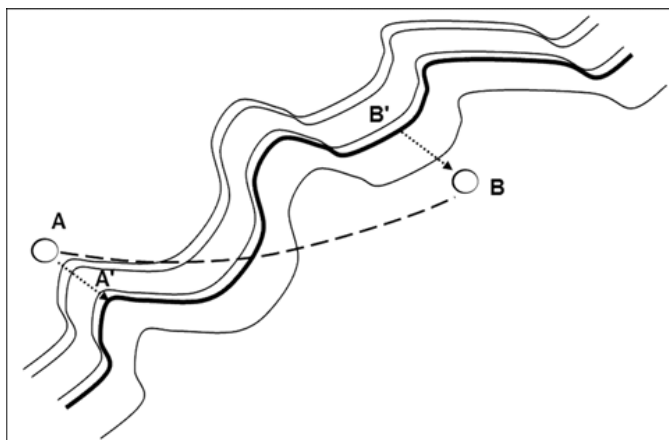


Fig. 2. Conceptual diagram for calculation of distances migrated between points A (tagging) and B (recapture). The total distance elapsed was calculated as the sum of 2 diffusion segments (A to A' and B' to B) and advection (A' to B'). The dashed line represents the great circle distance

Directional analysis

The fishing areas where capture and recapture took place were ordinated from 1 to 5, from west to east. Ordinal regression (Guisan & Harrell 2000), a type of generalized linear model (GLM), was utilized with area of recapture ($Area_R$) as the dependent variable, area of tagging ($Area_T$) and sex as predictor factors, and size (CL) at tagging (L_g , mm) and time at large (Δt , yr) as covariates in the main model:

$$Area_{R[1-5]} = Area_{T[1-5]} + sex_{[2]} + L_g + \Delta t \quad (1)$$

The bracketed subscripts indicate the number of levels of each discrete variable. As is normally the case in ordinal regression, the statistical output was a cumulative percentage; in the present case, of the dispersal of tagged lobsters to different areas. Ordinal regression was considered to be appropriate for

the analysis of direction, because the fishing grounds could be ordered in a geographic sequence (1 to 5, in that order) and we think that lobsters can only move between consecutive areas, as for instance from Area 3 to Area 4 or Area 2. Nevertheless, these grounds had different areas and distances that were not directly quantified in the model. Ordinal regression only requires the assumption that individuals migrated between areas, from west to east, or in the opposite direction, in a stepped manner, irrespective of distance.

In addition to the main model, a number of plausible interactions among variables were also included and tested. Different link functions were tried initially and on many occasions the ordered logit performed slightly better than other functions. The search for adequate error distributions was guided by the Akaike information criterion (AIC), but formal testing of the goodness of fit was performed with likelihood ratio tests (LRT) (Dick 2004). In order to search for possible effects of tagging on movement, the original datasets for each area were truncated by sequential removal of the lobsters according to their time at large. Thus, we tested the full dataset initially, then repeated the analyses after removing increasingly larger sub-sets of data. The criterion for removal was Δt , i.e. lobsters that were at liberty for shorter periods were removed first. If tagging induced some form of delay before the onset of movements, a disproportionately faster movement of lobsters at liberty for longer than the recovery period would be expected. The duration of the (average) recovery period would probably be indicated by a clear inflection in the expected movement.

Distance analysis

Advection distance (D_{adv} , km) was predicted by means of a GLM:

$$D_{adv} = ADV_1 + \text{sex}_{[2]} + L_g + \Delta t \quad (2)$$

In several trials we also included the individual observations of specific growth rate as a covariate in the model, calculated as $\ln(L_r/L_g)/\Delta t$, where L_r is size (CL) at recapture. The distribution of the observations used for the advection model presented some challenges that demanded a partition of the model. Some lobsters presented (generally small) negative values of advection from the datum along the reference bathymetric line, i.e. they moved from east to west. This could have been caused by actual dispersal in that direction or misreporting of the precise

position of recapture, or introduced by the calculation method itself or our simplistic formulation of advection. To obviate this, we transformed all advection distances into rational numbers equal to or larger than zero. Thus, this model considered only the absolute value of the movement rather than its direction, which was dealt with in the directional analysis above. The number of zeros (i.e. lobsters that apparently did not move by advection) was relatively large, and furthermore, the positive values of D_{adv} were considerably skewed to the right, i.e. towards long distance movements. This distribution (numerous zeros, strong positive skew) is frequent in fisheries data and is appropriately dealt with in 3 steps by hurdle models (Pennington 1983, Maunder & Punt 2004). In the first step, the probability of a non-zero advection was modelled by means of logistic regression using a GLM with an initial model structure similar to Eq. (2), and assuming a binomial error distribution. In the second step, only the positive (non-zero) movements were modelled using Eq. (2), and assuming a continuous error distribution of the exponential family. Analysis of the conditional data showed that the logarithm of the variance in distance migrated (advection) per unit time at large (Δt) related linearly to the logarithm of the mean distance with a slope of 2.1 (1.9 to 2.4, 95% CI). This is close to 2.0, the expected slope relationship for observations that have a constant coefficient of variation; these are appropriately described by a gamma error structure in GLMs (McCullagh & Nelder 2000). The final step involved combining the outputs from the 2 models in order to estimate the expected advection distance for a specific set of values of the explanatory variables.

Each tagged individual performed a diffusive movement from the tagging place to the median line, and from the median line to the recapture position. For simplification we modelled only the diffusion distance (D_{dif} , km) performed at recapture and generalized for all individuals in the 5 areas. The model structure could be greatly simplified in relation to that of advection without major loss of information:

$$D_{dif} = \text{Area}_{R[5]} \quad (3)$$

Although no zeros (i.e. no diffusion) were present, the distribution of observations was positively skewed. The variance to mean relationship of diffusion distance in the different areas had a slope of 1.6 (0.9 to 2.3, 95% CI), and therefore a GLM regression with gamma-distributed error and log link was selected. The gamma distribution is becoming increasingly used in studies of dispersal to describe the patterns of travel times and rate of spread in heterogeneous

populations (Yamamura 2002, Gurarie et al. 2009). All models tested included a constant, and only variables found significant ($p < 0.05$) in analysis of deviance were retained. Plausible first-order interactions were tested in the distance models, but none were significant and they were therefore omitted from the saturated models. Formal tests of the goodness of fit were performed using the LRT of the selected model against the null model (intercept only) and the saturated model. Confidence intervals for the estimates in Eqs. (2) (hurdle model) and (3) were obtained using parametric bootstrapping (see Fletcher et al. 2005). The estimates of the mean and SD of the parameters retained in the different models, as well as the constraining information contained in their covariance matrices, were used to generate 10 000 samples with replacement. These normal covariates were utilized to perform 10 000 realizations of the retained models for selected scenarios, and the confidence intervals were calculated from the 2.5th and 97.5th percentiles. All GLM fits and simulations were conducted using SPSS 19 (IBM) and R statistical software (www.r-project.org), including the libraries MASS and Rcmdr.

RESULTS

Depth of capture

The assumption that lobsters migrate within a defined bathymetric range (approximately 50 to 200 m depth) was supported by the available tagging and recapture data. Initial capture depth ranged between 71 and 200 m (median depth of 123.2 m, $n = 2758$), and recapture depth obtained from fisher logbooks ranged between 51 and 243 m (123.6 m, $n = 2752$). Most lobsters were captured and recaptured between 100 and 200 m depth (93.4 and 90.1%, respectively). Median depths by area were 125 m (Cape Agulhas), 165 and 145 m (West and East Agulhas Bank), 120 and 112 m (2 sections of the Mossel Bay to Algoa Bay area) and 110 m (Port Alfred).

Sex ratio and size composition

The sex-ratio of recaptured lobsters was generally skewed, with males predominating in 2348 recaptures made in Areas 1 to 4 (mean sex ratio of 1.6:1; Pearson's χ^2 test of independence; $p < 0.001$ in Areas 2 to 4), and females predominating in 317 recaptures made in Area 5 (0.5:1; $p < 0.001$). Lobsters were

clearly larger in Areas 3 and 4, but even in these areas, a number of smaller individuals were tagged (Fig. 3). The mean carapace length at tagging ($L_g \pm SD$) was 75.0 ± 9.9 mm, while after an average time at large of 2.0 ± 1.98 yr, recaptured lobsters had a mean carapace length (L_r) of 80.0 ± 10.0 mm. The minimum time at large was 4 d and the maximum 14.7 yr; however, only 9 lobsters were recaptured after 10 yr at liberty.

Heterogeneity of distance measurements

GC distances greatly underestimated the real distances moved by lobsters, particularly those that moved longer distances. On average the calculated advection distances alone exceeded the GC distances by 22%. This was most evident in small lobsters tagged in Area 1 and recaptured many years later in Areas 3 and 4. The distances migrated along the advection pathway were clearly longer than first expected from spherical geometry; for instance 900 versus 650 km in the furthest migration.

Delays in advective movements

Ordinal regressions of the expected areas of recapture for combinations of the 3 explanatory vari-

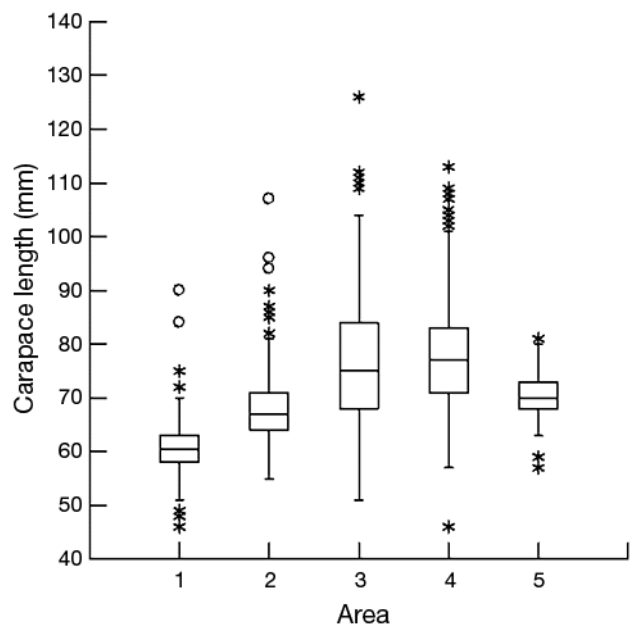


Fig. 3. *Palinurus gilchristi*. Carapace lengths (CL, mm) of spiny lobsters tagged in 5 areas, showing the median, 25th and 75th quartiles, the whiskers with maximum 1.5× interquartile range, outliers (asterisks), and far outliers (circles)

ables, area of tagging, lobster size and time at large (Fig. 4), showed no clear discontinuities indicative of delays in advection movement caused by tagging. Truncation of datasets by removing recaptures made within 6, 12, 18 and 24 mo of tagging made little difference to the location of recapture, as inferred from the narrow, parallel bands within which cumulative probabilities ranged. Thus, tagging did not appear to affect the observed movements, and further analyses were performed using the full datasets.

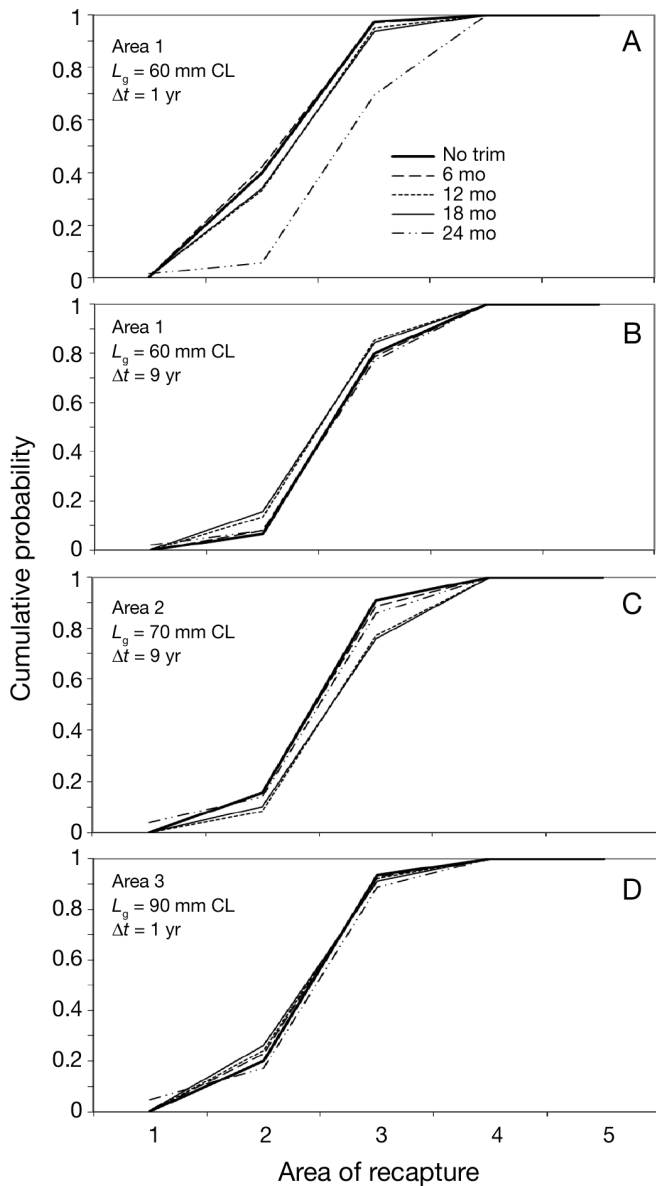


Fig. 4. *Palinurus gilchristi*. The cumulative probability of recapturing lobsters tagged in Areas 1 to 3 in any of the 5 areas, based on data truncated by sequentially removing individuals at large for periods between 6 mo and 2 yr

Area dispersal

Lobsters tagged in Areas 1 to 4 tended to accumulate in Areas 3 and 4, with very little straddling to Area 5 (Table 1). The ordinal regression predicted that after 5 yr at large, a lobster of 60 mm CL tagged in Area 1 would have a probability close to zero of being found in that area, increasing to about 15% in Area 2, 75% in Area 3, and 10% in Area 4, and it would not be expected to be found in Area 5 (Fig. 5A; upper dashed line). The same trend of advection northeastwards also occurred in Areas 2 and 3 and increased with time at large, but decreased significantly as the length at tagging increased (Table 2; Model 1, Fig. 5B–D). Thus, a lobster of 77 mm CL tagged in Area 3 had a 20% probability of being recaptured in the same area after 13 yr, and this probability increased strongly with size (Fig. 5B,C). A lobster of 78 mm CL in Area 4 is expected to remain within this area, with only about 2% probability of being recaptured in Area 5 after 9 yr at large (Fig. 5D). Similarly, a lobster of 71 mm CL in Area 5 will remain in the tagging area, with less than 1% probability of being recaptured in Area 4 after many years (Fig. 5E). These expected probabilities of straddling are larger than the observed frequencies: only 0.3% of the lobsters tagged in Areas 1 to 4 were found in Area 5, and 0.9% of the lobsters tagged in Area 5 were found in Area 4. The largest expected probabilities of straddling occurred only for long times at large (9 yr or longer), and are mainly extrapolations that are not well supported by the core of the field data.

Advection and diffusion distances

The probability of detecting advection movement in tagged lobsters declined solely as a function of geodetic distance in both Areas 1 to 4 and Area 5, with little improvement brought about by more com-

Table 1. *Palinurus gilchristi*. Individuals and corresponding areas of tagging and recapture considered in the present analysis (n = 2665)

Area of tagging	Area of recapture				
	1	2	3	4	5
1	3	60	49	37	1
2		121	52	31	–
3		32	644	74	2
4				1239	3
5				3	314

plex model formulations (Table 2; Models 2 and 5, LRT, D -statistic). For example, zero lobsters were stationary in Area 1, but a greater proportion of them made no advection movements in Areas 3 and 4. The

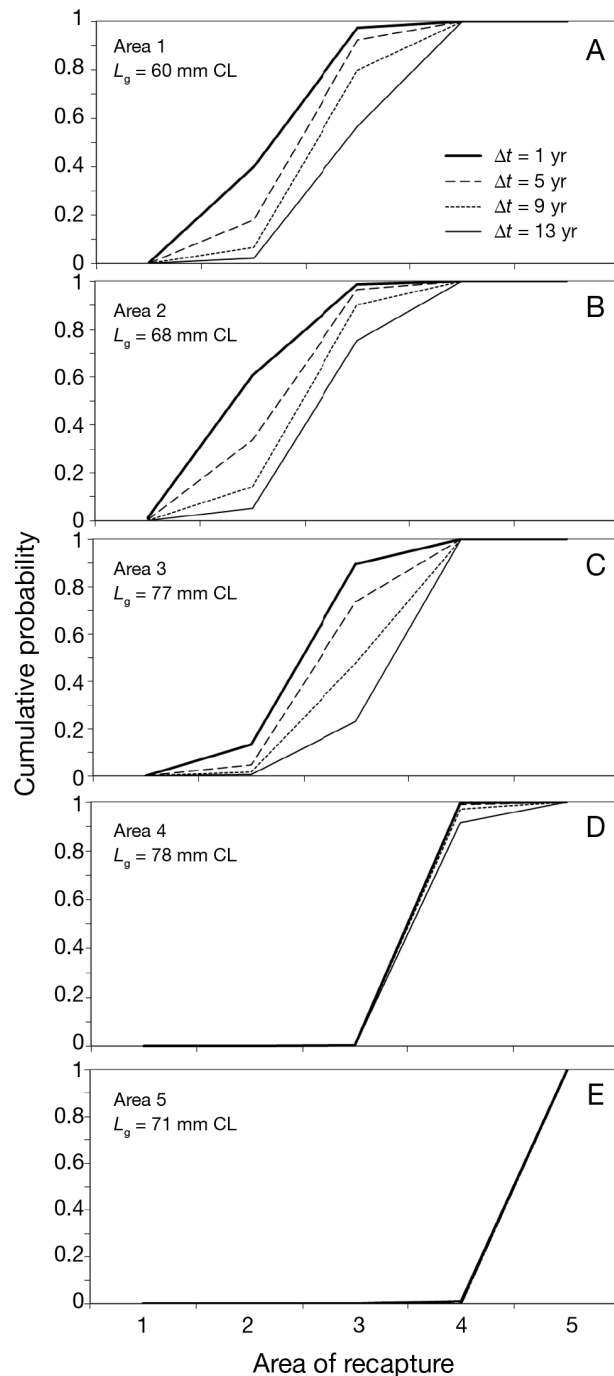


Fig. 5. *Palinurus gilchristi*. The cumulative probability of recapturing a lobster tagged in a given area in any of the 5 areas using the full dataset and the areal (directional) model, illustrated for a range of different lengths at tagging (L_g) and times at large (Δt)

range of advection distances covered (0 to 900 km) was large for a given time at large, particularly in Area 1 (Fig. 6). This was partially explained by the gamma model (Table 2; Model 3), which indicated that advection decreased with geodetic distance, but increased with time at large, and was partially sex-dependent. Although males tended to move longer distances than females in Areas 1 to 4, a gamma model without the sex variable also fitted the data well (AIC of 16 700 in the saturated model vs. AIC of 16 708 in sex-restricted model). On average, lobsters of both sexes and mean sizes 60, 70 and 80 mm CL released in Areas 1, 2 and 3, will have migrated about 330, 120 and 60 km towards the NE after 7 yr, respectively (Fig. 7). These differences conjugate the effects of release point and size at release. In all attempts to introduce the growth rate of lobster into the advection and diffusion models, this covariate failed to demonstrate significant effects ($p = 0.2$ to 0.6).

Modelling the extent of diffusion proved to be more difficult. Although the gamma error distribution provided the best fit, none of the covariates and factors, other than the area of release, provided a good description of the variability in diffusive distance (Table 2; Model 6). The average diffusion distance from the median depth was highest in Areas 1 and 3 (12 to 13 km), and in all other areas it ranged between 4.5 and 6.5 km from the median depth. As a consequence, the advection to diffusion ratio was very high for small lobsters that were advected long distances, but the 2 types of movements were virtually indistinguishable in lobsters >90 mm CL (Fig. 8). Although advection and diffusion distances could be distinguished in Areas 1 to 4 (Fig. 9A), the trend was different in Area 5, where advection and diffusion distances were similar, even for relatively small lobsters (Fig. 9B). It therefore appears that Area 5 was dominated by random diffusive dispersal. Although the available predictors could clarify much of the variability in elapsed distances over time, there appears to be some discrepancy between long-distance and short-distance migrants (see Fig. 6) that was difficult to account for.

DISCUSSION

The model of advection-diffusion along a bathymetric gradient realistically simulated the major migratory features of *Palinurus gilchristi* (see Groeneweld & Branch 2002): a west to east directionality without return migrations; migrants were mainly

Table 2. *Palinurus gilchristi*. Coefficients (\pm SE) of the parameters in the generalized linear models that describe the direction of movements (Model 1), and the distances advected (Models 2 to 5) and diffused (Model 6). Models indicated by Δ are hurdle models for a region, and variables or tests marked (–) were not relevant in particular models. The 5 areas are Cape Agulhas (1), West Agulhas Bank (2), East Agulhas Bank (3), Mossel Bay to Algoa Bay (4) and Port Alfred (5). The significance of the coefficients and the likelihood-ratio tests (LRT) of the selected model in relation to the null and the saturated models are also given. Significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Movement Area	Ordered (area) Areas 1–5	Advection (km) Areas 1–4		Advection (km) Area 5	Diffusion (km) Areas 1–5	
Model number	1	2	3	4	5	6
Error Link	Polytomous Ordered logit	Δ Binomial Logit	Δ Gamma (1) Log	Δ Binomial Logit	Δ Gamma Identity	Gamma Log
n	2665	2345	2072	320	227	2665
Intercept	–	3.5 (0.21)***	8.7 (0.34)***	1.32 (0.187)***	147 (40.2)***	2.5 (0.45)***
Length tag, L_g (mm)	–0.04 (0.005)***	–	–0.06 (0.004)***	–	–	–
Time at large, Δt (yr)	0.28 (0.031)***	–	0.16 (0.023)***	–0.18 (0.063)**	–	–
Sex (males)	–	–	0.20 (0.091)*	–	–	–
ADV1 (km)	–	–0.002 (0.0003)***	–0.002 (0.0002)***	–	–0.122 (0.035)***	–
Area tag 2	–0.53 (0.240)***	–	–	–	–	–
Area tag 3	2.1 (0.23)***	–	–	–	–	–
Area tag 4	10.3 (0.37)***	–	–	–	–	–
Area tag 5	20.3 (0.22)***	–	–	–	–	–
Area recapture 2	–7.4 (0.03)***	–	–	–	–	–0.95 (0.452)*
Area recapture 3	–2.4 (0.37)***	–	–	–	–	0.04 (0.449)
Area recapture 4	1.6 (0.38)***	–	–	–	–	–0.64 (0.449)
Area recapture 5	13.3 (0.55)***	–	–	–	–	–0.80 (0.451)
LRT- D (df) ^a null	4385 (9)***	70 (1)***	3114 (4)***	9 (1)**	12 (1)***	335 (4)***
LRT- D (df) saturated	1.2 (1)	2.5 (3)	–	2.7 (3)	10 (3)**	7.0 (3)*

^a D -statistic, chi-square distributed

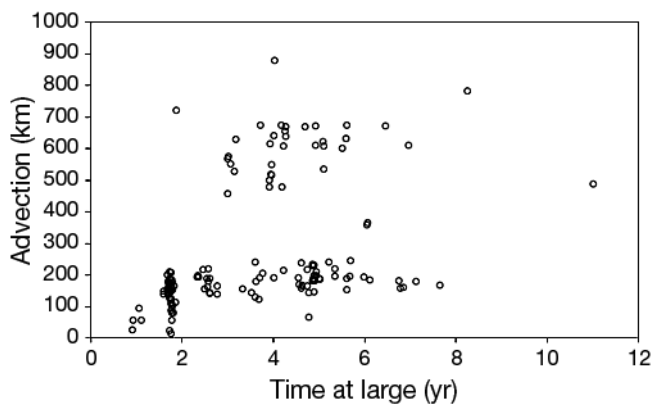


Fig. 6. *Palinurus gilchristi*. Advection distances as a function of time at large for small lobsters tagged in Area 1, showing a large degree of heterogeneity in distances advected (100 to 250 km and 400 to 900 km), irrespective of time, after >2 yr at large

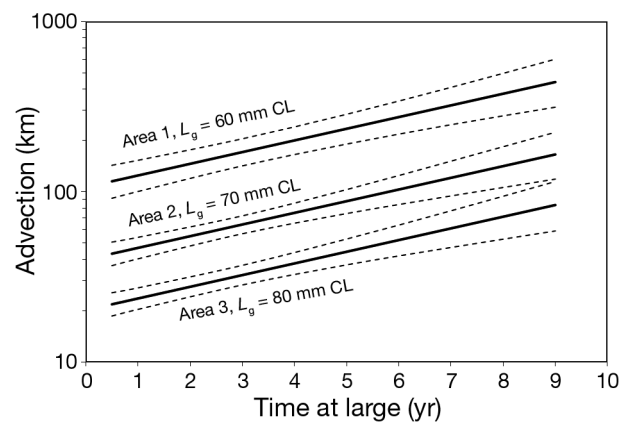


Fig. 7. *Palinurus gilchristi*. Predicted advection distances with increasing time at large for a selection of areas and lengths at tagging (L_g). Dashed lines indicate the 95% confidence limits of the distance estimates. Distances are given in logarithmic scale

small pre-adults; larger lobsters moved far less, or not at all; lobsters tagged near the downstream edge of the distribution range (Area 1; Cape Agulhas) were most likely to migrate, and travel furthest towards the east; and lobsters tagged near the upstream edge (Area 5) did not participate in migrations, other than

diffusive movements. The present migration analysis furthermore confirmed the presence of 2 populations, with no or little intermixing through benthic migrations: a southern population (Areas 1 to 4; Cape Agulhas to Algoa Bay) and an eastern population at Port Alfred (Area 5).

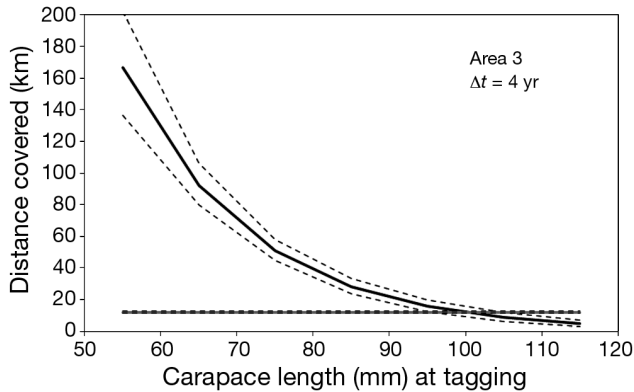


Fig. 8. *Palinurus gilchristi*. Predicted distances covered by advection (black line) and diffusion (grey line), respectively, of lobsters of a range of sizes tagged in Area 3 and at large for 4 yr. Dashed lines indicate the 95% confidence limits of the distance estimates

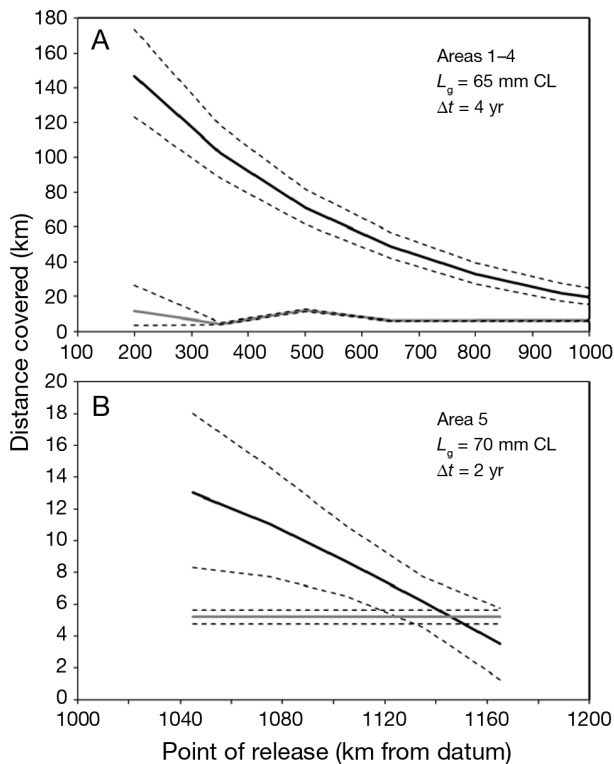


Fig. 9. *Palinurus gilchristi*. Relationship between point of release (i.e. distance from datum) and distance migrated by advection (black line) and diffusion (grey line), respectively, for lobsters of similar sizes tagged in (A) Areas 1 to 4 and (B) Area 5, and at large for 2 to 4 yr. The y-axes have different scales. Dashed lines indicate the 95% confidence limits of the distance estimates

The absence of benthic migrations between the southern and eastern populations is in contrast to the well-mixed gene pool shown for this species across all areas (Tolley et al. 2005). Presumably the absence

of genetic structure is a result of larval mixing by ocean currents during the pelagic stage (Groeneveld & Branch 2002). Whereas many larvae presumably drift towards the southwest to settle on the seafloor in Area 1 (Cape Agulhas hotspot), at least some of them must be retained near Area 5, or be returned there by counter currents, because the population at Port Alfred receives few benthic migrants from the west. Such retention and return of lobster larvae by eddies have been shown for *Jasus edwardsii* off New Zealand (Chiswell & Booth 1999). Further, even the small levels of inter-mixing (<2%) predicted in the present study between Areas 4 and 5 could give the appearance of panmixia owing to the sensitivity of molecular genetic methods to gene flow rates (Carvalho & Hauser 1994). However, in the ecological sense, and for management purposes, the populations should be considered structured (Area 5 separate from Areas 1 to 4).

The eastern population (Area 5) exhibits slower growth rates (Groeneveld 1997), smaller mean lobster size and size at sexual maturity (Groeneveld & Melville-Smith 1994), and lower fecundity (Groeneveld 2005) than the southern population (Areas 1 to 4). The lower productivity in Area 5 is presumably induced by a less favourable environment for *Palinurus gilchristi* towards the easternmost edge of its distribution range (Groeneveld 2005). This area has also been identified as a biogeographical boundary area, albeit based on intertidal rocky shores (Bustamante & Branch 1996). The physical cause for differences in population parameters (including a skewed sex ratio) is difficult to establish with certainty, because deep water and strong currents render the benthic environment and extant population difficult to sample with conventional means. Nevertheless, food availability, reduced foraging efficiency brought on by strong bottom currents near the Agulhas Current core, and density dependent effects have all been suggested as potential drivers of reduced lobster productivity (summarized by Groeneveld et al. 2013). Although the present study could confirm that lobsters in Area 5 undertake diffusive movements only, and are not regularly replenished by immigrants from the west, it provided no additional information on the cause of the observed population structure.

Estimates of migration distances along a convoluted bathymetric gradient were substantially further than those based on straight-line displacements (Groeneveld & Branch 2002) and GC distances. The latter 2 (shortest distance) estimates were clearly underestimates, because lobsters are unlikely to

move far out of their preferred habitat or depth range, and have not been observed there. Although more realistic, distance estimates based on the advection-diffusion model did bring about at least some bias: in Areas 1 to 4 the average real distance moved (using positive, zero and negative distances along the advection gradient) was approximately 100 km, some 4 km shorter than estimates based on absolute distances (zero or positive distances). This is well within the range of diffusion, which attained a minimum expected value of 4.5 km in Area 3. Thus, it may be that some of the tagged lobsters only performed random diffusive movements within a 360° radius from the site of first capture, and this accounts for the perceived negative advection of some. In Area 5, the difference was about 7 km, but also within the range of diffusive movements. However, these deviations can also be accounted for by small errors in the reporting of the coordinates of recapture.

Advantageous movements by spiny lobsters pervade every phase in the life cycle, can be sex or size dependent, and are mostly for foraging, finding shelter, reproduction or recruitment (Herrnkind 1980, Booth 1997, George 2005). The advection model in the present study confirmed size-specific migrations in *Palinurus gilchristi* shown by Groeneveld & Branch (2002), in which small individuals moved further and more frequently than larger adults, presumably to recruit to upstream adult habitats. The advection model also suggested that male *P. gilchristi* migrate further than females (Table 2; Model 3); however, this effect could not be discerned by Groeneveld & Branch (2002). The advection model may be more sensitive than the previous method, and explain some aspects of shorter sex-specific reproductive movements. Such movements have been shown for *P. delagoae* in eastern South Africa, where egg-bearing females aggregate in shallower water (150 to 275 m) in summer, and move deeper (>300 m) in autumn and winter, when eggs have hatched (Groeneveld et al. 2013). These reproductive migrations occur over short distances, because the continental shelf is steep in this region. *P. gilchristi* occurs in a similar environment, and a sex effect in the model would be plausible for similar reasons. Nevertheless, the sex effect was not disproportionate in the present models. Further, we could not detect a general trade-off between the distances covered and the growth rate of the individual lobsters.

Exclusion of short-term recaptures (at large for 6 mo to 2 yr) from the area analysis (Table 2; Model 1) provided no empirical evidence that tagging delayed

advective movements. This is in contrast with several previous lobster growth studies, which provided reasonable evidence that growth rates may be retarded by tagging injuries (Dubula et al. 2005, Brouwer et al. 2006). Nevertheless, assuming that some lobsters returned to the sea after tagging would have drifted away from their preferred habitat (a strong likelihood with the nearby Agulhas Current and considerable depth over the fishing grounds), some return movements (or homing) to suitable habitat would be expected. Such homing after being displaced from a capture site or home reef has previously been shown for spiny lobsters (Creaser & Travis 1950, Lozano-Álvarez et al. 2002). We assumed that homing would entail relatively short movements, aided by intrinsic orientation and navigation capabilities (Alerstam 2003, Boles & Lohmann 2003, Cain et al. 2005), infrequently extending across area boundaries, and thus not needing to be recorded as advection.

Earlier models of animal movement made the implicit assumption that populations are homogeneous, but more recently, a larger awareness of the heterogeneity of migration behaviour in populations has emerged (Gurarie et al. 2009). Our data also contained heterogeneous groups that even a skewed error distribution like the gamma had difficulties to accommodate (Fig. 6). The most prominent of these was a group of long-distance migrants tagged in Area 1 and recaptured in Area 4 (Fig. 1C), but these comprised a minority of the observations. Two clear groups were observed among lobsters tagged in Area 1 (a recruitment hotspot with a high probability of migration), irrespective of time at large longer than 2 yr: those travelling between 100 and 250 km to their adult habitats (Area 3; East Agulhas Bank) and those moving distances of between 400 and 900 km (Area 4; Mossel Bay to Algoa Bay). These 2 adult habitat areas are separated by a stretch of roughly 100 to 150 km (21 to 22° E) that is infrequently fished, presumably because it contains marginal habitat with low lobster densities. The existence of resident adult populations in Areas 3 and 4, and of the movement of smaller lobsters through Area 3, en route to Area 4, has been confirmed by length-frequency analysis (Groeneveld & Branch 2002).

Whereas the physical gap between Areas 3 and 4 can account for the difference in distance estimates of the 2 groups observed in Fig. 6, it remains difficult to explain why some lobsters stop when they reach Area 3, while others continue to Area 4. One reason may be that the inherited genetic programme for migration, which encodes both the distance and direction to migrate (see Gwinner & Helm 2003, Åkesson

& Hedenstrom 2007), retains elements of evolutionary inertia, and that migrants are genetically constrained to migrate to Area 3 or Area 4. This concept has previously been demonstrated for bird migrations, where expanding populations have retained their original, but now apparently sub-optimal, migration routes and destinations (Sutherland 1998, Alerstam et al. 2003). Importantly, all these cases referred to bird species where juveniles migrated independently from adults, thus relying on their genetic programming, and not on learning between generations. Assuming that migratory pathways reflect colonization routes during past range expansions (see Alerstam et al. 2003), it is possible that the differential migration pattern in lobster may have evolved during a series of successive range expansions caused by sea level changes coupled to habitat availability during glacial/interglacial periods (see Tolley et al. 2005).

Lohmann et al. (2007) provided examples of several animal taxa (including birds, sea turtles and spiny lobsters) that can detect Earth's magnetic field and use it as a cue in orientation and navigation. Boles & Lohmann (2003) provided strong evidence that the spiny lobster *Panulirus argus* possesses a magnetic map that facilitates navigation towards specific geographic areas. Should *P. gilchristi* also have similar magnetic navigation abilities, it might explain the inherited adherence to specific migration routes, independent of present habitat or resource availability.

Alternatively, the differential migration pattern may partially be driven by contemporary ecological factors, such as the availability of habitat, the density-dependent effect and competition (see Alerstam et al. 2003). For instance, migrant lobsters arriving at Area 3 might remain there if space and resources are available, but will continue to Area 4 if they are out-competed by the resident population. This scenario supposes a balance between the benefit of increased resource availability for migrants to Area 4, and the costs in time, energy and mortality associated with the migratory process. The weakness of this ecological hypothesis is that lobster densities in Area 3 are presumably moderated by fishing, and standardized catch rate trends indicate much lower lobster abundance in all areas (including 3 and 4) at present, compared to the 1970s and 1980s (Groeneveld et al. 2013). Nevertheless, a bimodal size frequency distribution in Area 3 has persisted over time (Pollock & Augustyn 1982, Groeneveld & Branch 2002), suggesting that small lobsters still transit through Area 3, despite lower lobster densities in this area, and pre-

sumably, the less intense competition for space and other resources in this area than in the past.

This study has major implications for the development of a spatial management strategy for the *Panulirus gilchristi* fishery, because the models can be used to predict and quantify lobster movements between fishing areas. It is, for instance, possible to simulate the dispersal of a single lobster, or of a legion of individual lobsters, by combining the direction sub-model, the advection sub-model, and the (2-sided) diffusive patterns induced by the third sub-model in each area. Since all these functions are dynamic and probabilistic, a multitude of individual dispersal behaviours can arise, including directional or turbulent flows. Further, dynamic cohort dispersal can be simulated by including information about population growth and mortality along the average paths. In principle, however, most lobsters from Area 1 (the recruitment hotspot; small immature individuals) are predicted to migrate through Area 2 to populate (after 9 yr) adult habitats in Area 3 (70%) and Area 4 (20%) (Fig. 4B). Only a minor proportion of lobsters (10%) are predicted to remain in transit Area 2, en route to adult habitats, and most of these are pre-adults. Therefore, closing Areas 1 and 2 to trap-fishing is likely to increase catches of larger lobsters in Areas 3 and 4, as well as the numbers of mature females in the population. This is one example of how the proposed advection-diffusion model can be used to assist in developing a spatial fishery management strategy.

The movement modelling demonstrated different life-history strategies in the same species, depending on their geographic location (southern area versus eastern area). The inference from this is that larval dispersal and settlement patterns are specific to these 2 areas, thus giving rise to migratory versus non-migratory populations. Furthermore, an interesting subject for future research is whether the differential migration routes in the southern area, starting at the same origin (Area 1) but with different destinations (Area 3 or Area 4), is a consequence of evolutionary inertia inherited as a result of adaptations to successive glaciation events, or whether it is a product of ecological factors.

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