

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

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10

11 **Abstract**

12

13 Advection-diffusion models were constructed to simulate migration patterns of juvenile
14 and adult spiny lobsters off southern South Africa. Models based on tag-recapture
15 information collected between 1978 and 2005 (2665 tag recaptures) were used to
16 quantify directional movements and to estimate distances moved along a bathymetric
17 gradient. Sex, length at tagging, tagging area and time at large were the main
18 explanatory variables considered . Empirical tests showed that tagging did not delay the
19 onset of advective movements. Lobsters advected from west to east, and no return
20 migrations were observed. Advection was strongly size dependent, with juvenile and
21 small mature individuals moving further than larger adults. Advection was also area
22 dependent, decreasing from west to east, and lobsters at the easternmost site did not
23 advect or receive immigrants from elsewhere. Juvenile lobsters tagged at a recruitment
24 hotspot at the westernmost site migrated 100 – 250 km far onto the Agulhas Bank (90%
25 probability after 5 years at large), or continued along the coast to more distant sites (400

26 – 900 km far; 10% after 5 years). This effect was stronger in males, but we could not
27 detect a trade-off in growth rate. Two theories are advanced to explain these migration
28 strategies - evolutionary effects of past range expansions and density dependence. A
29 novel approach for quantifying migrations in spiny lobsters is demonstrated, for
30 potential use in spatial fisheries management.

31

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

34

35 **Introduction**

36

37 Quantitative models to describe large scale movements are instrumental for the spatial
38 management of exploited fish populations, because they can be used to predict the
39 effects of a fishery operating in one area on the yield of a fishery operating elsewhere
40 (Sibert et al. 1999, Goethel et al. 2011). In general ecological research, these models
41 are not restricted to adult fishes that can be tagged and recaptured to infer movement
42 patterns, but have also been used to estimate larval dispersal patterns, based on
43 advection-diffusion concepts and oceanographic data (Hill 1990, Chiswell & Booth
44 1999, Largier 2003, Rudorff et al. 2009). Movement models are also useful for deciding
45 the configuration of marine reserves, where connectivity through larval and/or adult
46 dispersal is sought, particularly in areas with large alongshore advection rates
47 (Stockhausen et al. 2000, Kaplan 2006).

48

49 Several general classes of models can be applied to the quantitative analysis of fish
50 movements, as summarized by Sibert et al. (1999) and Goethel et al. (2011). Bulk-

51 transfer (or box-transfer) models, where exchange rates between regions are
52 characterized by transfer coefficients, have been applied to migratory tuna stocks
53 (Hilborn 1990, Hampton 1991), but they are not continuous in space and therefore
54 cannot predict the changes in population density at an arbitrary point. Diffusion models
55 have a long history in animal ecology (Skellam 1951). These models ultimately produce
56 a uniform distribution of a population at equilibrium, except if directional movements
57 are incorporated by adding ‘advective’ terms (Okubo 1980). Advection-diffusion
58 models have been applied to estimate movement parameters for yellow-fin (Deriso et
59 al. 1991) and skipjack tuna (Kleiber & Hampton 1994, Sibert et al. 1999), based on tag-
60 recapture data. State-space models that may require nonlinear methods to include
61 animal behaviour (i.e. changes between behavioural states) are described by Jonsen et
62 al. (2003). In the last few decades, tag-integrated stock assessment methods in fisheries
63 have allowed for the explicit incorporation of movement among spatially discrete sub-
64 populations (Goethel et al. 2011).

65

66 Spiny lobsters exhibit movement patterns that range from dispersal of pelagic larvae by
67 oceanic processes (Cobb 1997) to movements by juveniles or adults on the seafloor to
68 find food, shelter, or reproduce (Herrnkind 1980). The latter movements may be
69 nomadic or homing (periodic excursions from a shelter with subsequent return), or they
70 may be migratory, involving directional movements made by distinct parts of a
71 population over relatively long distances within a confined time period (Herrnkind
72 1980). Long-distance migrations on the seafloor are sometimes against prevailing
73 currents (contranatant; Meek 1915) to redress downstream dispersal of pelagic larvae,
74 and comprise pre-adult benthic individuals recruiting to adult populations (Moore &

75 Macfarlane 1984, Bell et al. 1987, Booth & Phillips 1994, Booth 1997, Groeneveld &
76 Branch 2002).

77

78 The most widely used technique to examine the movement patterns of marine animals
79 is the attachment of external tags, along with instructions for reporting of recaptured
80 animals (Semmens et al. 2007). In lobster research, anchor tags are typically inserted
81 into the abdominal muscle of lobsters, and recaptured individuals are used to evaluate
82 somatic growth, mortality rates or movement patterns. Long-term tagging programmes
83 exist for several commercially important lobster stocks (Phillips 1983, Haakonsen &
84 Anoruo 1994, Groeneveld & Branch 2002, Gardner et al. 2003, Linnane et al. 2005).

85 There are several potential disadvantages to using anchor tags, however, including
86 variable recapture and/or reporting rates (Frusher & Hoenig 2001), tag loss or shedding
87 (Montgomery & Brett 1996), and causing lethal or sub-lethal injuries (Brouwer et al.
88 2006). Lobster growth rates may be retarded as a result of physical injuries or
89 physiological stress (Vermeer 1987, Dubula et al. 2005, Haupt et al. 2006). Similarly,
90 tagged lobsters released at the sea surface may be displaced and disoriented by strong
91 currents, which could lead to a delay in the onset of migrations.

92

93 Commercial quantities of the spiny lobster *Palinurus gilchristi* were first discovered in
94 1974, and the species now supports the second largest lobster fishery in South Africa,
95 with landings of approximately 1000 t.year⁻¹ (Groeneveld et al. 2013). Fishing takes
96 place along the southern Cape coast, between Cape Point (18°E) and East London
97 (28°E) on rocky patches between 50 and 200 m depth (Fig. 1). Given its economic
98 importance, a management strategy for the fishery has been in place since the late 1970s
99 (Pollock & Augustyn 1982), and for this purpose catch, effort, length-composition and

100 tag-recapture data have been collected regularly and are used in annual resource
101 assessments (Groeneveld et al. 2013).

102

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

115

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

123

124 **Material and Methods**

125

126 *Field work*

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

133

134 Some tagging occurred in 1978 (see Pollock & Augustyn 1982), but the bulk of tagging
135 expeditions were undertaken between 1988 and 2005 (no tagging in 1989, 1991, 1994,
136 2000 and 2001). Due to the unfeasibility of tagging lobsters in all 5 areas in each year,
137 greatest effort was concentrated at Mossel Bay–Algoa Bay (the largest area; 8 trips),
138 followed by West and East Agulhas Bank (4 trips each), and Port Alfred and Cape
139 Agulhas (2 trips each).

140

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

148

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

155

156 *Quality control of data*

157 The full set of observations consisted of 2665 recaptured lobsters out of 40030 tagged
158 individuals between 1989 and 2005 (6.7% recapture rate). The tagging location, time,
159 depth, sex, and size variables were measured by researchers, and the quality of these
160 observations was therefore considered to be better than the recapture coordinates, time
161 and depth, which were measured by fishermen, and sometimes coarsely or poorly
162 recorded in logbooks. Certain observations were thus discarded if they clearly indicated
163 unlikely recapture positions.

164

165 *Movement and distance*

166 The distance between the points of capture and recapture was calculated in two ways.
167 The first was the shortest distance between two points on the surface of the globe,
168 namely an arc commonly denominated as the great circle (GC) distance. The
169 distribution of the points of capture and recapture (Fig. 1) seemed, however, to indicate
170 convoluted dispersal paths along defined bathymetric lines. A more realistic description
171 of distance was thus calculated using the median depth of captures and recaptures in
172 each fishing area, and assuming an advection pathway along a bathymetric contour
173 connecting these median points. The western-most point of tagging (Lat: -34.084, Lon:

174 18.212) was defined as the origin (the geodetic datum) of the advection pathway, i.e.
175 km 0. The local perpendicular deviation of each sampling point to the advection
176 pathway, either at tagging or at re-capture, was considered to be a measurement of
177 diffusion (Fig. 2). The total distance elapsed was thus considered to be the sum of two
178 diffusion segments (A–A' and B'–B) and advection (A'–B'). The advection (ADV)
179 distance was measured as $ADV_2 - ADV_1$, which correspond to the distances in km along
180 the datum line for points B' and A', respectively.

181

182 The calculation of all lobster movements was performed using the ArcMap 9.2 GIS
183 software package. The software features used included topo-to-raster interpolation,
184 surface length 3-dimensional distance calculation, as well as the lines to points and
185 distance between points Hawth's Tools plugins. The data projection used was the World
186 Geodetic System WGS_1984_UTM_Zone_34S. Bathymetry data was obtained from
187 Shuttle Radar Topography Mission SRTM30_Plus, a global 30 arc second grid of depth
188 values, derived from a compilation of single and multibeam echo-soundings (Becker et
189 al. 2009). The first movement calculation method, the straight-line distance, involved
190 evaluating the total distance travelled from point A to point B, using the surface length
191 tool. For the second method, a Digital Elevation Model was first created from SRTM
192 bathymetry lines using the topo-to-raster interpolation tool, and median depths were
193 determined from extracted z values of all tag and recapture points in each area (area 4
194 was split into 4a and 4b). A shapefile containing numbered points (ADV_s) at 1 km
195 intervals along the unified and smoothed median depth line was then generated using
196 the lines to points Hawth's Tools plugin. Using this shapefile, the 3 distance
197 components (tag points to nearest ADV₁, ADV₁ to ADV₂, and recapture points to
198 nearest ADV₂) were calculated with the distance between points Hawth's Tools plugin.

199

200 *Data analysis*

201 The movement model comprised three probabilistic and independent sub-models: the
 202 first was an analysis of the direction of movement; the second was a quantification of
 203 the advection distance along the median depth, and the third was a model of the
 204 diffusion distance from the median line. The sum of advection and diffusion to and
 205 from the median line is here called the dispersal distance. It is important that the
 206 resulting dispersal model be simple and robust to be useful for prediction of individual
 207 migration and in population management. Preliminary analyses were performed to test
 208 whether tagging itself interfered with lobster movements between areas. The latter
 209 analysis investigated whether truncation of the data would remediate bias. Truncation
 210 of observations based on increasing time-at-large could correct for initial retardation of
 211 body growth as a result of tagging effects (J. Santos pers. obs.).

212

213 *Directional analysis*

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

219

$$220 \quad Area_{R[1-5]} = Area_{T[1-5]} + sex_{[2]} + L_g + \Delta t \quad (\text{equation 1})$$

221

222 The bracketed subscripts indicate the number of levels of each discrete variable. As is
 223 normally the case in ordinal regression, the statistical output was a cumulative

224 percentage; in the present case, of the dispersal of tagged lobsters to different areas.
225 Ordinal regression was considered to be appropriate for the analysis of direction,
226 because the fishing grounds could be ordered in a geographic sequence (1 to 5, in that
227 order) and we believe that lobsters can only move between consecutive areas, as for
228 instance from area 3 to area 4 or area 2. Nevertheless, these grounds had different areas
229 and distances that were not directly quantified in the model. Ordinal regression only
230 requires the assumption that individuals migrated between areas, from west to east, or
231 in the opposite direction, in a stepped manner, irrespective of distance.

232

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

247

248 *Distance analysis*

249 Advection distance (D_{adv} , km) was predicted by means of a generalized linear model,

250

$$251 \quad D_{adv} = ADV_1 + sex_{[2]} + L_g + \Delta t \quad (\text{equation 2})$$

252

253 In several trials we also included the individual observations of specific growth rate,

254 calculated as $\ln(L_r/L_g)/\Delta t$, as a covariate in the model. The distribution of the

255 observations used for the advection model presented some challenges that demanded a

256 partition of the model. Some lobsters presented (generally small) negative values of

257 advection from the datum along the reference bathymetric line, i.e. they moved from

258 east to west. This could have been caused by actual dispersal in that direction,

259 misreporting of the precise position of recapture, or introduced by the calculation

260 method itself or our simplistic formulation of advection. To obviate this we transformed

261 all advection distances into rational numbers equal to or larger than zero. Thus, this

262 model considered only the absolute values of movement rather than its direction, which

263 was dealt with in the directional analysis above. The number of zeroes (i.e. lobsters that

264 apparently did not move by advection) was relatively large, and furthermore, the

265 positive values of D_{adv} were considerably skewed to the right, i.e. towards long distance

266 movements. This distribution (numerous zeroes, strong positive skew) is frequent in

267 fisheries data and is appropriately dealt with in 3 steps by hurdle models (Pennington

268 1983, Maunder & Punt 2004). In a first step, the probability of a non-zero advection

269 was modelled by means of logistic regression using a GLM with an initial model

270 structure similar to equation 2, and assuming a binomial error distribution. In a second

271 step, only the positive (non-zero) movements were modelled using equation 2, and

272 assuming a continuous error distribution of the exponential family. Analysis of the

273 conditional data showed that the logarithm of the variance in distance migrated

274 (advection) per unit time at large (Δt) related linearly to the logarithm of the mean
 275 distance with a slope of 2.1 (1.9–2.4, 95% CI). This is close to 2.0, the expected slope
 276 relationship for observations that have a constant coefficient of variation; these are
 277 appropriately described by a gamma error structure in generalized linear models
 278 (McCullagh & Nelder 2000). The final step involved combining the outputs from the
 279 two models in order to estimate the expected distance advected for a specific set of
 280 values of the explanatory variables.

281

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

287
$$D_{dif} = Area_{R[5]} \text{ (equation 3)}$$

288 Although no zeroes (i.e. no diffusion) were present, the distribution of observations was
 289 positively skewed. The variance to mean relationship of diffusion distance in the
 290 different areas had a slope of 1.6 (0.9–2.3, 95% C.I.), and therefore a GLM regression
 291 with gamma distributed error and log link was selected. The gamma distribution is
 292 becoming increasingly used in studies of dispersal to describe the patterns of travel
 293 times and rate of spread in heterogeneous populations (Yamamura 2002, Gurarie et al.
 294 2009). All models tested included a constant, and only variables found significant ($p <$
 295 0.05) in analysis of deviance were retained. Plausible first-order interactions were tested
 296 in the distance models, but none were significant and they were therefore omitted from
 297 the saturated models. Formal tests of the goodness of fit were performed using the LRT
 298 of the selected model against the null model (intercept only) and the saturated model.

299 Confidence intervals for the estimates in equations (2) (hurdle model) and (3) were
300 obtained using parametric bootstrapping (see Fletcher et al. 2005). The estimates of the
301 mean and standard deviation of the parameters retained in the different models, as well
302 as the constraining information contained in their covariance matrices, were used to
303 generate 10000 samples with replacement. These normal covariates were utilized to
304 perform 10000 realizations of the retained models for selected scenarios, and the
305 confidence intervals were calculated from the 2.5th and 97.5th percentiles. All GLM fits
306 and simulations were conducted using SPSS 19 (IBM) and R statistical software
307 (www.r-project.org), including the libraries MASS and Rcmdr.

308

309 **Results**

310

311 *Depth of capture*

312 The assumption that lobsters migrate within a defined bathymetric range
313 (approximately 50 to 200 m depth) was supported by the available tagging and
314 recapture data. Initial capture depth ranged between 71 and 200 m (median depth of
315 123.2 m, n = 2758), and recapture depth obtained from fisher logbooks ranged between
316 51 and 243 m (123.6 m, n = 2752). Most lobsters were captured and recaptured between
317 100 and 200 m depth (93.4% and 90.1%, respectively). Median depths by area were
318 125 m (Cape Agulhas), 165 and 145 m (West and East Agulhas Bank), 120 and 112 m
319 (two sections of the Mossel Bay–Algoa Bay area) and 110 m (Port Alfred).

320

321 *Sex ratio and size composition*

322 The sex-ratio of recaptured lobsters was generally skewed, with males predominating
323 in 2348 recaptures made in areas 1 to 4 (mean sex-ratio of 1.6:1; Pearson's χ^2 test of

324 independence; $p < 0.001$ in areas 2 to 4), and females predominating in 317 recaptures
325 made in area 5 (0.5:1; $p < 0.001$). Lobsters were clearly larger in areas 3 and 4, but even
326 in these areas a number of smaller individuals were tagged (Fig. 3). The mean carapace
327 length at tagging ($L_g \pm sd$) was 75.0 ± 9.9 mm, while after an average time at large of
328 2.0 ± 1.98 years, recaptured lobsters had a mean carapace length (L_r) of 80.0 ± 10.0
329 mm. The minimum time at large was 4 days and the maximum 14.7 years, however
330 only 9 lobsters were recaptured after 10 years at liberty.

331

332 *Heterogeneity of distance measurements*

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

339

340 *Delays in advective movements*

341 Ordinal regressions of the expected areas of recapture for combinations of the three
342 explanatory variables, area of tagging, lobster size and time-at-large (Fig. 4a-d) showed
343 no clear discontinuities indicative of delays in advection movement caused by tagging.
344 Truncation of datasets by removing recaptures made within 6, 12, 18 and 24 months of
345 tagging made little difference to the location of recapture, as inferred from the narrow,
346 parallel bands within which cumulative probabilities ranged. Thus, tagging did not
347 appear to affect the observed movements, and further analyses were performed using
348 the full data sets.

349

350 *Area dispersal*

351 Lobsters tagged in areas 1 to 4 tended to accumulate in areas 3 and 4, with very little
352 straddling to area 5 (Table 1). The ordinal regression predicted that after 5 years at
353 large, a lobster of 60 mm CL tagged in area 1 would have a probability close to zero of
354 being found in that area, increasing to about 15% in area 2, 75% in area 3, and 10% in
355 area 4, and it would not be expected to be found in area 5 (Fig. 5a; top stippled line).
356 The same trend of advection northeastwards also occurred in areas 2 and 3 and
357 increased with time at large, but decreased significantly as the length at tagging
358 increased (Table 2; model 1, Fig. 5b-d). Thus, a lobster of mean size 77 mm tagged in
359 area 3 had a 20% probability of being recaptured in the same area after 13 years, and
360 this probability increased strongly with size (Fig. 5b, c). A lobster of average size (78
361 mm) in area 4 is expected to remain within this area, with only about 2 % probability
362 of being recaptured in area 5 after 9 years at large (Fig. 5d). Similarly, a lobster of
363 average size 71 mm in area 5 will remain in the tagging area, with less than 1%
364 probability of being recaptured in area 4 after many years (Fig. 5e). These expected
365 probabilities of straddling are larger than the observed frequencies: only 0.3 % of the
366 lobsters tagged in areas 1 to 4 were found in area 5, and 0.9% of the lobsters tagged in
367 area 5 were found in area 4. The largest expected probabilities of straddling occurred
368 only for long times at large (9 years or longer), and are mainly extrapolations that are
369 not well supported by the core of the field data.

370

371 *Advection and diffusion distances*

372 The probability of detecting advection movement in tagged lobsters declined solely as
373 a function of geodetic distance in both areas 1 to 4 and area 5, with little improvement

374 brought about by more complex model formulations (Table 2; models 2 and 5, LRT –
375 D statistic). For example, zero lobsters were stationary in area 1, but a greater
376 proportion of them made no advection movements in areas 3 and 4. The range of
377 advection distances covered (0–900 km) was large for a given time at large, particularly
378 in area 1 (Fig. 6). This was partially explained by the gamma model (Table 2; model
379 3), which indicated that advection decreased with geodetic distance, but increased with
380 time-at-large, and was partially sex-dependent. Although in areas 1 to 4 males tended
381 to move longer distances than females, a gamma model without the sex variable also
382 fitted the data well (AIC of 16700 in the saturated model v. AIC of 16708 in sex-
383 restricted model). On average, lobsters of both sexes and mean sizes 60, 70 and 80 mm
384 CL released in areas 1, 2 and 3, will have migrated about 330, 120 and 60 km towards
385 the NE after 7 years, respectively (Fig. 7). These differences conjugate the effects of
386 release point and size at release. In all attempts to introduce the growth rate of lobster
387 in the advection and diffusion models this covariate failed to demonstrate significant
388 effects ($P= 0.2 - 0.6$).

389

390 Modeling the extent of diffusion proved to be more difficult. Although the gamma error
391 distribution provided the best fit, none of the covariates and factors, other than the area
392 of release, provided a good description of the variability in diffusive distance (Table 2;
393 model 6). The average diffusion distance from the median depth was highest in areas 1
394 and 3 (12 to 13 km), and in all other areas it ranged between 4.5 and 6.5 km from the
395 median depth. As a consequence, the advection to diffusion ratio was very high for
396 small lobsters that advected long distances, but the two types of movements were
397 virtually indistinguishable in lobsters >90 mm CL (Fig. 8). Although advection and
398 diffusion distances could be distinguished in areas 1 to 4 (Fig. 9, top), the trend was

399 different in area 5, where advection and diffusion distances were similar, even for
400 relatively small lobsters (Fig. 9, bottom). It therefore appears that area 5 was dominated
401 by random diffusive dispersal. Although the available predictors could clarify much of
402 the variability in elapsed distances over time, there appears to be some discrepancy
403 between long-distance and short-distance migrants (see Fig. 6) that was difficult to
404 account for.

405

406 **Discussion**

407

408 The model of advection-diffusion along a bathymetric gradient realistically simulated
409 the major migratory features of *Palinurus gilchristi* (see Groeneveld & Branch 2002):
410 a west to east directionality without return migrations; that migrants were mainly small
411 pre-adults; that larger lobsters moved far less, or not at all; that lobsters tagged near the
412 downstream edge of the distribution range (area 1; Cape Agulhas) were most likely to
413 migrate, and travel furthest towards the east; and that lobsters tagged near the upstream
414 edge (area 5) did not participate in migrations, other than diffusive movements. The
415 present migration analysis furthermore confirmed the presence of 2 populations, with
416 no or little intermixing through benthic migrations; a southern population (areas 1 to 4;
417 Cape Agulhas to Algoa Bay) and an eastern population at Port Alfred (area 5).

418

419 The absence of benthic migrations between the southern and eastern populations is in
420 contrast to the well-mixed gene pool shown for this species across all areas (Tolley et
421 al. 2005). Presumably the absence of genetic structure is as a result of larval mixing by
422 ocean currents during the pelagic stage (Groeneveld & Branch 2002). Whereas many
423 larvae presumably drift towards the southwest to settle on the seafloor in area 1 (Cape

424 Agulhas hotspot), at least some of them must be retained near area 5, or be returned
425 there by counter currents, because the population at Port Alfred receives few benthic
426 migrants from the west. Such retention and return of lobster larvae by eddies have been
427 shown for *Jasus edwardsii* off New Zealand (Chiswell & Booth 1999). Further, even
428 the small levels of inter-mixing (<2%) predicted in the present study between areas 4
429 and 5 could give the appearance of panmixia owing to the sensitivity of molecular
430 genetic methods to gene flow rates (Carvalho & Hauser 1994). However, in the
431 ecological sense, and for management purposes, the populations should be considered
432 structured (area 5 separate from areas 1-4).

433

434 The eastern population (area 5) exhibits slower growth rates (Groeneveld 1997),
435 smaller mean lobster size and size at sexual maturity (Groeneveld and Melville-Smith
436 1994), and lower fecundity (Groeneveld 2005) than the southern population (areas 1-
437 4). The lower productivity in area 5 is presumably induced by a less favourable
438 environment for *P. gilchristi* towards the easternmost edge of its distribution range
439 (Groeneveld 2005). This area has also been identified as a biogeographical boundary
440 area, albeit based on intertidal rocky shores (Bustamante & Branch 1996). The physical
441 cause for differences in population parameters (including a skewed sex ratio) is difficult
442 to establish with certainty, because deep water and strong currents render the benthic
443 environment and extant population difficult to sample with conventional means.
444 Nevertheless, food availability, reduced foraging efficiency brought on by strong
445 bottom currents near the Agulhas Current core, and density dependent effects have all
446 been suggested as potential drivers of reduced lobster productivity (summarized by
447 Groeneveld et al. 2013). Although the present study could confirm that lobsters in area
448 5 undertake diffusive movements only, and are not regularly replenished by immigrants

449 from the west, it provided no additional information on the cause of the observed
450 population structure.

451

452 Estimates of migration distances along a convoluted bathymetric gradient were
453 substantially further than those based on straight-line displacements (Groeneveld &
454 Branch 2002) and GC distances. The latter two (shortest distance) estimates were
455 clearly underestimates, because lobsters are unlikely to move far out of their preferred
456 habitat or depth range, and have not been observed there. Although more realistic,
457 distance estimates based on the advection-diffusion model did bring about at least some
458 bias; in areas 1 to 4 the average real distance moved (using positive, zero and negative
459 distances along the advection gradient) was approximately 100 km, some 4 km shorter
460 than estimates based on absolute distances (zero or positive distances). This is well
461 within the range of diffusion, which attained a minimum expected value of 4.5 km in
462 area 3. Thus, it may be that some of the tagged lobsters only performed random
463 diffusive movements within a 360° radius from the site of first capture, and this
464 accounts for the perceived negative advection of some. In area 5 the difference was
465 about 7 km, but also within the range of diffusive movements. However, these
466 deviations can also be accounted for by small errors in the reporting of the coordinates
467 of recapture.

468

469 Advantageous movements by spiny lobsters pervade every phase in the life cycle, can
470 be sex or size dependent, and are mostly for foraging, finding shelter, reproduction or
471 recruitment (Herrnkind 1980, Booth 1997, George 2005). The advection model in the
472 present study confirmed size-specific migrations in *P. gilchristi* shown by Groeneveld
473 & Branch (2002), in which small individuals moved further and more frequently than

474 larger adults, presumably to recruit to upstream adult habitats. The advection model
475 also suggested that male *P. gilchristi* migrate further than females (Table 2; model 3),
476 however this effect could not be discerned by Groeneveld & Branch (2002). The
477 advection model may be more sensitive than the previous method, and explain some
478 aspects of shorter sex-specific reproductive movements. Such movements have been
479 shown for *Palinurus delagoae* in eastern South Africa, where egg-bearing females
480 aggregate in shallower water (150–275 m) in summer, and move deeper (> 300 m) in
481 autumn and winter, when eggs have hatched (Groeneveld et al. 2013). These
482 reproductive migrations occur over short distances, because the continental shelf is
483 steep in this region. *P. gilchristi* occurs in a similar environment, and a sex effect in the
484 model would be plausible for similar reasons. Nevertheless, the sex effect was not
485 disproportionate in the present models.. Further, we could not detect a general trade-
486 off between the distances covered and the growth rate of the individual lobsters.

487

488 Exclusion of short-term recaptures (at large for 6 months to 2 years) from the area
489 analysis (Table 2, model 1) provided no empirical evidence that tagging delayed
490 advective movements. This is in contrast with several previous lobster growth studies,
491 which provided reasonable evidence that growth rates may be retarded by tagging
492 injuries (Dubula et al. 2005, Brouwer et al. 2006). Nevertheless, assuming that some
493 lobsters returned to the sea after tagging would have drifted away from their preferred
494 habitat (a strong likelihood with the nearby Agulhas Current and considerable depth
495 over the fishing grounds), some return movements (or homing) to suitable habitat would
496 be expected. Such homing after being displaced from a capture site or home reef has
497 previously been shown for spiny lobsters (Creaser & Travis 1950, Lozano-Álvarez et
498 al. 2002). We assumed that homing would entail relatively short movements, aided by

499 intrinsic orientation and navigation capabilities (Alerstam 2003, Boles & Lohmann
500 2003, Cain et al. 2005), infrequently extending across area boundaries, and thus not
501 needing to be recorded as advection.

502

503 Earlier models of animal movement made the implicit assumption that populations are
504 homogeneous, but more recently a larger awareness about the heterogeneity of
505 migration behaviour in populations has emerged (Gurarie et al. 2009). Our data also
506 contained heterogeneous groups that even a skewed error distribution like the gamma
507 had difficulties to accommodate (Fig. 6). The most prominent of these was a group of
508 long-distance migrants tagged in area 1 and recaptured in area 4 (Fig. 1C), but these
509 comprised a minority of the observations. Two clear groups were observed among
510 lobsters tagged at area 1 (a recruitment hotspot with a high probability of migration),
511 irrespective of time at large longer than two years: those travelling between 100 and
512 250 km to their adult habitats (area 3; East Agulhas Bank) and those moving distances
513 of between 400 and 900 km (area 4; Mossel Bay–Algoa Bay). These two adult habitat
514 areas are separated by a stretch of roughly 100–150 km (21–22°E) that is infrequently
515 fished, presumably because it contains marginal habitat with low lobster densities. The
516 existence of resident adult populations at areas 3 and 4, and of the movement of smaller
517 lobsters through area 3, en route to area 4, has been confirmed by length-frequency
518 analysis (Groeneveld & Branch 2002).

519

520 Whereas the physical gap between areas 3 and 4 can account for the difference in
521 distance estimates of the two groups observed in Fig. 6, it remains difficult to explain
522 why some lobsters stop when they reach areas 3, while others continue to area 4. One
523 reason may be that the inherited genetic programme for migration, which encodes both

524 the distance and direction to migrate (see Gwinner & Helm 2003, Åkesson &
525 Hedenstrom 2007), retains elements of evolutionary inertia, and that migrants are
526 genetically constrained to migrate to area 3 or area 4. This concept has previously been
527 demonstrated for bird migrations, where expanding populations have retained their
528 original, but now apparently sub-optimal, migration routes and destinations (Sutherland
529 1998; Alerstam et al. 2003). Importantly, all these cases referred to bird species where
530 juveniles migrated independently from adults, thus relying on their genetic
531 programming, and not on learning between generations. Assuming that migratory
532 pathways reflect colonization routes during past range expansions (see Alerstam et al.
533 2003), it is possible that the differential migration pattern in lobster may have evolved
534 during a series of successive range expansions caused by sea level changes coupled to
535 habitat availability during glacial / interglacial periods (see Tolley et al. 2005) .

536

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

544

545 Alternatively, the differential migration pattern may partially be driven by
546 contemporary ecological factors, such as the availability of habitat, the density
547 dependent effect and competition (see Alerstam et al. 2003). For instance, migrant
548 lobsters arriving at area 3 might remain there if space and resources are available, but

549 will continue to area 4 if they are outcompeted by the resident population. This scenario
550 supposes a balance between the benefit of increased resource availability for migrants
551 to area 4, and the costs in time, energy and mortality associated with the migratory
552 process. The weakness of this ecological hypothesis is that lobster densities in area 3
553 are presumably moderated by fishing, and standardized catch rate trends indicate much
554 lower lobster abundance in all areas (including 3 and 4) at present, compared to the
555 1970s and 1980s (Groeneveld et al. 2013). Nevertheless, a bimodal size frequency
556 distribution in area 3 has persisted over time (Pollock & Augustyn 1982, Groeneveld &
557 Branch 2002), suggesting that small lobsters still transit through area 3, despite lower
558 lobster densities in this area, and presumably, the less intense competition for space and
559 other resources in this area than in the past.

560

561 This study has major implications for the development of a spatial management strategy
562 for the *Palinurus gilchristi* fishery, because the models can be used to predict and
563 quantify lobster movements between fishing areas. It is, for instance, possible to
564 simulate the dispersal of a single lobster, or of a legion of individual lobsters, by
565 combining the direction sub-model, the advection sub-model, and the (two-sided)
566 diffusive patterns induced by the third sub-model in each area. Since all these functions
567 are dynamic and probabilistic, a multitude of individual dispersal behaviours can arise,
568 including directional or turbulent flows. Further, dynamic cohort dispersal can be
569 simulated by including information about population growth and mortality along the
570 average paths. In principle, however, most lobsters from area 1 (the recruitment hotspot;
571 small immature individuals) are predicted to migrate through area 2 to populate adult
572 habitats in area 3 (70 %) and area 4 (20 % after nine years) (Fig. 4b). Only a minor
573 proportion of lobsters (10 %) are predicted to remain in transit area 2, en route to adult

574 habitats, and most of these are pre-adults. Therefore, closing areas 1 and 2 to trap-
575 fishing is likely to increase catches of larger lobsters in areas 3 and 4, as well as the
576 numbers of mature females in the population. This is one example of how the proposed
577 advection-diffusion model can be used to assist in developing a spatial fishery
578 management strategy.

579

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

589

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597

598 **References**

599

600 Åkesson S, Hedenstrom A (2007) How migrants get there: migratory performance and
601 orientation. *BioScience* 57:123–133

602 Alerstam T (2003) The lobster navigators. *Nature* 421:27–28

603 Alerstam T, Hedenstrom A, Åkesson S (2003) Long-distance migration: evolution and
604 determinants. *Oikos* 103:247–260

605 Becker JJ, Sandwell DT, Smith WHF, Braud J, Binder B, Depner J, Fabre D, Factor J,
606 Ingalls S, Kim S-H, Ladner R, Marks K, Nelson S, Pharaoh A, Trimmer R, Von
607 Rosenberg J, Wallace G, Weatherall, P (2009) Global Bathymetry and Elevation
608 Data at 30 Arc Seconds Resolution: SRTM30 PLUS', *Marine Geodesy* 32:355–
609 371

610 Bell RS, Channells PW, MacFarlane JW, Moore R, Phillips BF (1987) Movements and
611 breeding of the ornate rock lobster, *Panulirus ornatus*, in Torres Strait and on
612 the north-east coast of Queensland. *Aust J Mar Freshw Res* 38:197–210

613 Boles LC, Lohmann KJ (2003) True navigation and magnetic maps in spiny lobsters.
614 *Nature* 421:60–63

615 Booth JD (1997) Long-distance movements in *Jasus* spp. and their role in larval
616 recruitment. *Bull Mar Sci* 61:111–128

617 Booth JD, Phillips BF (1994) Early life history of spiny lobster. *Crustaceana* 66:271–
618 294

619 Brouwer SL, Groeneveld JC, Blows B (2006) The effects of appendage loss on growth
620 of South African West Coast rock lobster *Jasus lalandii*. *Fish Res* 78:236–242

621 Bustamante R, Branch GM (1996) Large scale patterns and trophic structure of southern
622 African rocky shores: the roles of geographic variation and wave exposure. *J.*
623 *Biogeogr* 23:339-351

- 624 Cain SD, Boles LC, Wang JH, Lohmann KJ (2005) Magnetic orientation and navigation
625 in marine turtles, lobsters, and molluscs: concepts and conundrums. *Integr*
626 *Comp Biol* 45:539–546
- 627 Carvalho GR, Hauser L (1994) Molecular genetics and the stock concept in fisheries.
628 *Rev Fish Biol Fisheries* 4:326–350
- 629 Chiswell SM, Booth JD (1999) Rock lobster *Jasus edwardsii* larval retention by the
630 Wairarapa eddy off New Zealand. *Mar Ecol Prog Ser* 183:227–240
- 631 Cobb JS (1997) Oceanic processes affecting lobster larvae: report from a workshop.
632 *Mar Freshw Res* 48:771–775
- 633 Creaser EP, Travis D (1950) Evidence of a homing instinct in the Bermuda spiny
634 lobster. *Science* 112:169–170
- 635 Deriso RB, Punsley RG, Bayliff WH (1991) A Markov movement model of yellowfin
636 tuna in the Eastern Pacific Ocean and some analyses for international
637 management. *Fish Res* 11:375–395
- 638 Dick, EJ (2004) Beyond ‘lognormal versus gamma’: discrimination among error
639 distributions for generalized linear models. *Fish Res* 70:351–366
- 640 Dubula O, Groeneveld JC, Santos J, van Zyl DL, Brouwer S, van den Heever N, McCue
641 SA (2005) Effects of tag-related injuries and timing of tagging on growth of
642 rock lobster, *Jasus lalandii*. *Fish Res* 74:1–10
- 643 Fletcher D, MacKenzie D, Villouta E (2005) Modelling skewed data with many zeros:
644 A simple approach combining ordinary and logistic regression. *Environ Ecol*
645 *Stat* 12:45–54
- 646 Frusher SD, Hoenig JM (2001) Estimating natural and fishing mortality and tag
647 reporting rate of southern rock lobster (*Jasus edwardsii*) from a multiyear
648 tagging model. *Can J Fish Aquat Sci* 58:2490–2501

- 649 Gardner C, Frusher S, Haddon M, Buxton C (2003) Movements of the southern rock
650 lobster *Jasus edwardsii* in Tasmania, Australia. Bull Mar Sci 73:653–671
- 651 George RW (2005) Review: Evolution of life cycles, including migration, in spiny
652 lobsters (Palinuridae). NZ J Mar Freshw Res 39:503-514
- 653 Goethel DR, Quinn TJ, Cadrin SX (2011) Incorporating spatial structure in stock
654 assessment: movement modelling in marine fish populations. Rev Fish Sci
655 19:119–136
- 656 Groeneveld JC (1997) Growth of spiny lobster *Palinurus gilchristi* (Decapoda:
657 Palinuridae) off South Africa. S Afr J Mar Sci 18:19–30
- 658 Groeneveld JC (2005) Fecundity of spiny lobster *Palinurus gilchristi* (Decapoda:
659 Palinuridae) off South Africa. Afr J Mar Sci 27:231–237
- 660 Groeneveld JC, Branch GM (2002) Long-distance migration of South African deep-
661 water rock lobster *Palinurus gilchristi*. Mar Ecol Prog Ser 232:225–238
- 662 Groeneveld JC, Goñi R, Díaz D (2013) *Palinurus* species. In: Phillips BF (ed) Lobsters:
663 Biology, management, aquaculture and fisheries 2nd edition. John Wiley &
664 Sons, p 326–356
- 665 Groeneveld JC, Melville-Smith R (1994) Size at onset of sexual maturity in the South
666 Coast rock lobster *Palinurus gilchristi* (Decapoda: Palinuridae). S Afr J Mar Sci
667 14:219-223
- 668 Guisan A, Harrell FE (2000) Ordinal response regression models in ecology. J Veg Sci
669 11:617–626
- 670 Gurarie E, Anderson JA, Zabel RW (2009) Continuous models of population-level
671 heterogeneity inform analysis of animal dispersal and migration. Ecology
672 90:2233–2242

- 673 Gwinner E, Helm B (2003) Circannual and circadian contributions to the timing of
674 avian migration. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian
675 migration. Springer, Berlin, p 81–95
- 676 Haakonsen HO, Anoruo AO (1994) Tagging and migration of the American lobster
677 *Homarus americanus*. Rev Fish Sci 2:79–93
- 678 Hampton J (1991) Estimation of southern bluefin tuna, *Thunnus maccoyii*, natural
679 mortality and movement rates from tagging experiments. Fish Bull 89:591–610
- 680 Haupt P, Brouwer SL, Branch GM, Gäde G (2006) Effects of exposure to air on the
681 escape behaviour and haemolymph chemistry of the South African Cape lobster,
682 *Jasus lalandii*. Fish Res 81:210–218
- 683 Herrnkind WF (1980) Spiny lobsters: patterns of movement. In: Cobb JS, Phillips BF
684 (eds) The biology and management of lobsters, Vol I. Physiology and
685 behaviour. Academic Press, New York, p 349–407
- 686 Hilborn R (1990) Determination of fish movement patterns from tag recoveries using
687 maximum likelihood estimators. Can J Fish Aquat Sci 47:635–643
- 688 Hill AE (1990) Pelagic dispersal of Norway lobster *Nephrops norvegicus* larvae
689 examined using an advection-diffusion-mortality model. Mar Ecol Prog Ser
690 64:217–226
- 691 Jonsen ID, Myers RA, Mills Fleming J (2003) Meta-analysis of animal movement using
692 state-space models. Ecology 84:3055–3063
- 693 Kaplan DM (2006) Alongshore advection and marine reserves: consequences for
694 modeling and management. Mar Ecol Prog Ser 309:11–24
- 695 Kleiber P, Hampton J (1994) Modeling effects of FADs and islands on movement of
696 skipjack tuna (*Katsuwonus pelamis*): estimating parameters from tagging data.
697 Can J Fish Aquat Sci 51:2642–2653

- 698 Largier JL (2003) Considerations in estimating larval dispersal distances from
699 oceanographic data. *Ecol Appl* 13:S71–S89
- 700 Linnane A, Dimmlich W, Ward T (2005) Movement patterns of the southern rock
701 lobster, *Jasus edwardsii*, off South Australia. *NZ J Mar Freshw Res* 39:335–
702 346
- 703 Lohmann KJ, Lohmann CM, Putman NF (2007) Magnetic maps in animals: nature's
704 GPS. *J Exp Biol* 210:3697-3705
- 705 Lozano-Álvarez E, Carrasco-Zanjini G, Briones-Fourzán P (2002) Homing and
706 orientation in the spotted spiny lobster, *Panulirus guttatus* (Decapoda,
707 Palinuridae), towards a subtidal coral reef habitat. *Crustaceana* 75:859–874
- 708 Maunder MN, Punt AE (2004) Standardizing catch and effort data: a review of recent
709 approaches. *Fish Res* 70:141–159
- 710 McCullagh P, Nelder JA (2000) *Generalized Linear Models*, Chapman and Hall,
711 London, UK (2nd Edition)
- 712 Meek A (1915) Migrations in the sea. *Nature* 95:231
- 713 Montgomery SS, Brett PA (1996) Tagging eastern rock lobsters *Jasus verreauxi*:
714 effectiveness of several types of tag. *Fish Res* 27: 141–152
- 715 Moore R, MacFarlane JW (1984) Migration of the ornate rock lobster, *Panulirus*
716 *ornatus* (Fabricius), in Papua New Guinea. *Aus J Mar Freshw Res* 35:197–212
- 717 Okubo A (1980) *Diffusion and ecological problems: mathematical models*. Springer,
718 NY, 254 p
- 719 Pennington M (1983) Efficient estimators of abundance for fish and plankton surveys.
720 *Biometrics* 39:281–286
- 721 Phillips BF (1983) Migrations of pre-adult western rock lobsters, *Panulirus cygnus*, in
722 Western Australia. *Mar Biol* 76:311–318

- 723 Pollock DE, Augustyn CJ (1982) Biology of the rock lobster *Palinurus gilchristi* with
724 notes on the South African fishery. Fish Bull S Afr 16:57–73
- 725 Rudorff CAG, Lorenzetti JA, Gherardi DFM (2009) Modeling spiny lobster larval
726 dispersion in the Tropical Atlantic. Fish Res 96:206–215
- 727 Semmens JM, Pecl GT, Gillanders BM, Waluda CM, Shea EK, Jouffre D, Ichii T,
728 Zumholz K, Katugin ON, Leporati SC, Shaw PW (2007) Approaches to
729 resolving cephalopod movement and migration patterns. Rev Fish Biol
730 Fisheries 17:401–423
- 731 Sibert JR, Hampton J, Fournier DA, Bills PJ (1999) An advection-diffusion-reaction
732 model for the estimation of fish movement parameters from tagging data, with
733 application to skipjack tuna (*Katsuwonus pelamis*). Can J Fish Aquat Sci
734 56:925–938
- 735 Skellam JG (1951) Random dispersal in theoretical populations. Biometrika 38:196–
736 218
- 737 Stockhausen WT, Lipcius RN, Hickey BM (2000) Joint effects of larval dispersal,
738 population regulation, marine reserve design, and exploitation on production
739 and recruitment in the Caribbean spiny lobster. Bull Mar Sci 66:957–990
- 740 Sutherland WI (1998) Evidence for flexibility and constraint in migration systems. J
741 Avian Biol 29:441–446
- 742 Tolley KA, Groeneveld JC, Gopal K, Mathee CA (2005) Mitochondrial DNA
743 panmixia in spiny lobster *Palinurus gilchristi* suggests a population expansion.
744 Mar Ecol Prog Ser 297:225–231
- 745 Vermeer GK (1987) Effects of air exposure on desiccation rate, hemolymph chemistry,
746 and escape behaviour of the spiny lobster, *Panulirus argus*. Fish Bull 85:45–51

747 Yamamura K (2002) Dispersal distance of heterogeneous populations. *Popul Ecol*
748 44:93–101

749

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

751

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

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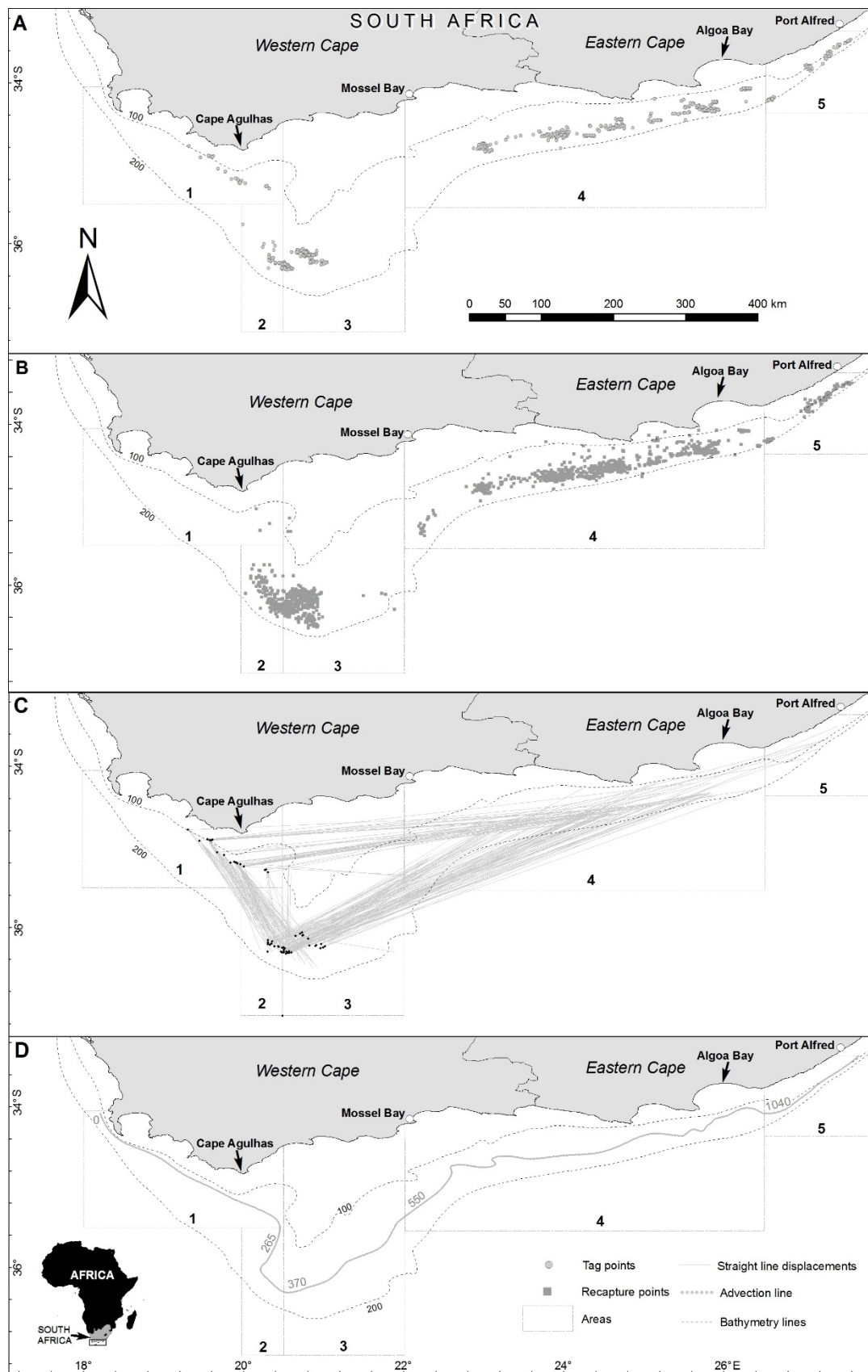
760 Table 2: *Palinurus gilchristi*. Coefficients (\pm SE) of the parameters in the generalized linear models that describe the direction of movements (model 1), and
 761 the distances advected (models 2 to 5) and diffused (model 6). Models indicated by (Δ) are hurdle models for a region, and variables or tests marked (-) were
 762 not relevant in particular models. The five areas are Cape Agulhas (1), West Agulhas Bank (2), East Agulhas Bank (3), Mossel Bay-Algoa Bay (4) and Port
 763 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
 764 given.

Movement	Ordered (area)	Advection (km)			Advection (km)		Diffusion (km)
Area	Areas 1-5	Areas 1-4		Area 5		Areas 1-5	
Model number	1	2	3	4	5	6	
Error	Polytomous	Δ Binomial	Δ Gamma (1)	Δ Binomial	Δ Gamma	Gamma	
Link	Ordered logit	Logit	Log	Logit	Identity	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, lg (mm)	-0.04 (0.005) ***		-0.06 (0.004) ***				
Time at large, ΔT (y)	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; significance * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

765

766 Figures and legends



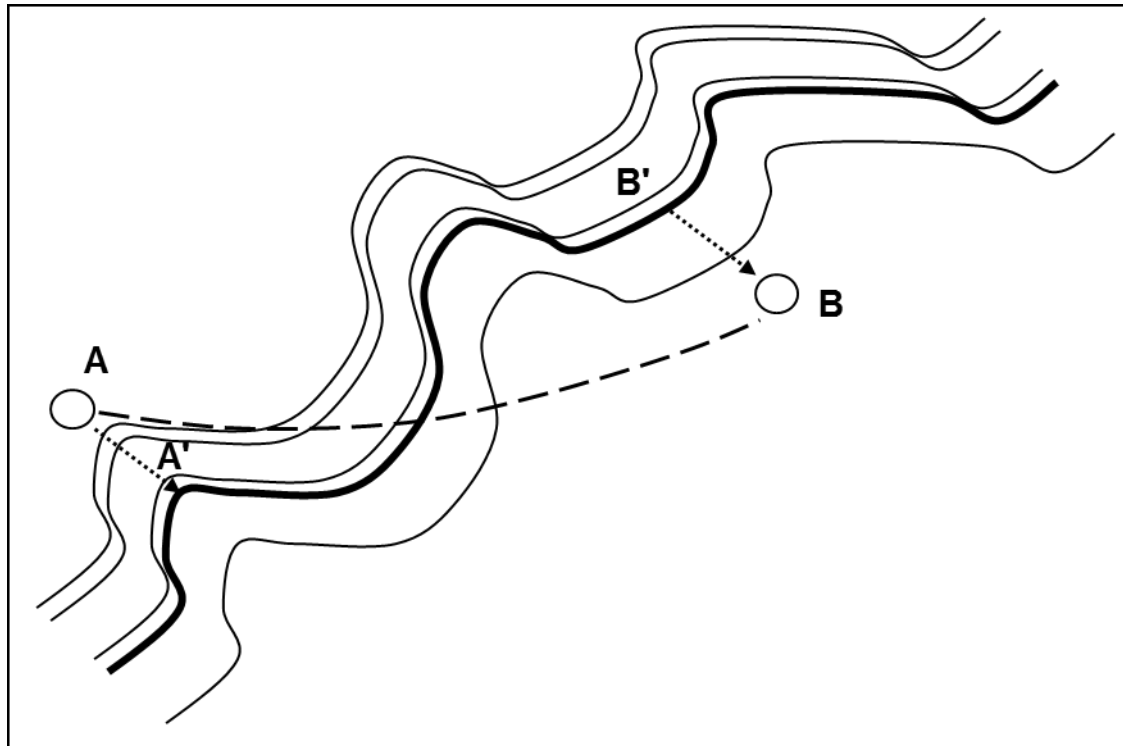
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768 Figure 1 (legend below)

769

770 Fig. 1. The southern coast of South Africa showing the 5 sampling areas, Cape Agulhas
771 (1), West Agulhas Bank (2), East Agulhas Bank (3), Mossel Bay–Algoa Bay (4), and
772 Port Alfred (5). (A) Locations of release of tagged lobsters in batches; (B) individual
773 recapture positions; (C) Straightline trajectories of lobsters that moved >100 km – all
774 movements of this distance were in an eastwards direction; and (D) the proposed
775 advection gradient. Distances measured at the boundaries of the 5 sampling areas are
776 relative to the geodetic datum (0 km) at the westernmost origin of the migration path.

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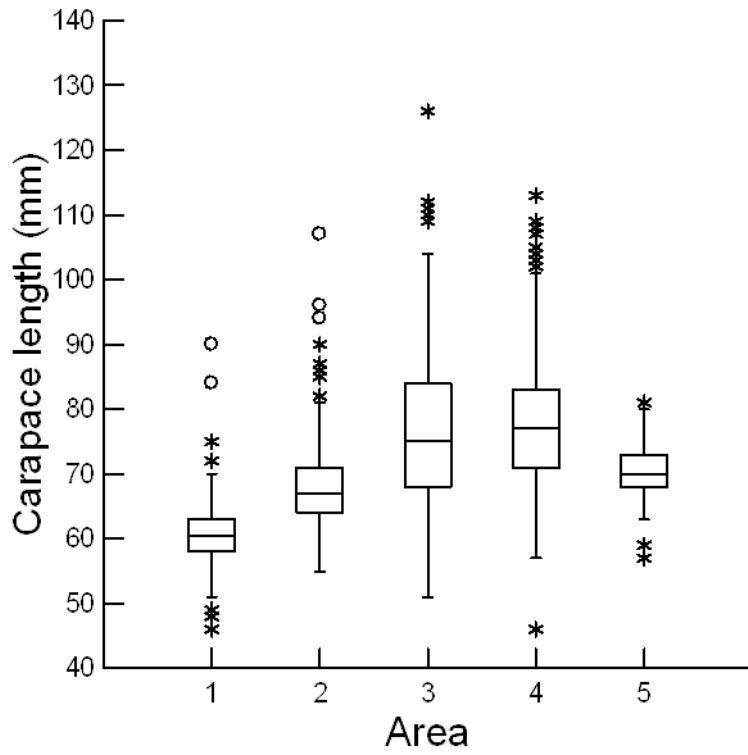
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781 Fig. 2. Conceptual diagram for calculation of distances migrated between points A
782 (tagging) and B (recapture). The total distance elapsed was calculated as the sum of
783 two diffusion segments (A–A' and B'–B) and advection (A'–B'), where the advection
784 distance was measured as $ADV_2 - ADV_1$, which correspond to the distances in km along
785 the datum line for points B' and A', respectively. The stippled line represents the great
786 circle distance.

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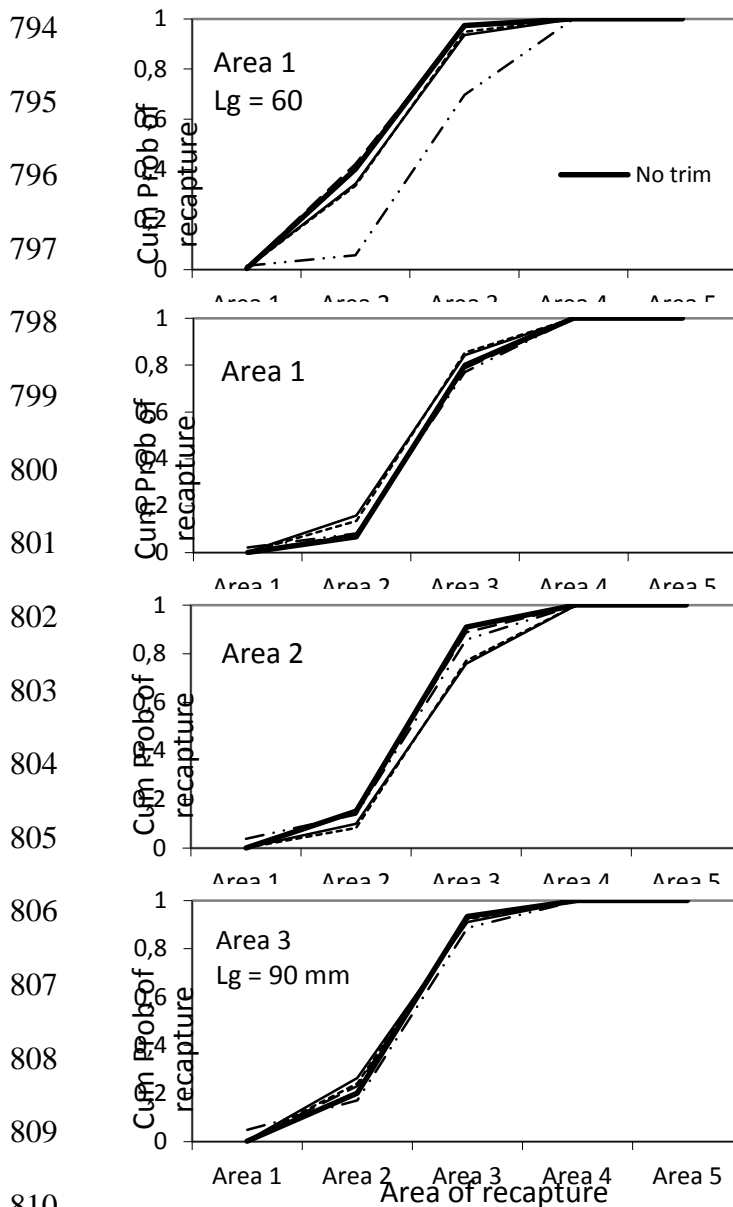


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789

790 Fig. 3. *Palinurus gilchristi*. Box-plot of carapace lengths (CL, mm) of spiny lobsters
791 tagged at 5 areas, showing the median, 25th and 75th quartiles, the whiskers with
792 maximum 1.5 interquartile range, and outliers.

793

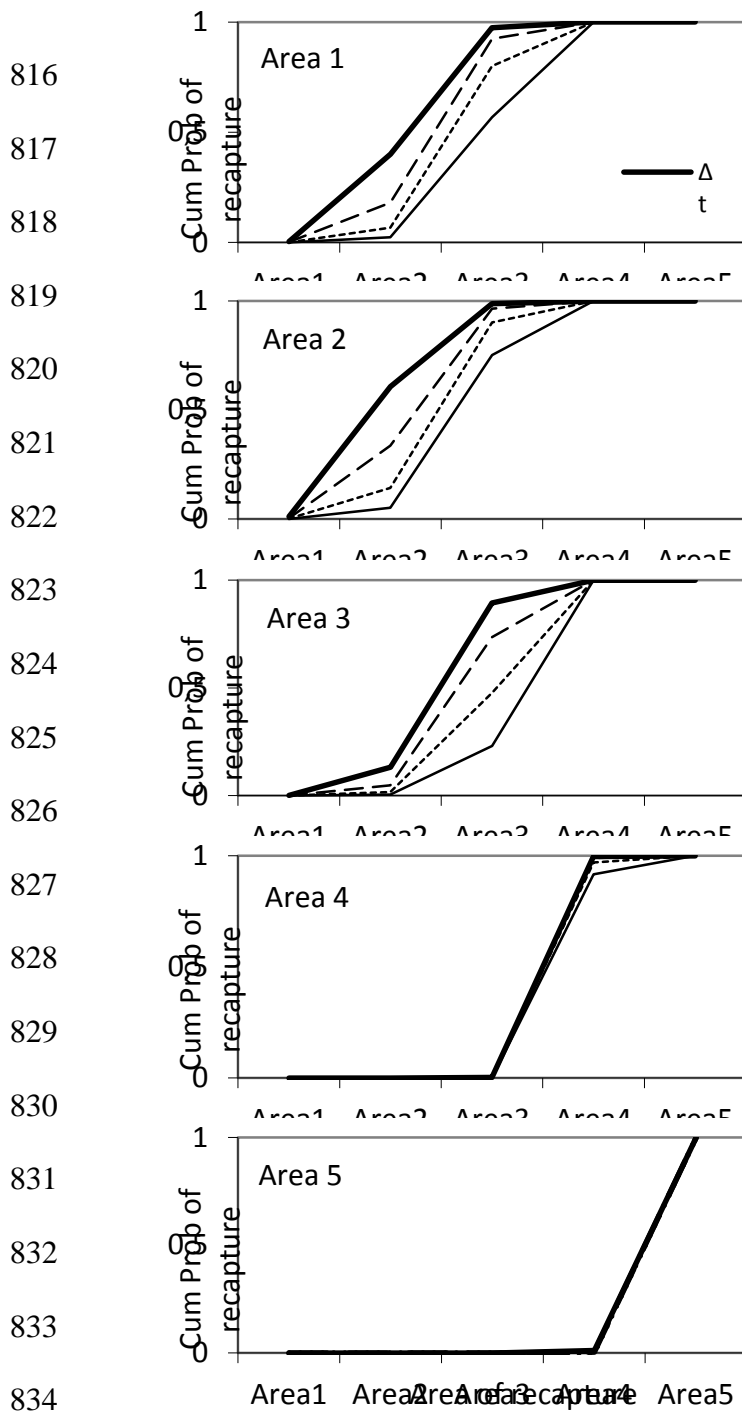


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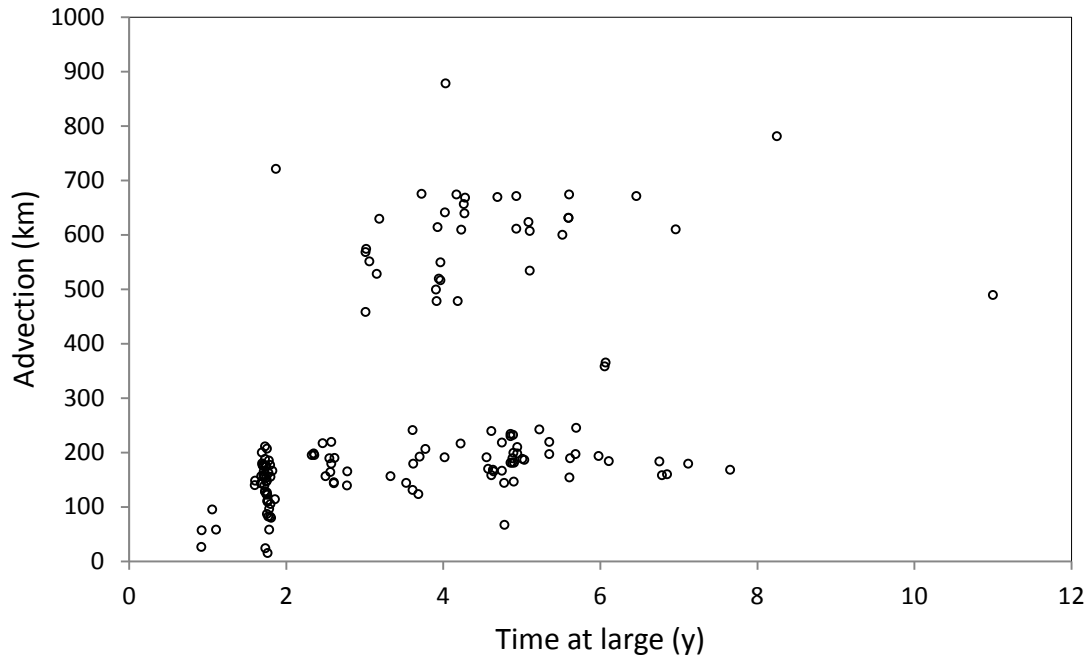
811

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

815



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

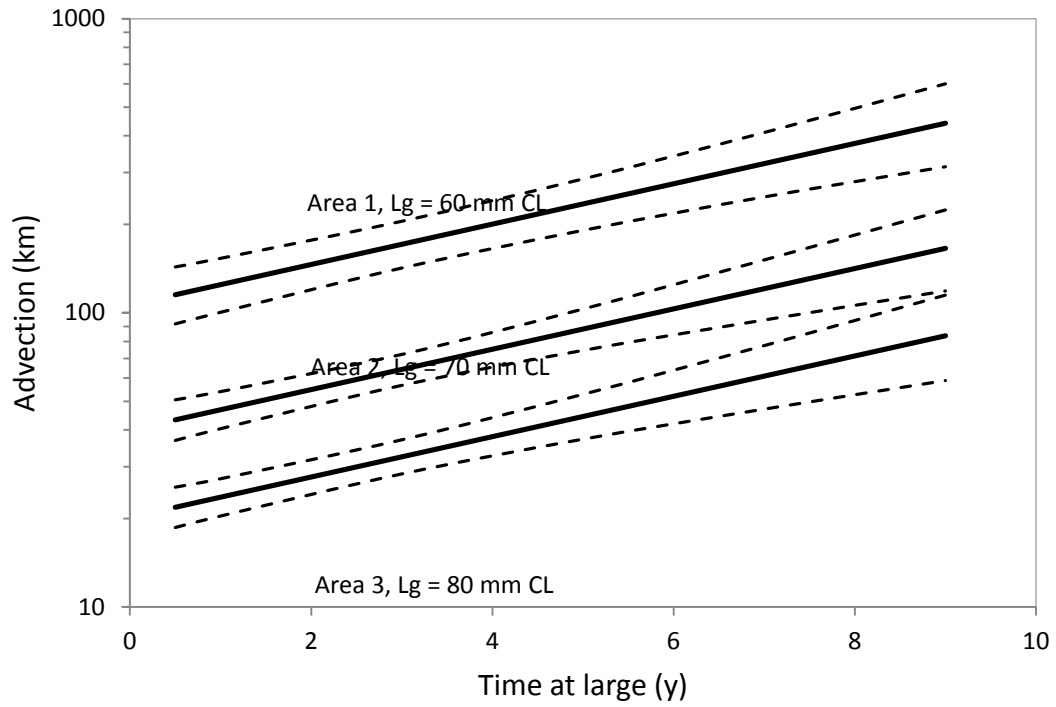


838

839 Fig. 6. *Palinurus gilchristi*. Advection distances as a function of time at large for
840 lobsters tagged in area 1, showing a large degree of heterogeneity found in small
841 lobsters tagged in this area.

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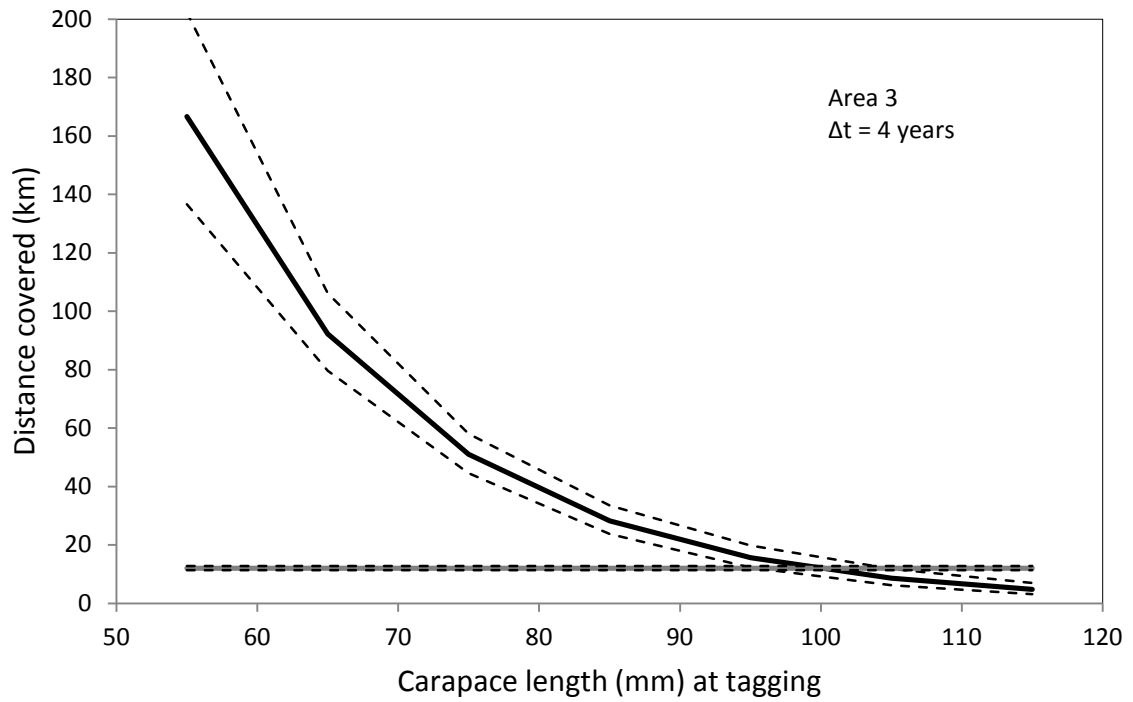
845

846 Fig. 7. *Palinurus gilchristi*. Predicted advection distances with increasing time at large

847 for a selection of areas and lengths at tagging (Lg). Stippled lines indicate the 95%

848 confidence limits of the distance estimates. Distances are given in logarithmic scale.

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852 Fig. 8. *Palinurus gilchristi*. Predicted distances covered by advection (black line) and
853 diffusion (gray line), respectively, of lobsters of a range of sizes tagged in area 3 and at
854 large for 4 years. Stippled lines indicate the 95% confidence limits of the distance
855 estimates.

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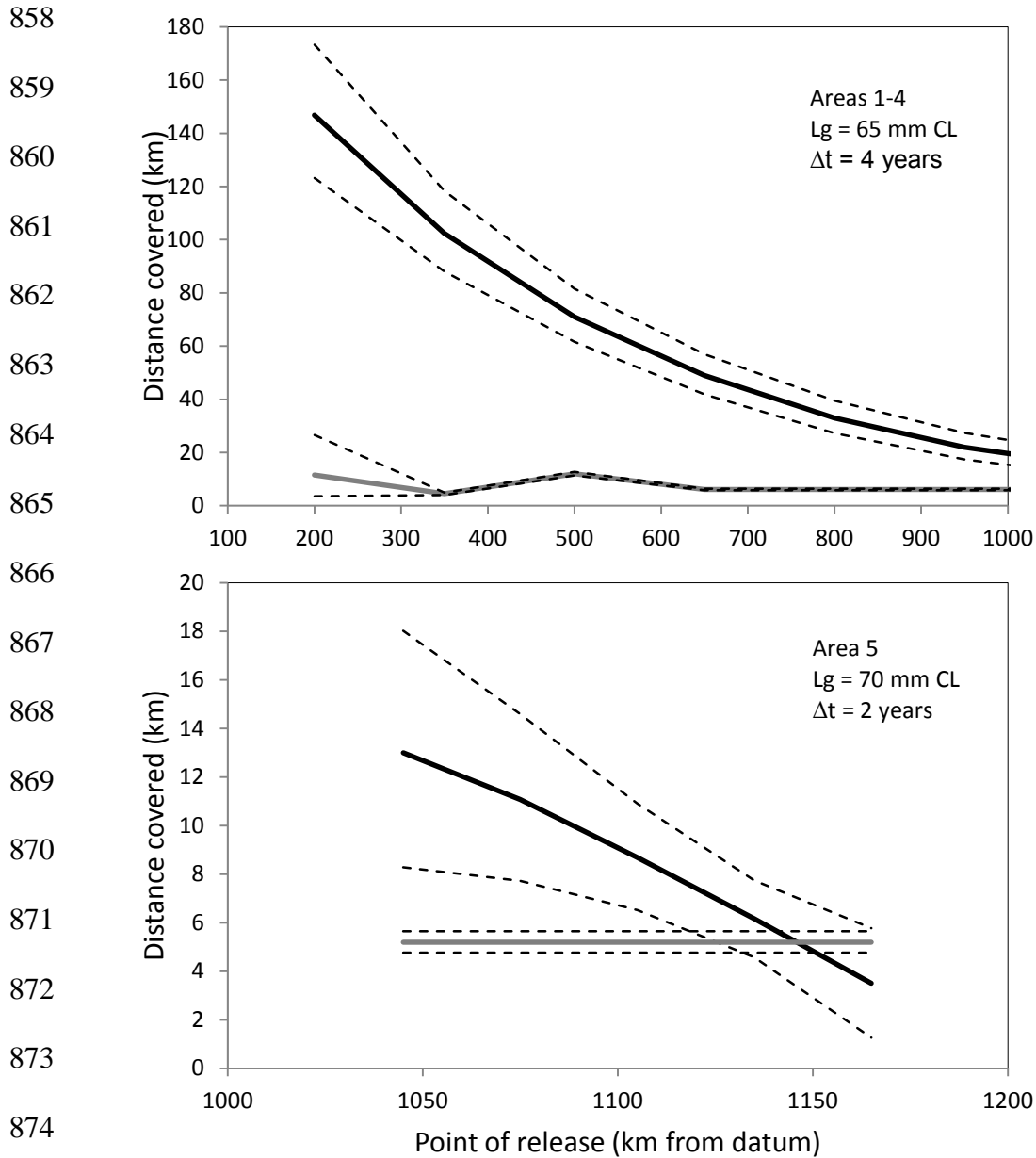


Fig. 9. *Palinurus gilchristi*. Relationship between point of release (i.e. distance from datum) and distance migrated by advection (black line) and diffusion (gray line), respectively, for lobsters of similar sizes tagged in areas 1-4 (top) and 5 (bottom) and at large for 2 to 4 years. The y-axes have different scales.