

Diffusion of American lobster (*Homarus americanus*) in Northumberland Strait, Canada

Cornelia Elizabeth den Heyer, E. Michael P. Chadwick, and Jeffrey A. Hutchings

Abstract: We tested the hypothesis that American lobster (*Homarus americanus*) movement can be described as diffusion. In 2001 and 2002, 3689 lobsters, captured by experimental trap and trawl surveys, were tagged and released in Northumberland Strait, Canada. Recaptures ($n = 413$) were reported by roughly 200 commercial fishermen, up to 3 years after release. Only six lobsters, all females, were recaptured more than once. Recapture rates were marginally higher for males (male 12%, female 10%) and varied with area of release (range: 5%–12%) and the fishing gear used for tagging (trap 12%, trawl 11%). Maximum and mean displacements between release and recapture were 58.3 and 12.3 km, respectively. The positive linear correlation between mean square displacement (MSD) and time between release and recapture provides evidence for diffusion. We calculate a diffusion coefficient (D) of $13 \text{ km}^2\text{-week}^{-1}$; there was no difference in D between sexes. A power analysis showed that MSD is underestimated at small sample sizes. There were insufficient data to test for differences in D associated with sexual maturity or shell hardness at time of release. During the summer in Northumberland Strait, the lobster population spreads about 20 km. The demographic consequences of seasonal diffusion of lobster warrant study.

Résumé : Nous évaluons l'hypothèse selon laquelle les déplacements du homard d'Amérique (*Homarus americanus*) peuvent être interprétés comme des diffusions. En 2001 et 2002, nous avons marqué et relâché 3689 homards capturés lors d'inventaires au casier expérimental et au chalut dans le détroit de Northumberland. Les recaptures ($n = 413$) ont été signalées par environ 200 pêcheurs commerciaux, jusqu'à 3 ans après la libération. Seuls six homards, tous femelles, ont été capturés plus d'une fois. Les taux de recapture étaient légèrement plus élevés chez les mâles (mâles 12%, femelles 10%) et variaient en fonction du point de libération (étendue: 5–12%) et l'engin de pêche utilisé lors du marquage (casier 12%, chalut 11%). Les distances maximale et minimale des déplacements entre la libération et la recapture étaient respectivement de 58,3 et 12,3 km. La corrélation linéaire positive entre le déplacement moyen au carré (MSD) et le temps entre la libération et la recapture est une indication de diffusion. Nous calculons que le coefficient de diffusion (D) est de $13 \text{ km}^2\text{-semaine}^{-1}$, sans différence de D entre les sexes. Une analyse de puissance montre que MSD est sous-estimé dans les petits échantillons. Il n'y a pas suffisamment de données pour tester les différences de D associées à la maturité sexuelle ou à la dureté de la carapace au moment de la libération. Durant l'été dans le détroit de Northumberland, la population de homards s'étend d'environ 20 km. Il y aurait intérêt à étudier les conséquences de cette diffusion saisonnière des homards.

[Traduit par la Rédaction]

Introduction

Individual lifetime net displacement, or dispersal, can result from large-scale movements or an accumulation of small-scale movements attributable to behaviours associated with foraging, mating, and predator avoidance (Dingle 1996). Dispersal defines populations and metapopulations (Dobzhansky and Wright 1943; Pulliam 1988; Lebreton et

al. 1992), enables range expansion (Skellam 1951; Kot et al. 1996; Clark et al. 1998), and contributes to population persistence in temporally variable environments (Roff 1975, 1986, 1994).

Individual and mass mark–recapture studies are commonly used to study animal movement. Both empirical and theoretical models can be used to describe the density–distance distributions of individual net displacements and extrapolate population redistribution (Kot et al. 1996; Turchin 1998; Clark et al. 1999). Diffusion or random walk models that assume movement is equally probable in all directions or random with respect to space are commonly used as null models. In a homogeneous space, with no boundaries and individuals with identical movement behaviour, diffusion predicts a normal density–distance distribution. The regression of the mean square displacement (MSD), which measures population dispersion, on time at large can be used to test for diffusion and estimate the diffusion coefficient (Kareiva 1983; Rudd and McEvoy 1996). Deviations from the predicted normal density–distance distribution may indicate population or habitat heterogeneity (Dobzhansky and Wright 1943; Kareiva 1983; Skalski and Gilliam 2000).

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C.E. den Heyer.¹ Fisheries and Oceans Canada, Bedford Institute of Oceanography, 1 Challenger Drive, Dartmouth, NS B3H 4J1, Canada.

E.M.P. Chadwick. Fisheries and Oceans Canada, Gulf Fisheries Centre, P.O. Box 5030, Moncton, NB E1C 9B6, Canada.

J.A. Hutchings. Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.

¹Corresponding author (e-mail: Nell.denHeyer@mar.dfo-mpo.gc.ca).

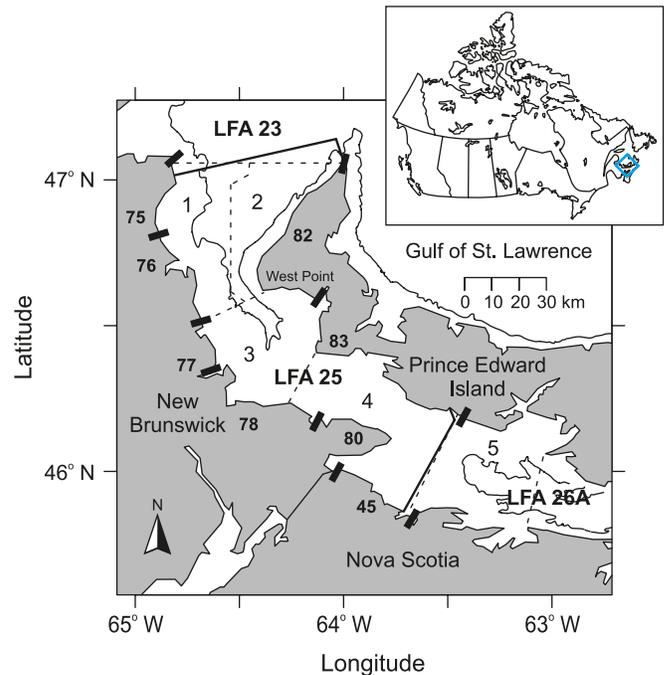
The American lobster (*Homarus americanus*) is economically and socially important to Atlantic Canada. Facilitated by an intense commercial fishery, large body size, and ease of handling, mark-recapture tagging studies have been used to quantify exploitation rate, growth, and movement in this species (reviewed by Krouse 1980; Haakonsen and Anoruo 1994; Comeau and Savoie 2002). These studies have generally found that lobsters, recruited to the fishery, can be highly mobile. Displacements of more than $1 \text{ km}\cdot\text{day}^{-1}$ are not uncommon, although mean and median displacements over months and years are often less than 5 km.

Lobsters exhibit a variety of individual movement behaviours and patterns. Movements that allow individuals to maintain single or multiple dens or depressions in close proximity to one another are described as being characteristic of resident behaviour, while movements that do not contribute to the maintenance of a home range are described as transient or nomadic (Herrnkind 1980; Ennis 1984; Karnofsky et al. 1989a). Individuals may alternate between resident and transient behaviour throughout warmer summer months, but are generally less active, and hence more resident, during winter months (Ennis 1984; Karnofsky et al. 1989b; Watson et al. 1999).

Heterogeneity in movement behaviour may also be linked to intrinsic factors such as size, sex, and maturity. As lobsters grow, they become increasingly mobile (review by Lawton and Lavalli 1995). While tagging studies conducted off southwestern Nova Scotia found that mature lobsters moved farther than immature lobsters (Campbell and Stasko 1985, 1986; Campbell 1989), studies in southern Gulf of St. Lawrence (sGSL) do not show strong evidence of a size bias (Comeau and Savoie 2002; Bowlby et al. 2007). In the sGSL, lobsters mature at a smaller size than elsewhere (Fisheries Resource Conservation Council 2007). The size of 50% maturity has been estimated to range between 69 and 73 mm carapace length (CL) for lobsters landed at seven fishing ports in northeastern Nova Scotia (Watson 1988) and New Brunswick (Comeau and Savoie 2002), while off the southern coast of Nova Scotia and New Brunswick the size at 50% maturity ranges between 95 and 105 mm CL (Fisheries Resource Conservation Council 2007).

Sex-biased dispersal in both birds and small mammals has been linked to nesting behaviour and mating strategies (Greenwood 1980; Clarke et al. 1997). However, mark-recapture tagging studies commonly find no difference in movement between the sexes in fish, although there are a few exceptions, including two species of marine fish (lingcod, *Ophiodon elongatus* (Smith et al. 1990); rig, *Mustelus lenticulus* (Francis 1988, cited in Attwood and Bennett 1994)) with female-biased movement, and one population of brook trout, *Salvelinus fontinalis*, in which males disperse farther than females (Hutchings and Gerber 2002). Female-biased movement of lobsters may be associated with mating and reproduction. Male lobsters are territorial and defend one or more dens, while females choose mates and (or) dens (Atema et al. 1979; Karnofsky and Price 1989) and hence may be more mobile than males. Female-biased movement may also be associated with achieving optimal temperatures for egg development (Campbell 1989). Alternatively, the greater physiological tolerance of male lobsters to high temperatures and low salinities (Jury et al. 1994a, 1994b) may result in male-

Fig. 1. Map of the study area, showing its partitioning into five strata bounded by broken lines. The lobster fishing areas (LFAs 23, 25, and 26A) are bounded by solid lines. Indicated in bold numerals (45, 75, 76, 77, 78, 80, 82, and 83) and demarcated by ticks are the statistical districts in which lobster landings are reported. Also indicated is the 20 m depth contour. Northumberland Strait is in the southern Gulf of St. Lawrence and is bounded by Prince Edward Island, New Brunswick, and Nova Scotia.



biased lobster dispersal in estuaries and bays (Munro and Therriault 1983; Howell et al. 1999; Watson et al. 1999).

Some lobster tagging studies have documented distinct directed return movements to and from specific areas (Campbell 1986; Pezzack and Duggan 1986). Seasonal inshore-offshore migration or mass movement has also been inferred from changes in abundance and distribution (Munro and Therriault 1983; Roddick and Miller 1992; Howell et al. 1999). While previous mark-recapture tagging studies in Northumberland Strait (Fig. 1) provided little or no evidence of directed movements (Comeau and Savoie 2002), a recent study with acoustic tags, which tracked individuals released during the fall (August–October) fishery through the winter and into the following summer, suggested a seasonal pattern of migration out of the Strait in the fall and returning in the spring (Bowlby et al. 2007).

Here we report the analysis of a 2-year mark-recapture tagging study of lobsters in Northumberland Strait, Canada. Our objectives were threefold: (i) to quantify seasonal patterns in lobster movement; (ii) to test the hypothesis that lobster movement can be described as diffusion; and (iii) to examine whether lobster movement is related to sexual maturity or sex.

Materials and methods

Study area

The focal area for the present study was the western half of Northumberland Strait, which encompasses lobster fishing

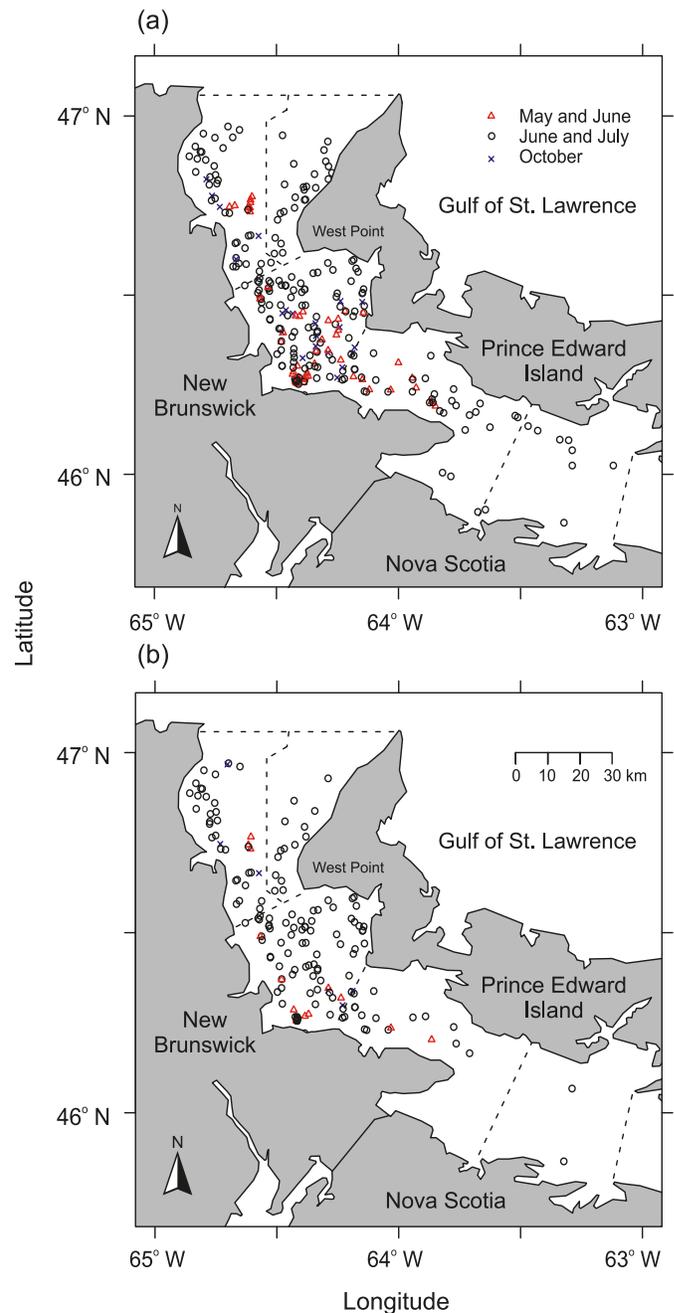
Table 1. Number of tagged lobsters cross-classified according to recapture, sex, release strata, and release season.

Release season	Release stratum	Not recaptured		Recaptured in 2001, 2002	
		Male	Female	Male	Female
May, June	1	26	23	1	2
	2	0	0	0	0
	3	53	86	2	10
	4	13	23	0	2
	5	0	0	0	0
July, August	1	382	334	51	45
	2	161	194	19	21
	3	660	754	113	102
	4	134	192	15	10
	5	26	26	3	0
October	1	54	63	0	3
	2	0	0	0	0
	3	43	40	1	2
	4	0	0	0	0
	5	0	0	0	0

area (LFA) 25 and the western edge of LFA 26A. Northumberland Strait separates Prince Edward Island from New Brunswick and mainland Nova Scotia (Fig. 1). It is approximately 320 km long and between 13 and 48 km wide. Water flows from west to east. The net flow is on the order of centimetres per day (J. Chassé, Bedford Institute of Oceanography, 1 Challenger Drive, Dartmouth, Nova Scotia, Canada, personal communication). Tides inside the Strait are semidiurnal, with a maximum tidal range of 2 m. During summer, bottom water temperatures can approach 20 °C inside the Strait (Fisheries and Oceans Canada 2001). In winter, ice covers much of the Strait. The study area was divided into five strata (Fig. 1), defined by the Fisheries and Oceans Canada (DFO) trawl survey described below.

In Canada, the lobster fishery is regulated by effort control and restrictions on the size and condition of landed lobsters. The number of lobster harvesters in the Strait has dropped slightly from 887 in 1995 to 843 in 2006 (Fisheries Resource Conservation Council 2007). Ovigerous female lobsters are prohibited from the landings, and the minimum legal CL of lobsters landed in LFA 25 was 67.5 mm in 2001 and 2002. LFA 25 has a fall (August–October) fishery, while all others in sGSL have spring (May–June) fisheries. Also, unlike the other lobster fisheries in sGSL, fishermen in LFA 25 do not have areas of traditional use, but are free to move throughout the LFA; most fishermen set one or two traps per buoy and it is not unusual for them to move their traps.

Prior to the 2002 lobster fishery in LFA 25, a total of 3689 lobsters were tagged with streamer tags (manufactured by Hallprint Pty. Ltd., 27 Jacobsen Crescent, Holden Hill, South Australia, Australia 5088) sewn through the dorsal musculature between the carapace and tail (Table 1). Lobsters were caught by experimental trapping in the spring and early summer, by the prefishery DFO trawl surveys in May and July, and by the postfishery trawl survey in August and October (Fig. 2). CL was measured from the eye socket to the end of the cephalothorax in a line parallel to the mid-

Fig. 2. Map of the release sites (a) and recapture sites (b). The symbols indicate the season of release. More than one individual was released at most release sites.

dorsal line. Softness of the shell to the left and right of the mid-dorsal line and at the lower edge of the cephalothorax was noted. The sex and absence or presence of eggs was also recorded.

Trawl survey

To estimate the exploitation rate of the lobster fishery in Northumberland Strait, DFO conducted a trawl survey of lobster abundance before and after the fishery between 2000 and 2003 (Comeau et al. 2004). Trawl stations were established on a 3.1 km (2 nautical miles) grid of areas deeper than 5 m and suitable for trawl gear. A No. 286 trawl with

rockhopper footgear was towed for 15 min at 4.6 km (2.5 nautical miles) per hour at stations chosen randomly in five strata. The net had a 17.7 m (58 foot) head rope and a 21.9 m (72 foot) ground rope (see Comeau et al. 2004 for further details). Owing to weather and time constraints, the May and October trawls surveys focused on the central part of LFA 25, between West Point and Confederation Bridge, while the July and August surveys encompassed all of LFA 25 (Fig. 2a). During the trawl surveys, tagged lobsters were usually held on board for 15 min prior to release; tags were removed from unresponsive lobsters (approximately 2% of lobsters tagged).

Trap survey

To monitor the distribution of lobsters in May, June, and July in 2001 and 2002, five commercial fishermen participated in an experimental trap survey in strata 1 and 3 (Fig. 1). The design and deployment of experimental traps varied among fishermen (den Heyer 2006), but all possessed blocked escape vents to increase the capture probability of small lobsters. During the trap surveys, tagged lobsters were released immediately after tagging.

Tag recaptures and reports

Prior to the fishing seasons in both 2001 and 2002, fishermen were mailed information about the tagging study. There were 793 licence holders in LFA 25 in 2001 (Fisheries and Oceans Canada 2002). The Maritimes Fishermen's Union (MFU) wharf representatives, DFO biologists, and province of Prince Edward Island (PEI) biologists also helped by collecting tag returns and posting information about the research project. The MFU and PEI Fishermen's Association published articles on the research in their newsletters, and DFO maintained a toll-free number to receive tag reports. (In the fall of 2001, a public service commission strike left the DFO phones unattended during the fishing season and some tag reports were not received.) In 2002, in addition to notification of the tagging study, a tally sheet for recording information on tagged lobsters was sent to fishermen with the lobster licence. Also in 2002, one of us (CdH) visited all 30 wharves at least once during the fishing season, and for those fishermen who reported catching tagged lobsters, there was a draw for two hand-held GPS units (approximate value of \$400).

Tests of hypotheses

Basic statistical analyses and data presentations such as maps, histograms, and linear regressions were produced in R 2.7.0 (R Development Core Team 2008). Differences in the probability of capture and recapture can bias interpretation of movement data. While the distribution of release effort is known, with mark-recapture studies that rely on the tag reports from commercial harvest, the distribution of fishing effort, as well as the fishing gear and practices, can result in spatial and temporal variability in the probability of recapture as well as differences in recapture probability among segments of the population. We used log-linear models (Poisson distribution) to test whether the probability of recapture was independent of several factors: year of release (2001, 2002); capture method (trap, trawl); sex (male, female); shell hardness (hard, soft); and release stratum (1, 2, 3, 4, 5). The capture frequencies (y_{ij}) were modeled as function recapture ($R(i)$) and test effect ($T(j)$):

$$\log y_{ij} = \mu + \mu_{R(i)} + \mu_{T(j)}$$

Unpaired t tests were used to compare mean displacement distances. Kolmogorov–Smirnov tests were used to compare the size distributions of lobsters tagged and released by trap and trawl and recaptured by the fishery.

Movement direction

The diffusion null hypothesis is that the direction of movement is random. A Rayleigh test of the mean vector (ρ), where

$$\rho = 1/n \times \left[\left(\sum \cos \theta \right)^2 + \left(\sum \sin \theta \right)^2 \right]^{1/2}$$

was used to test for a random distribution of directions (Batschelet 1981) of displacement distance between capture and release sites with tags and release with tags and recapture. The Rayleigh test was completed using CircStats package (Lund 2001).

Movement rate

The diffusion model predicts that the spatial distribution of individuals (x and y coordinates) released from a point will be bivariate normal and that the probability density function for net displacement (r) will be a function of the diffusion coefficient (D) and time (t).

$$(1) \quad f(r) = \frac{1}{2Dt} e^{-(r^2/4Dt)}$$

This density function is a special case of a Weibull density function ($\nu = 2$, $\lambda = 1/4Dt$, see below) called the Rayleigh distribution. Assuming no change in the population size (no mortality and no recruitment), the rate of population spread (c^*) can be estimated from the diffusion coefficient,

$$(2) \quad c^* = 2\sqrt{D}$$

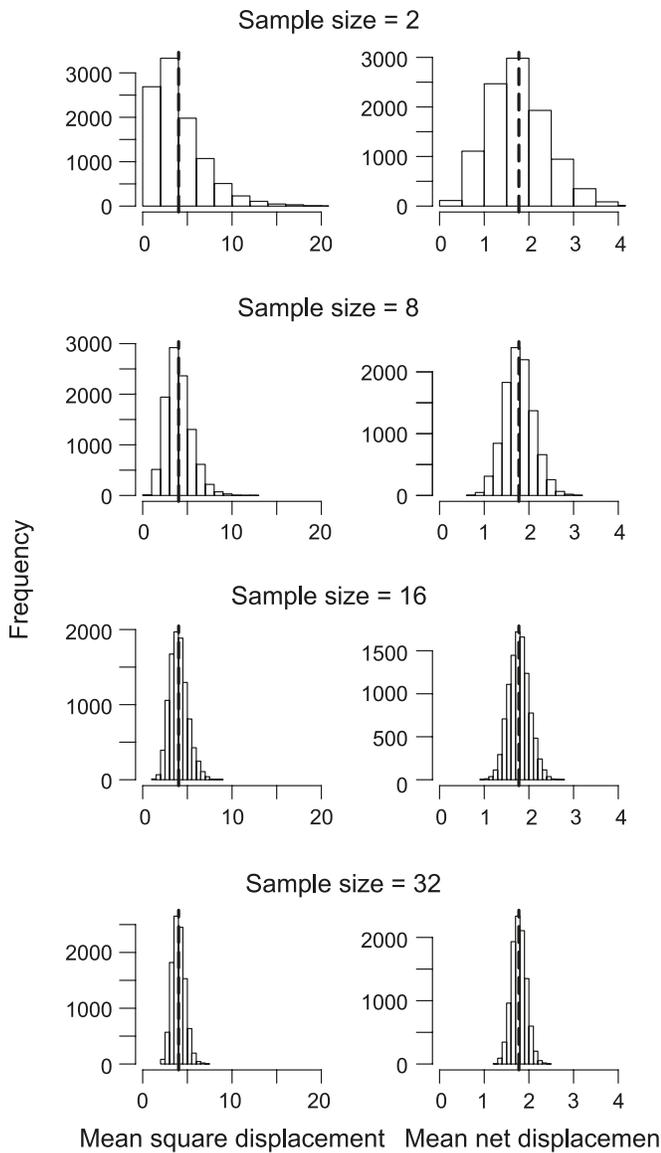
At any point in time, D can be estimated from the mean square displacement (MSD) divided by $4t$ (Skellam 1951; Kareiva 1983; Rudd and McEvoy 1996). However, estimates of MSD at low sample sizes are more variable than estimates of mean net displacement and are skewed to the left (Fig. 3). To determine the appropriate sample size for estimating MSD, we generated a data set of 10 000 observations from a Weibull distribution ($\nu = 2$, $\lambda = 2, 18$, or 32 , for example $D = 1$ and $t = 1, 3$, or 4) from which we sampled 1000 times at a range of sample sizes (2 to 100). The plot of the proportion of samples that estimated the MSD plus or minus 33% is asymptotic (Fig. 4) and is not influenced by the scale value. A sample size between 20 and 30 will provide an estimate of MSD plus or minus 33% 9 times out of 10.

The linear regression of the MSD and time between release and recapture provides a test for random movement (Kareiva 1983, Rudd and McEvoy 1996). If the relationship between MSD and time can be described by a straight line, the diffusion model is accepted. We fit a linear model:

$$y_i = \mu + \mu_{W(i)}$$

where MSD (y_i) is a function of the weeks at large ($W(i)$). This relationship has been used in other studies for which there was not a single point of release (Kareiva 1983; Rudd

Fig. 3. Histograms of 1000 estimates of mean square displacement (MSD) and mean net displacement by randomly sampling data ($N = 10\,000$) generated from a Weibull distribution with shape of 2 and scale of 2. The vertical lines indicate the population MSD (4.00) and mean net displacement (1.77).



and McEvoy 1996). We tested for the effect of sexual maturity, shell hardness, and sex by including a covariate ($S(j)$) in the model:

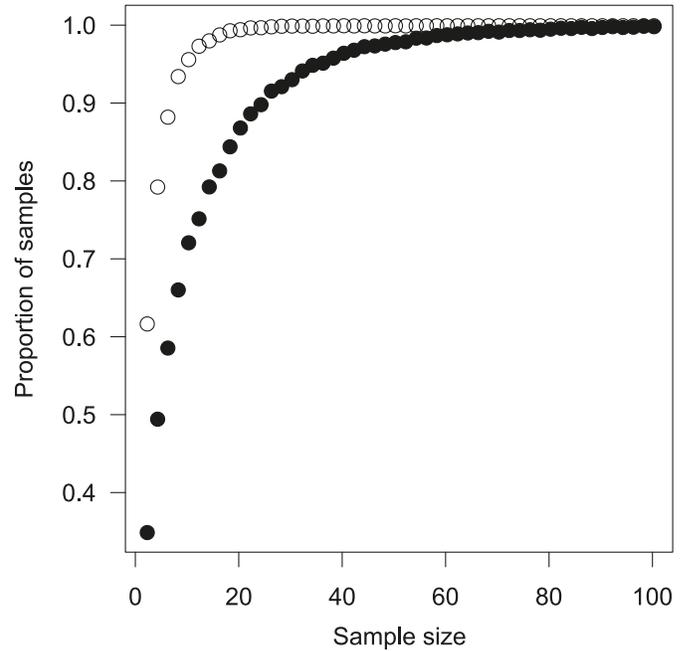
$$y_{ij} = \mu + \mu_{W(i)} + \mu_{S(j)} + \mu_{WS(ij)}$$

Here, we accept 70 mm CL as the 50% size at maturity for lobsters in the sGSL (Miller et al. 2006). To ensure that we are not using adjacent size classes in the comparison of mature and immature lobsters, immature lobsters are defined as <68 mm CL and mature lobsters as $\text{CL} \geq 72$ mm.

Density–distance distributions

A variety of empirical models have been used to describe density–distance distributions (Turchin 1998; Clark et al.

Fig. 4. Plot of the proportion of samples ($n = 1000$) that are plus or minus 33% of the mean square displacement (MSD, solid circles) and the mean net displacement (open circles) of generated data (Weibull distribution, shape = 2, scale = 2, $N = 10\,000$) versus the sample size.



1999). Here, we use the two-parameter Weibull probability density function:

$$f(x) = \nu\lambda x^{(\nu-1)} e^{-(\lambda x^\nu)}$$

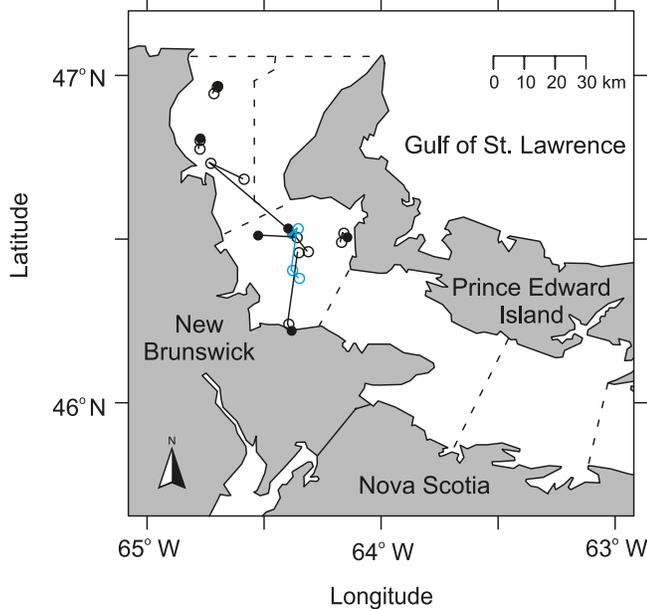
with shape parameter (ν) and scale parameter (λ), because the Weibull distribution is very flexible and can describe Rayleigh distributions ($\nu = 2$) that result from diffusion, as well as long- and fat-tailed distributions, which are common for density–distance distributions of animal movement (Rudd and McEvoy 1996; Morales et al. 2004). The shape and scale parameters for the Weibull were estimated using Markov chain Monte Carlo (MCMC) techniques with WinBUGS 1.4 (see www.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml for further information) called through the BRugs R package (Thomas et al. 2006). Hyperpriors were used for both ν and λ (gamma: shape = 1, scale = 1). The model was solved for 20 000 iterations.

Results

Recapture data

Approximately 200 commercial fishermen in LFA 25 reported the tag number, date, and location (GPS or LoranC coordinates) of the capture of tagged lobster. 11% (402) of lobsters released prior to the 2002 lobster fishery were recaptured and reported (Table 1). Two reports were excluded because the recapture positions were in serious error; the positions reported were outside of LFA 25 in an area that was not open to fishing at that time. A third report was discounted because the lobster CL was 10 mm less when recaptured than that recorded at time of release, and the recapture date was also misreported. Three recapture dates

Fig. 5. The tracks of the six lobsters recaptured twice (black) and the one lobster recaptured three times (blue). The solid circles indicate the initial release sites; open circles show the capture sites.

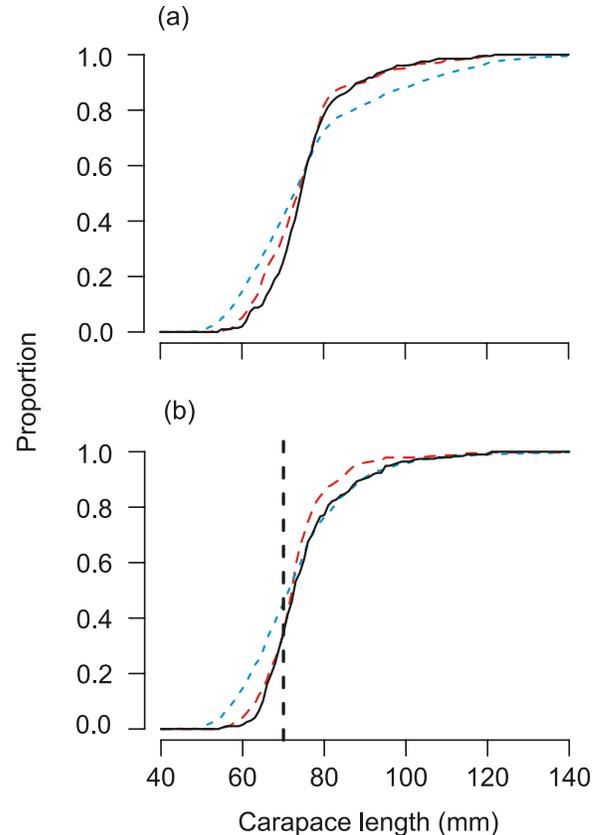


were not included in analysis that involved time at large because the dates of reporting were a few days before the fishery opened. Seven small (CL at time of initial release 65–77 mm) female lobsters were released by fishermen and reported a second time; one was reported a third time (Fig. 5). The recaptures of two tagged lobsters were reported in 2003 and 2004. Both were females with eggs at time of release in July and May 2002, respectively. In total, there were 386 reports that could be used to calculate displacement distance and 348 reports that could be used to calculate the displacement and the days between release and recapture.

There was a significantly higher recapture rate in 2002 than in 2001 for those lobsters that were released in the 9 months prior to the fishery (7.9% and 11.1% recaptured in 2001 and 2002, respectively; $p < 0.001$). Male lobsters were more likely to be recaptured than female lobsters (Table 1, $p < 0.01$), and lobsters that were soft at the time of tagging were less likely to be recaptured (10.5% and 7.4% recaptured for hard- and soft-shelled individuals, respectively; $p < 0.001$). The proportion recaptured varied between the release strata (Table 1, $p < 0.001$). Lobsters that were captured and tagged by trap survey had a higher rate of recapture than lobsters tagged during the trawl survey (9.5% and 11.1% recaptured for trawls and traps, respectively; $p < 0.001$). Although there was no difference in the size distribution (Fig. 6, Kolmogorov–Smirnov; $p = 0.174$) of lobsters tagged by trap survey ($n = 753$, mean = 74.4 mm, range = 53–141 mm) and recaptured by the fishery ($n = 402$, mean = 76.0 mm, range = 55–122 mm), the fishery caught a smaller size range of lobsters than the trawl survey ($n = 2931$, mean = 75.1 mm, range = 43–153 mm) (Kolmogorov–Smirnov; $p < 0.001$).

Half (50.5%) of the tagged lobsters were released in stratum 3 (Table 1). Lobsters were more likely to be recaptured and reported if they were released in strata 1, 2, or 3 (10%–

Fig. 6. Cumulative distribution of size at time of release of male (a) and female (b) lobsters that were recaptured by the fishery (solid black line), tagged during the trawl survey (broken blue line), and tagged during the trap survey (broken red line). The broken vertical line is the size at maturity for female lobsters (70 mm carapace length).



12%) than if they had been released in strata 4 or 5 (5%–7%). The number of reports of tagged lobsters in each district in 2002 was positively correlated with the lobster landings in 2001 (Fig. 7). The landings in 2001 were used as a surrogate for landings in 2002, as there is very little difference between landings in 2001 and 2002 (Comeau et al. 2004). In both 2001 and 2002, reports per landing were highest in the central part of the Strait (districts 77, 78, and 83).

Movement direction

Although there was no significant tendency in the direction of displacements for lobsters released in stratum 1 (Table 2, Fig. 8a), there was a southward tendency in displacements of lobsters released in stratum 2 (Fig. 8b) and a northward tendency for lobsters released in strata 3 and 4 (Figs. 8c and 8d). Overall, there was a small northward tendency in the direction of displacements between release and recapture (Table 2, Fig. 8f).

Movement rate

50% of lobsters tagged and released in Northumberland Strait moved less than 9 km (Table 3). The largest displace-

Fig. 7. Plot of landings in 2001 and reports of recaptured tagged lobsters by statistical district. The statistical districts are identified across the top; open triangles are 2001 and solid triangles are 2002. The regression lines are plotted. There are two data points hidden.

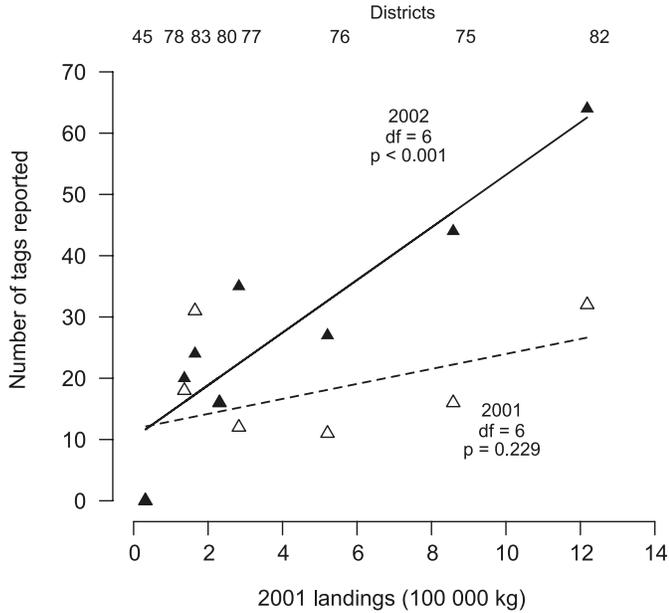
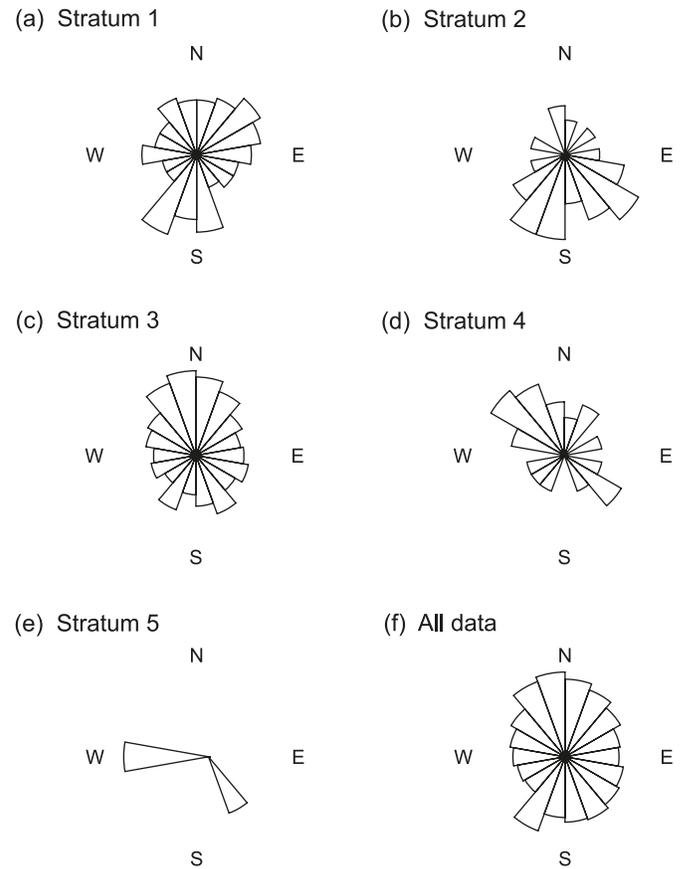


Table 2. Summary of Rayleigh test for bias in direction on displacement between release and recapture.

Release stratum	<i>n</i>	θ_m (°)	ρ	<i>p</i>
1	95	106.2	0.0756	0.5810
2	37	167.9	0.5557	<0.001
3	226	2.5	0.2399	<0.001
4	25	-31.3	0.3632	0.0353
5	3	-112.7	0.5002	0.5139
All	386	10.8	0.1035	0.0160

ment was 58.3 km and the mean displacement was 12.3 km. On average, lobsters were at large for 56 days and the rate of displacement ranged from 0 to 12.11 km·day⁻¹, with a mean of 0.56 km·day⁻¹. The mean displacement for female lobsters (*n* = 176, mean = 13.8 km) was greater than that for males (*n* = 172, mean = 10.9 km) (*df* = 330.123, *p* = 0.014), but there was no difference in displacement per day (male: mean = 0.48 km·day⁻¹, *n* = 172; female: mean = 0.63 km·day⁻¹, *n* = 176; *p* = 0.1446). Only 59 immature lobsters (CL < 68 mm) were recaptured. There was no difference (*p* = 0.80) between the mean net displacement of immature (mean = 12.9 km, *n* = 59) and mature lobsters (mean = 12.4 km, *n* = 227), nor was there a difference in the displacement per day (immature: mean = 0.40 km·day⁻¹, *n* = 59; mature: mean = 0.61 km·day⁻¹, *n* = 227; *p* = 0.3184). The mean net displacement for lobsters tagged during the trap survey (*n* = 87, mean = 17.8 km) was significantly greater than that for lobsters tagged during the trawl survey (*n* = 253, mean = 10.8 km; *p* < 0.001), but there was no difference in displacement per day (trap: mean = 0.51 km·day⁻¹, *n* = 87; trawl: mean = 0.52 km·day⁻¹, *n* = 87; *p* = 0.782). The difference between the mean net displacement of lobsters with hard shells at time of release

Fig. 8. Rose diagrams of the direction of displacements between release and recapture by stratum (a–e) and for all the tag reports (f). North is at 0°. The class width is 20°, and the radius is scaled to the square root of the class frequency.



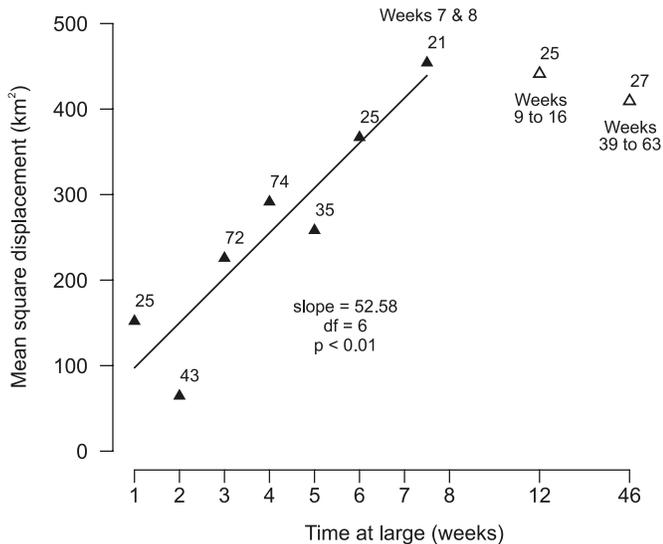
(mean = 12.9 km, *n* = 289) and those with soft shells at time of release (mean = 10.4 km, *n* = 50) was not significant (*p* = 0.065). There was also no significant difference (*p* = 0.207) in the displacement per day for lobster with hard shells (mean = 0.53 km·day⁻¹, *n* = 289) and those with soft shells at the time of release (mean = 0.44 km·day⁻¹, *n* = 50).

The MSD was positively correlated to time between release and recapture for lobsters at large less than 8 weeks (Fig. 9). Estimates of MSD are sensitive to variance, and for small sample sizes the MSD tends to be underestimated. Here, we lump weeks 7 and 8 to achieve a sample size greater than 20. The diffusion coefficient (*D*), estimated from the slope divided by 4, is 13 km·week⁻¹ or 1.88 km·day⁻¹. The MSD for lobsters at large for 9–16 weeks and for 39–63 weeks was 411 and 409 km², respectively. There was no difference in the slope of the regression of MSD on time between males and females (Fig. 10a). Only 53 immature lobsters (CL < 68 mm) were recaptured, having been at large less than 8 weeks. As none of the 1-week intervals had more than 10 displacements of mature lobsters (Fig. 10b), there were insufficient data to test for differences between the mature and immature lobsters using the regression of MSD on time. Similarly, the data were insufficient to compare *D*, estimated from the slope of the regression of MSD on time at large, for lobsters with soft or hard shells at time of release (Fig. 10c).

Table 3. Summary of the distribution of net displacement of lobsters in intervals between release and recapture.

Interval (weeks)	<i>n</i>	Distance (km)			Weibull parameters	
		Min.	Max.	Mean	ν (2.5% and 97.5% CIs)	λ (2.5% and 97.5% CIs)
1	25	0.8	44.0	6.9	0.8743 (0.6501, 1.120)	0.2115 (0.0961, 0.3794)
2	43	0.3	19.9	6.1	1.1060 (0.8597, 1.384)	0.1373 (0.0652, 0.2408)
3	72	0.5	42.5	11.8	1.2630 (1.0450, 1.490)	0.0433 (0.0204, 0.0791)
4	74	0.3	44.6	13.8	1.2430 (1.0230, 1.480)	0.0381 (0.0168, 0.0711)
5	35	0.5	42.3	11.8	1.0160 (0.7667, 1.293)	0.0887 (0.0339, 0.1766)
6	25	1.2	53.4	13.8	1.0030 (0.7204, 1.320)	0.0816 (0.0253, 0.1819)
7, 8	21	0.6	36.6	18.2	1.2980 (0.8735, 1.793)	0.0290 (0.0042, 0.0893)
9 to 16	25	0.5	58.3	16.6	1.1580 (0.8257, 1.533)	0.0442 (0.0106, 0.1125)
39 to 63	27	1.7	51.4	15.4	1.1040 (0.8024, 1.447)	0.0548 (0.0150, 0.1294)

Fig. 9. Plot of the mean square displacement (MSD) versus weeks at large. The regression line was fit to the MSD of lobsters at large and the number of weeks between release and recapture (Time at large). Weeks 7 and 8 were lumped together because of low sample size. Also plotted are the MSDs of lobsters at large between 9 and 16 weeks and between 39 and 63 weeks. The number of lobsters in the calculation of MSD is indicated for each datum.



Density–distance distributions

Weibull distributions were fit to the density–distance distributions for displacements during each time interval (Fig. 11, Table 3). There was very little variation in ν among intervals, and none of the curves fit by maximum likelihood were described by the Rayleigh distribution ($\nu = 2$). There was more variation in λ . In general, λ declined with more time at large, but the 95% confidence interval tended to be quite large. For comparison, we plotted the sum of the density distributions for diffusion (eq. 1, D of $1.88 \text{ km}\cdot\text{day}^{-1}$ ($13 \text{ km}\cdot\text{week}^{-1}$), $t = \text{days at large}$), weighted by the proportion of recaptures for each day at large in that release period.

Discussion

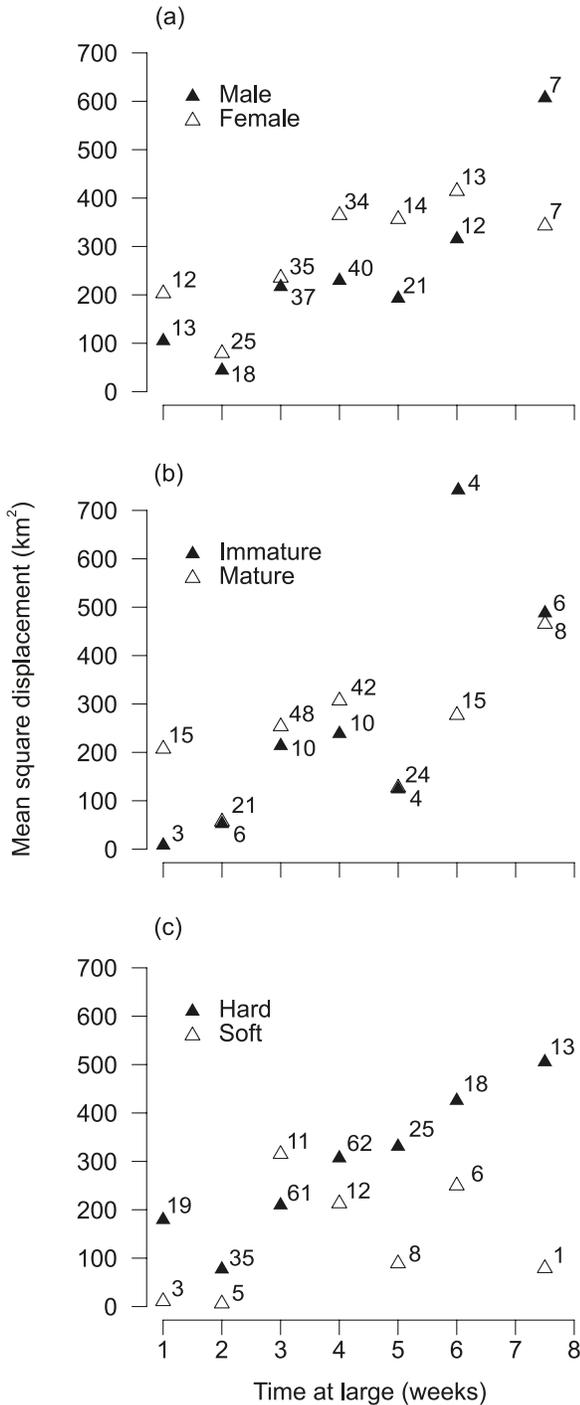
We apply standard quantitative analysis of the displacement of lobsters between mark and recapture to test the hypothesis that movement by American lobsters can be described by diffusion. We find that movement by lobsters

in Northumberland Strait during summer can be described by diffusion (i.e., a random walk). From the regression of MSD on time, we estimate the diffusion coefficient (D), which is a measure of population redistribution that incorporates both a measure of variance in movement and time at large.

One constraint of our study was that tagged lobsters had to be both recaptured and reported by fishermen. Although the fishery in LFA 25 can be intensive (in 2003, the fishery caught 75% of the exploitable biomass; Fisheries Resource Conservation Council 2007), only about one-quarter of the fishermen participated in our study. In 2002, after increasing our effort to collect tag reports by offering prizes and visiting all the wharves in LFA 25, the return rate of tagged lobsters increased from 7% to 11%. Previous tagging studies in the sGSL have documented higher tag returns (Comeau and Savoie 2002), possibly because tagging in discrete locations facilitates communication with lobster fishermen. The difference in size-selectivity between the fishery and the trawl survey may also have reduced the probability of recapture of lobsters tagged during the trawl survey. Further, low tag retention and high tag mortality could contribute to low return rates. Capture by trawl and handling in midsummer may have contributed to increased mortality, and while we do not have moult stage information for hard lobsters, a previous summer tagging study in this area attributed lower recapture rates to higher tag loss and tag-induced mortality for lobsters tagged during the premoult stage (Comeau and Mallet 2003).

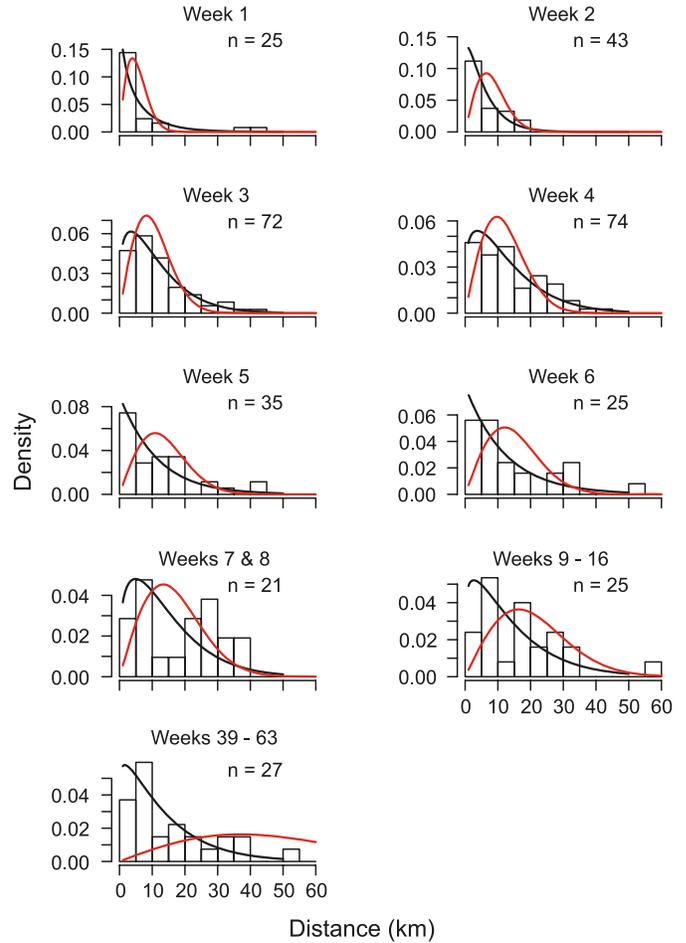
The extrapolation of tagging studies to population-level processes assumes that the individuals sampled are representative of the population. However, mark–recapture studies rarely sample all individuals with equal probability (Turchin 1998). Often the probability of recapture is highest near release sites, leading to an under-sampling of the tails of the density–distance curve (Barrowclough 1978; Baker et al. 1995; Koenig et al. 1996), which represent the rare long-distance movements that may be of particular importance to population spread (Kot et al. 1996; Clark et al. 1998). While participation of the commercial fishermen allowed this study to be executed at a spatial scale that would have been impractical for fisheries-independent research, the distribution of fishing effort and spatial variation in the participation of fishermen may have biased the distribution of recaptures and hence the magnitude and direction of displacements between release and recapture. Further, variation in fishing gear and practices also might have in-

Fig. 10. Plot of mean square displacement versus weeks at large for male and female lobsters (a), for mature and immature lobsters (b), and for lobster with hard and soft shells at time of release (c).



fluenced recapture probability. Both intrinsic factors, such as size, sex, maturity, and moult stage, and extrinsic factors, such as season, weather, and water temperature can influence catchability (Miller 1990; Tremblay and Smith 2001; Tremblay et al. 2006). Lobsters that were soft at the time of release were slightly less likely to be recaptured. Male lobsters were also marginally more likely to be recaptured than female lobsters, possibly because fishermen are prohibited from landing ovigerous females, and the re-

Fig. 11. Histograms of net displacements for time intervals at large, with the Weibull curves (black line) fit to the displacement data and time-integrated density distribution (red line) predicted by simple diffusion ($D = 1.88$).



duced time spent handling ovigerous lobsters may reduce the likelihood of identifying tags, or fishermen might avoid areas where they are likely to catch ovigerous females.

Overall, the distribution of releases and recaptures are similar. Half of the releases were in stratum 3, and just a little under half of the tagged lobsters that were recaptured (caught and reported) were in stratum 3. Lobsters were more likely to be recaptured if they were released in strata 1, 2, or 3 (10%–12%) than if they had been released in strata 4 or 5 (5%–7%). The higher probability of recapture in the more westerly strata probably reflects the distribution of fishing effort. Fishermen in LFA 25 do not have to report where they fish, but the distribution of fishing effort would be expected to reflect lobster distribution (Campbell 1986, Swain and Wade 2003). The trawl survey prior to the fishery in LFA 25 identified high densities of lobsters in stratum 1 and off West Point, PEI, on the southern edge of stratum 2 and the northern edge of stratum 3 (Comeau et al. 2004), where recaptures were concentrated. Additionally, the number of recaptures in a statistical district was positively correlated to the landings.

Undirected or random movement with respect to space is an assumption of the diffusion model. This does not necessarily mean that the animals are moving at random, but

rather that the movements are unbiased with respect to space or that a movement in one direction is as likely as a movement in another direction, as might happen if resources were homogeneously distributed. The directional bias of displacements in strata 2, 3, and 4 may have resulted from a concentration of recapture effort off West Point, which would have biased recaptures to the south in stratum 2 and to the north in stratum 3. Overall, there was a weak bias in the displacements to the north, which we feel resulted from differences in the distribution of release and recapture effort and not from directional bias in lobster movement.

The significant positive linear relationship between the MSD and time at large is evidence of diffusion or random movement. The diffusion coefficient can also be estimated from density–distance curves described by Rayleigh distributions. All of the density–distance distributions for the 1-week and several week time intervals are more leptokurtic than predicted by the Rayleigh distribution. The time-integrated curves for release intervals less than 4 weeks describe the density–distance distributions better than those for longer release periods. Over time, spatial heterogeneity, such as shape of the study area and spatial variability in recapture effort, could result in a left skew. For lobsters released in stratum 3 (50% of the releases), the maximum displacement detectable by the LFA 25 fishery was roughly 100 km to either north or southeast, but much less in other directions as defined by the edges of the Strait. D can be estimated from density distributions in areas with reflecting and absorbing boundaries (Kareiva 1982; Turchin 1998), such as the edges of the Strait and the adjacent fishing areas, and density–distance distributions can be corrected by weighting the observed displacements by the observation effort (Barrowclough 1978; Baker et al. 1995; Koenig et al. 1996). Kareiva (1983) suggests applying a correction for a truncated density–distance distribution when 10%–15% of the individuals reach the limit of detection. Unfortunately we cannot easily apply a correction to our estimates of diffusion because we released individuals over such a large area and cannot quantify the distribution of fishing effort. Population heterogeneity in movement behaviour may also be contributing to the leptokurtosis (Dobzhansky and Wright 1943; Clark et al. 1998; Skalski and Gilliam 2000). Recently, Bowlby et al. (2007) identified resident and dispersive lobsters in the western part of the Northumberland Strait (strata 2 and 3) by fitting a switching model (Morales et al. 2004) to lobster movements tracked over the winter.

Previous tagging studies in the sGSL also have found the highest mean displacements (5.4–19.4 km) of lobsters to be in Northumberland Strait (Comeau and Savoie 2002). In the present study, most lobsters were at large for less than 3 months, averaging $0.56 \text{ km}\cdot\text{day}^{-1}$, with a maximum of $12.11 \text{ km}\cdot\text{day}^{-1}$ for an individual that was at large for less than 1 week. A recent study with acoustic tags in the same study area also reported high movement rates ($>7 \text{ km}\cdot\text{day}^{-1}$) for lobsters at large for less than 3 months (Bowlby et al. 2007). High movement rates during short release intervals can be indicative of tag-induced movement. The process of being caught and brought to the surface, as well as handling during tagging, may elicit a stress response in lobsters that could induce high rates of movement. The only other lobster

tagging study in which we have found reports of such high rates of movement for American lobster was conducted on the southern New England continental shelf; 31 individuals that had a net displacement of more than 185 km averaged between 1.8 and $10.2 \text{ km}\cdot\text{day}^{-1}$ (Uzmann et al. 1977). It has been suggested that the relatively flat homogeneous bottom of Northumberland Strait facilitates lobster movement (Stasko 1980; Comeau and Savoie 2002) and that the pan-shaped Strait provides a large area in which lobster can move (Comeau and Savoie 2002). Perhaps the relatively homogeneous and shallowly sloped bottom of Continental Shelf also provides opportunity for lobster movement. The lack of physical shelters that might cue settling or resident behaviour might also contribute to higher movement rates. Further, the bottom water temperatures in Northumberland Strait during the summer are the highest in sGSL (Fisheries and Oceans Canada 2001). The warmer water may result in higher activity and higher movement rates (McLeese and Wilder 1958; Karnofsky et al. 1989b; Watson et al. 1999). Alternatively, lobsters in Northumberland Strait may be composed of a greater proportion of dispersive lobsters (Bowlby et al. 2007) than areas with more larval settlement and (or) higher juvenile survival, which would sustain a larger population of less mobile or more resident lobsters.

In sGSL, lobster tagging studies have documented both male and female bias in mean net displacement (Comeau and Savoie 2002). Although we found a small but statistically significant difference in mean net displacement between male and female lobsters, there was no difference in the estimate of D between sexes. As in many of the earlier tagging studies, our large sample size makes it possible to detect statistically significant, albeit biologically insignificant, differences in mean net displacement. D incorporates both the variance in displacements and the time between release and recapture. Unfortunately, achieving precise and unbiased estimates of D requires more data than that required for estimating net displacement, and detecting differences between D becomes increasingly difficult with greater time intervals (Cain 1991).

Ontogenetic changes in lobster behaviour from shelter-restricted early benthic stages to the increasingly vagile juveniles have been well documented (Lawton and Lavalli 1995). The net displacement reported here for sexually mature lobsters is comparable with the displacements of large mature lobsters off southwestern Nova Scotia (Campbell and Stasko 1985, 1986). We found there to be no difference in the mean net displacement of immature (CL < 68 mm) and mature (CL ≥ 72 mm) lobsters. Unfortunately, it was not possible to fit a regression line for MSD on time at large with only 53 immature lobsters recaptured with less than 8 weeks at large.

MSD does not increase linearly for release intervals of 3–4 months and 6–13 months. The levelling off of MSD may result from spatial or temporal heterogeneity in movement behaviour. As discussed above, with more time at large, movement may be limited by the shape of the Strait or long-distance displacements may not be detected because of the reduced probability of reporting of tagged lobsters caught in adjacent fishing areas, where there was no direct effort to solicit reports. Temporal variation in movement behaviours can also result from periods of inactivity or settlement. In Northumberland Strait, MSD increases for 7–8 weeks during the

warmer summer months. In the colder winter months, lobsters are generally less active and more resident (Ennis 1984; Karnofsky et al. 1989b; Watson et al. 1999), while lobster activity increases with temperature (McLeese and Wilder 1958). Similarly, during summer months, there may also be a period of reduced movement as lobsters seek shelter and feed less often during ecdysis and the stages immediately following the moult (Aiken and Waddy 1980). Although there is not enough data to test for differences in *D* between lobsters that were hard and soft at time of release, net displacement is slightly lower for lobsters that had soft shells at time of release, probably reflecting reduced mobility of lobster with soft shells.

Superimposed on directionally arbitrary diffusive movement in summer may be directed seasonal migration into and out of the Strait. Bowlby et al. (2007) tracked large (CL = 81–89 mm) lobsters leaving the Strait in autumn. A small shift in the distribution to deeper water in winter has been documented off the coast of Newfoundland (Ennis 1984), while off southwestern Nova Scotia and Maine shifts to deeper water are of greater magnitude (Uzmann et al. 1977; Campbell 1986; Pezzack and Duggan 1986). In spring, lobsters may undertake a directed inshore migration into warmer water for moulting and mating (Munro and Therriault 1983; Campbell 1986; Moriyasu et al. 1999) or may disperse into seasonally available habitat (Jeffries and Johnson 1974; Karnofsky et al. 1989b; Howell et al. 1999). In the present study, we found no evidence for directed movement into the Strait, but our tagging in May, June, and early July would have captured primarily the resident overwintering lobsters. The relatively flat and homogeneous bottom of the Strait may provide limited overwintering habitat, and individuals that have not secured shelter for the winter may undertake directed movement to deeper water.

Diffusion of lobsters in Northumberland Strait for only 2–3 months a year could result in a population (demographic unit) spread of about 20 km·year⁻¹. Based on landings data (Miller et al. 2006) and the DFO trawl survey (Comeau et al. 2004), a high proportion of the lobsters in the central part of Northumberland Strait (strata 3, 4, and 5 and the adjacent area to the east) are larger than 81 mm CL. The mean size of lobsters landed to the east of the present study area has historically (data from 1930–1932, 1940, 1947–1950, 1975, and 1999) been one–two moult sizes greater than other areas around Prince Edward Island (Miller et al. 2006). Diffusion of lobsters from areas with greater abundance of smaller lobsters in the northern part of the Strait (stratum 1), or even outside of the Strait, could account for the observed greater proportion of large lobsters in landings from that area.

An understanding of adult movement could help define demographic units and, in conjunction with research on larval dispersion, could help to identify population structure. Unfortunately, basic distribution and abundance data are missing for American lobster (Steneck and Wilson 2001). Most data on lobster distribution and abundance are fishery-dependent and limited to harvestable size classes and, in Canada, to particular seasons. On the Atlantic coast, where surveys of settlement and juvenile lobsters have been undertaken, larval settlement is spatially variable (Incze et al. 1997; Wahle and Incze 1997), and the distribution of early benthic stages is more variable than that of adults (Palma et

al. 1999). Dispersal could be density or shelter dependent (Steneck 2006) and (or) part of an ontogenetic habitat shift, such as that which has been documented in blue crab (*Callinectes sapidus*) (Pardieck et al. 1999) and spiny lobster (*Panulirus argus*) (Lipcius et al. 1997). For animals with water-borne larval stages, diffusion away from shallow settlement areas may constitute a contranatal migration. A recent analysis of fishery-independent trawl surveys off New England identified a greater proportion of larger lobsters at depths greater than 50–100 m (Chen et al. 2006), which could be explained by diffusion away from settlement areas. Steneck (2006) explored the ecological implications of demographic diffusion or dispersal of adult lobsters on the Atlantic coast, where an offshore mass migration may provide a refuge from the intense inshore fishery. In the Gulf of St. Lawrence, the cold intermediate layer (CIL), a layer of cold water averaging 0.02 °C (1961–1990) (Fisheries and Oceans Canada 2001), is expected to limit offshore movement of lobsters to less than 30 m (Stasko 1980; Comeau and Savoie 2002), which is the upper limit of the CIL. Instead of providing a refuge, lobster diffusion between LFA 25 and adjacent fishing areas with spring fisheries may increase fishing pressure.

Here, we have shown that lobsters in Northumberland Strait are diffusing during the summer months. The large number of observations with short release times have also allowed for a rigorous test of sex-biased dispersal. While we see no evidence for directed movement of lobsters into and out of the Strait, the high mobility of individuals suggests that lobsters in Northumberland Strait are not distinct from those in the sGSL.

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