

# Stock structure and seasonal distribution patterns of American lobster, *Homarus americanus*, inferred through movement analyses

Heather D. Bowlby<sup>a,\*</sup>, J. Mark Hanson<sup>b</sup>, Jeffrey A. Hutchings<sup>a</sup>

<sup>a</sup> Department of Biology, Dalhousie University, Halifax, NS, Canada B3H 4J1

<sup>b</sup> Department of Fisheries and Oceans, P.O. Box 5030, Moncton, NB, Canada E1C 9B6

Received 14 May 2007; received in revised form 22 October 2007; accepted 2 November 2007

## Abstract

Movement influences the annual distribution patterns of a species and is an important determinant of stock structure. In situations where monitoring programs have quantified movement or distribution patterns by sampling during particular times of the year, seasonal changes in abundance as well as the degree of connectivity among adjacent stocks can be underestimated. Here, a summer abundance trawl survey was combined with a 1-year mark-recapture tagging study to infer seasonal changes in distribution within and among American lobster (*Homarus americanus*) stocks. Within the study area, lobsters were concentrated in central Northumberland Strait (Canada) during August, yet their observed dispersal behaviour implied that density declined in the central portion and increased in the northern portion of Northumberland Strait during winter. Stock mixing among management zones was not observed and individual tendencies to move were predicted to decline precipitously in early December. These movement patterns are consistent with the hypothesis of seasonal limitation by hard-substrate habitat availability causing population redistribution. Such information can ultimately be useful when assessing changes in abundance or exploitation rates, and for guiding management efforts.

Crown Copyright © 2007 Published by Elsevier B.V. All rights reserved.

**Keywords:** Stock structure; Dispersal; Acoustic tagging; Mark-recapture; American lobster

## 1. Introduction

For the purposes of fishery management, a stock is most commonly defined as all individuals of a particular species that reside within the boundaries of a legislated fishing zone (Thorpe et al., 2000; Smith and Addison, 2003). According to this definition, a stock is a management unit rather than an ecologically-defined group of organisms (Harding et al., 1993; Lawton and Lavalli, 1995), and only rarely do stocks correspond to genetically isolated populations (Thorpe et al., 2000). Therefore, the ecological processes structuring populations can vary among or within stocks, particularly when management boundaries are based on governmental jurisdiction rather than an understanding of the life histories of resident organisms (Harding et al., 1993; Vecchione and Collette, 1996; Pollock et al., 2002). For highly mobile species, seasonal or ontogenetic changes in distribution within or among management units can introduce significant

bias into monitoring data used in stock assessment, particularly when estimating abundance or recruitment (Schwarz and Seber, 1999; Gerber et al., 2003). For exploited populations, such parameters must be quantified in order to effectively set harvesting limits (Frank and Brickman, 2001), forecast population trends (Harwood and Stokes, 2003; Fogarty and Gendron, 2004) or undertake remediation projects (Kelly et al., 2000; French McCay et al., 2003). The collapse of many fished stocks (Frank and Brickman, 2001; Myers and Worm, 2003; Hutchings and Baum, 2005) underscores the importance of understanding the spatial dynamics of populations (Vecchione and Collette, 1996; Hutchings and Reynolds, 2004).

American lobsters (*Homarus americanus*) are distributed along the east coast of North America from North Carolina, USA, to Labrador, Canada (Pezack, 1992). Throughout these waters, coastal lobster populations are believed to be locally self-sustaining, with replenishment through reproduction rather than dispersal (Haakonsen and Anoruo, 1994; Lawton and Lavalli, 1995; Comeau and Savoie, 2002). In Canada, fishery management is based on effort control and management regulations are specific to large geographical zones called Lobster Fishing

\* Corresponding author. Tel.: +1 902 494 6279; fax: +1 902 494 3736.  
E-mail address: [hbowlby@dal.ca](mailto:hbowlby@dal.ca) (H.D. Bowlby).

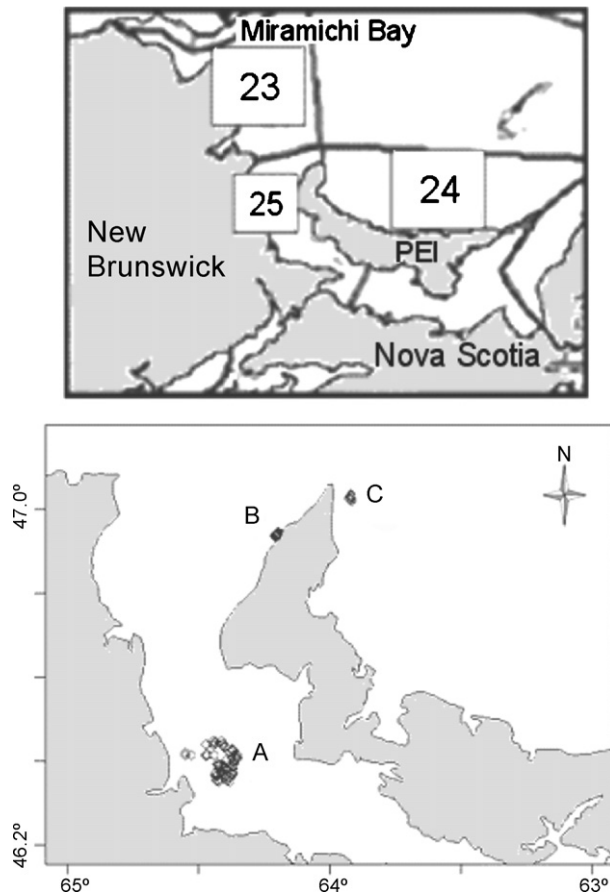


Fig. 1. Geographic map of the study area, showing the location within Atlantic Canada (first panel), as well as the boundaries of the three LFAs from which data were collected (LFA 23, 24 and 25). The silhouette map (second panel) depicts a close-up of the release locations for ultrasonically tagged lobsters: A – central LFA 25 ( $n = 119$ ; 27 August to 7 September 2004), B – northern LFA 25 ( $n = 20$ ; 7 October 2004) and C – western LFA 24 ( $n = 20$ ; 24 September 2004).

Areas (LFAs; Fig. 1). Summer bottom trawl surveys in Northumberland Strait (LFA 25) have identified two areas of high lobster density, one in the central region and one in the northwest region of LFA 25 (Comeau et al., 2004). Although these surveys provide point estimates of the population in time and can be used to track net changes in abundance (Dunnington et al., 2005), they cannot be used to evaluate the seasonal gains and losses of individuals that determine stock structure, defined throughout this manuscript as the degree of genetic isolation, or conversely, the population connectivity, of a species among management units (Pollock et al., 2002).

Given that movement contributes to inter-annual variability in long-term abundance or distribution patterns (Inchausti and Weimerskirch, 2002; Bell et al., 2003; Fisher and Frank, 2004), much marine fisheries research has attempted to quantify movement, often using single mark-recapture tagging studies (Pittman and McAlpine, 2003; Smith and Addison, 2003). For the majority of coastal American lobster populations, such studies have not found evidence of quantifiable movement patterns or predominant long-distance movement by adults (Haakonsen and Anoruo, 1994; Lawton and Lavalli, 1995; Comeau and Savoie, 2002). This suggests that there is little exchange of individuals

among areas, and that seasonal distribution patterns are relatively constant. However, as in abundance surveys, tagging studies can erroneously imply extremely localized stocks if data collection is restricted to specific times of year, such as discrete fishing seasons (Diamond and Hankin, 1985). A recent study with expanded temporal coverage reported distinct resident and disperser movement types in a coastal lobster population for which long-distance dispersal behaviour (median rate = 2.5 km/day) was the predominant strategy (Bowlby et al., 2007). If such patterns are common, stock mixing could be much more prevalent than previously thought.

Ultrasonic telemetry is a relatively new tagging methodology that has the potential to reduce the biases inherent in mark-recapture research while not sacrificing spatial or temporal resolution in data collection (Freire and Gonzalez-Gurriaran, 1998; Schwarz and Seber, 1999). The main benefit is that animals can be recaptured outside of discrete fishing seasons and over large geographical areas concurrently (Kimley et al., 1998). Categorizing the resulting recaptures allows one to compare movement characteristics between fishery-dependent and -independent methods, thus partially controlling for the biases introduced by observation error and catchability (Freire and Gonzalez-Gurriaran, 1998; Sibert and Fournier, 2001). However, for species that are expected to move very little, reliance on remote-sensing techniques may be tenuous when attempting to differentiate between animals that move very little and lost tags. Given that ultrasonic telemetry has not been widely used on crustaceans, there is no well-tested methodology for tag attachment and subsequent tag loss has not been well documented.

To address the issue of stock structure, the present study aimed to quantify lobster movement patterns among LFAs and/or to detect differences in movement behaviour among lobsters originating in different geographical areas, either within or outside of LFA 25. Movement characteristics could then be analyzed relative to summer distribution patterns to infer seasonal changes in distribution as well as the degree of population isolation within or among management units. Such information on the spatial characteristics of the lobster stock in LFA 25 can ultimately be used to guide future regulatory changes and management efforts.

## 2. Methods

### 2.1. Laboratory tagging experiment

The tag attachment experiment was done using a random block design with two tanks (randomly assigned as either treatment or control) and three replicates. Due to space limitations, the replications were consecutive, beginning on 26 October 2005, 25 November 2005, and 6 January 2006, respectively, and lasting 28 days. For each trial, groups of 20 adult lobsters (81–89 mm carapace length, 1:1 sex ratio) were purchased from Clearwater® Lobster Shops (Bedford, Nova Scotia, Canada), tagged, and randomly assigned to one of the two aquaria (1.5 m × 1.5 m × 1.0 m). The control aquarium contained sand substrate and no shelter, while the treatment aquarium contained sand substrate plus two wire lobster traps (hoop size

92 mm) and two concrete cinderblocks. To ensure that the lobsters would remain active and to standardize conditions between trials, the water temperature was held constant ( $14 \pm 1^\circ\text{C}$ ), using a heat-exchanger. The experimental protocol adhered to Canadian Council on Animal Care guidelines on the ethical treatment of animals.

The dummy tag was superficially identical to the acoustic tag used for field data collection (model V13-1L-69 kHz; Vemco Ltd., Nova Scotia, Canada), yet lacked internal electronic circuitry and external numbers. Tags (weighing  $\sim 11$  g in air) were attached to the dorsal carapace surface, offset from the median groove, using 5-min epoxy (Mastercraft®; Canadian Tire Corporation, Canada). To ensure good adhesion, both the lobster's carapace and the dummy tag were roughened with 200 grit sandpaper and dried thoroughly. Lobsters were placed in a partially open cooler while the epoxy hardened (approximately 30 min). Although it was not possible to fully approximate field tagging conditions (ambient temperature, water temperature, weather, and time of year) in the laboratory, the experimental conditions were within the variability experienced during field tagging (27 August to 7 October 2004). Tag retention was confirmed daily and individuals were not disturbed except to determine their sex if their tag had detached.

## 2.2. Field methods

Although the study was initiated in LFA 25, it incorporated information collected from adjacent fishing areas to the north (LFA 23 and 24; Fig. 1). Geographically, LFA 25 encompasses the waterway between Prince Edward Island (PEI) and the mainlands of New Brunswick and Nova Scotia (Northumberland Strait), while LFA 23 lies off northern New Brunswick and the Miramichi Bay, and LFA 24 extends offshore of northern PEI (Fig. 1). The physical oceanography of central LFA 25 is different from more northerly areas, particularly in sediment composition and bottom topography. Central LFA 25 is characterized by shallow water depths (average  $< 20$  m), soft sediment, and extreme seasonal temperature variation ( $< 0$  to  $> 20^\circ\text{C}$ ) owing to wind-driven mixing of the water column. Northern LFA 25 is thermally stratified and experiences much less severe temperature fluctuation in deeper ( $> 40$  m) water yet differs in substrate composition and topography from east to west. Sand and gravel bottom substrate extends along the New Brunswick coast in northern LFA 25, but is more frequently interspersed with cobble and rocky reefs. The PEI-side of northern LFA 25 is predominantly rocky sediment with much steeper bottom topography (Loring and Nota, 1973; Hanson and Courtenay, 1996; Hanson and Lanteigne, 2000).

In 2004, the summer (July/August) trawl survey in Northumberland Strait/LFA 25 (described in detail by Voutier and Hanson (2008)) was undertaken from 17 July to 19 August in waters greater than 4 m in depth (Fig. 2). Randomly selected stations ( $n = 156$ ) from a  $3.7 \text{ km} \times 3.7 \text{ km}$  grid were sampled by an otter trawl equipped with rock-hopper footgear and towed at  $4.6 \text{ km/h}$  for 15 min (Comeau et al., 2004; Voutier and Hanson, 2008). Given that towing stations were restricted to relatively flat bottom types (but various substrate types), adult lobster catchability

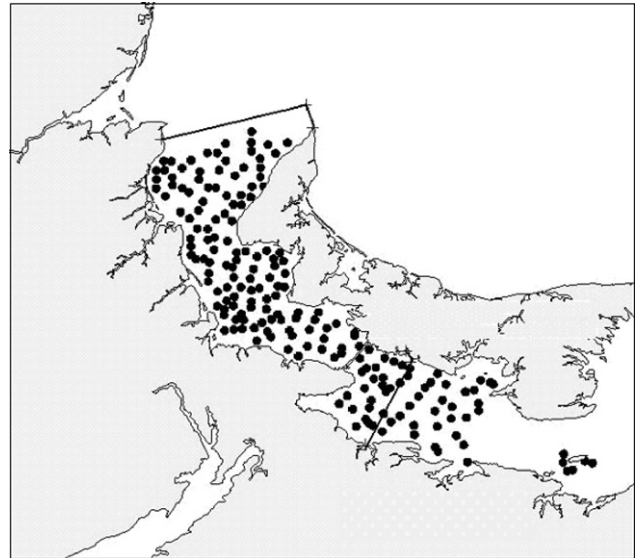


Fig. 2. Locations sampled ( $n = 156$ ) during the 2004 summer trawl survey in Northumberland Strait. Thin black lines denote the boundaries of LFA 25.

was assumed to be constant among stations. Lobster counts per tow were standardized to number per  $\text{km}^2$  to permit comparison among stations. Contour maps of the distribution of adult lobsters ( $\text{CL} > 80$  mm) were generated using point kriging (Comeau et al., 2004).

In autumn of 2004, three groups of lobsters were tagged with ultrasonic transmitters (methodology detailed by Bowlby et al. (2007)) and released: the first in central LFA 25 (released between 27th August and 7th September,  $n = 119$ ); the second in western LFA 24 (released on 24th September,  $n = 20$ ); and the third in northern LFA 25 (released on 7th October,  $n = 20$ ) (Fig. 1). The latter two groups of 20 animals each are collectively referred to as the PEI releases. In each group, individuals were of a standard size (81–89 mm carapace length) and comprised a sex ratio of 1:1. Lobsters were recaptured using three methods: (1) harvester reports, for which fishermen recorded the date, location and tag number of any acoustically-tagged lobsters landed in commercial traps while fishing, before re-releasing the animal; (2) moored hydrophone receivers (model VR2, Vemco Ltd., Shad Bay, Nova Scotia, Canada), where each listening station decoded any tag transmissions in the vicinity and recorded a time and date stamp with each detection; and (3) active tracking with a mobile receiver (model VR60, Vemco Ltd.), during which tags were detected using an omnidirectional hydrophone (model VR65, Vemco Ltd.) suspended below the keel depth of the sampling boat. Each tag transmitted a unique acoustic signal and was externally numbered to permit identification by fishermen. Harvester recaptures were possible from mid-August to mid-October 2004 within LFA 25 and from the start of May to the end of June 2005 in all other LFAs. Fishing effort within each LFA is high (198,250 allowable traps fished daily in LFA 25, 184,200 in LFA 24, and 216,600 in LFA 23) and traps are distributed throughout the available area, with a slight bias towards shallower water as the fishing season progressed (Lanteigne et al., 2004). Passive listening stations were operational from August 2004 to August 2005, excluding the month

of June in central LFA 25, and from August to mid-October 2004 in northern LFA 25. Receivers were positioned in two lines: one spanning the width of the Strait approximately 20 km north of the release sites in central LFA 25 and the second followed the northern boundary of LFA 25, from the New Brunswick shore to 18 km offshore. Active tracking took place during May to August 2005 and was concentrated around the release sites, along the PEI coast, and within 15 km of the line of VR2 receivers in central LFA 25 (Bowlby et al., 2007). Sampling sites ( $n = 1300$ ) were searched following a grid pattern, with stations 500 m apart over the 2004 release sites and 1000 m apart in other areas. The precision of location estimates ranged from 300 to 500 m for active or passive tracking yet could not be determined for harvester recaptures. Errors in position estimates were assumed to be randomly distributed. Lobsters released in central LFA 25 were detected multiple times during 2004 and 2005, while lobsters released off PEI were detected once in the spring/summer of 2005, either by the fishery in LFA 24 (May–June 2005) or by active tracking.

### 2.3. Statistics and modeling

Each individual lobster's recapture history in the wild was transformed from geographical coordinates to rectangular coordinates for further analysis and straight-line movement between locations was assumed (Batschelet, 1981). As such, each movement between two consecutive points became a vector with two components: step length (distance in km) and trajectory angle (radians). To account for the varying number of days between each release and recapture event, step length was standardized to a movement rate or distance per day. Movement vectors were found to be independent by Schoener's Ratio Test (Schoener, 1981), so data from central LFA 25 were pooled and categorized according to season: autumn (recaptures occurring in August to November 2004), winter (occurring in November 2004 to May 2005), and spring/summer (occurring in May to August 2005) for analyses. Data from the two PEI releases were pooled to obtain a sufficiently large sample size, yet were considered to be a separate category from 'winter' even though the recaptures took place during a similar timeframe (November to June 2005).

For each category, the observed distribution of trajectory angles was compared with a uniform distribution using Moore's modified Rayleigh test (Moore, 1980). Compared to a standard Rayleigh test, MRT is less sensitive to variation in displacement because angular observations are weighted as a function of their rank distance prior to calculating the test statistic. This gives little weight to small movements in a particular direction and more weight to large movements. Therefore, it is believed to more accurately represent the behavioural choices of individuals and significance suggested that animals were moving in a preferred direction (Diamond and Hankin, 1985). Step length was compared among categories using a Kruskal–Wallis Rank Sum Test, followed by multiple Mann–Whitney  $U$ -tests. The Kruskal–Wallis and Mann–Whitney tests were chosen over a one factor ANOVA and two-sample  $t$ -tests because movement data tends to be leptokurtic (Turchin, 1998). In all cases, the null hypothesis is that observations are taken from a single distribu-

tion; biologically, this would indicate no difference in median movement distance among categories. Changes in movement rate within a season were shown by fitting a non-parametric lowess smoother to daily displacement during autumn (Crawley, 2002). For time-series data, the lowess smoother is an improvement over traditional least-squares methods in that observations need not be equally spaced through time. All analysis techniques were programmed using the statistical software package 'R' (R Core Development Team, 2004).

Non-random searching effort is known to confound the results of population-level movement studies, particularly when describing movement trajectories (Diamond and Hankin, 1985; Freire and Gonzalez-Gurriaran, 1998). Although commercial fishing effort was evenly distributed throughout LFA 25 during autumn (Lanteigne et al., 2004), the listening stations and active tracking sites were exclusively located to the north of the release sites in central LFA 25. This could have introduced bias into the observed distribution of trajectory angles or step lengths recorded. To test for such bias, the data was partitioned into two parts. The first contained all movement vectors from release up to an animal's first detection by a listening station, while the second contained all subsequent movement vectors. Using the MRT and Kuskal–Wallis tests described above, the entire data set plus the two sub-sets were compared for differences in mean trajectory angle and/or mean step length. No significant differences were found, so the distribution of sampling effort was assumed to have introduced minimal bias into the estimates of displacement. Similarly, Bowlby et al. (2007) found that the tag detection method for mobile lobsters (harvester recaptures or listening stations) had no effect on recorded movements.

Lobsters tagged in central LFA 25 were classified as 'residents' (individuals that remained in the vicinity of release and turned randomly while moving) or 'dispersers' (individuals that exhibited long-distance, directional movement patterns) by Bowlby et al. (2007). Such behavioural differences in the tendency to move could influence the degree to which individuals are susceptible to the commercial fishery, by affecting their ability and motivation to locate and occupy baited traps (Jury et al., 2001). Therefore, we used Fisher's exact test (Zar, 1999) to determine if the proportion of individuals recaptured by harvesters relative to active tracking was the same for both residents and dispersers. If movement behaviour was not correlated with lobster catchability, one would expect the proportions to be equal.

## 3. Results

### 3.1. Experimental tag loss

There were no incidences of tag loss among control animals and total tag loss varied among trials for treatment animals (3/10, 3/10, and 0/10 for each of the three replicates). The majority of tag losses in each trial occurred within the first 6 days of tagging and was rare in subsequent weeks (one lost tag on day 25 in trial 2). Although tag loss did not appear to be sex-biased (pooling data from all trials), the sample size was insufficient for statistical analysis. Mean tag loss over 28 days was estimated to be 20% (95% CI=0.08, 0.39) assuming that

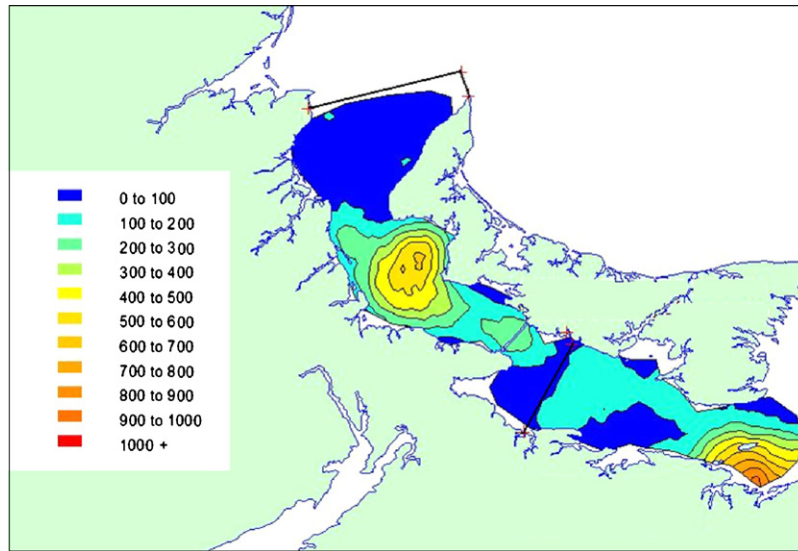


Fig. 3. Adult lobster abundance patterns (number per km) in Northumberland Strait during summer, 2004. Samples were standardized to a 2 km tow length, and were generalized from discrete to continuous data using point kriging. Black lines denote the boundaries of LFA 25.

lobsters encountered hard-substrate features continually and that the time of year had little effect on lobster activity relative to water temperature (Drinkwater et al., 2006). Based on this estimate, 32 of the 159 lobster marked in the field are predicted to have lost their tags soon after release. Study animals were all newly molted when tagged in the field (Bowlby et al., 2007) and lobster activity levels would have declined during winter and spring due to water temperature (Aiken and Waddy, 1986; Karnofsky et al., 1989) so it is likely that few additional tag losses occurred over the duration of the study.

### 3.2. Lobster distribution and movement patterns

In summer (prior to the fishery), adult lobster were concentrated in central LFA 25 and become progressively scarcer to the north, based on catch rate data obtained from the trawl survey. The mean ( $\pm$ S.E.) numbers per square kilometer estimated from the survey were:  $400 \pm 50$  per  $\text{km}^2$  ( $n = 76$ ) in central LFA 25,  $230 \pm 80$  per  $\text{km}^2$  ( $n = 31$ ) along the NB side of northern LFA 25, and  $70 \pm 20$  per  $\text{km}^2$  ( $n = 29$ ) along the PEI side of northern LFA 25 (Fig. 3). Although errors in these estimates resulting from differential catchability among stations are likely to be small, the values are considered to represent relative rather than absolute estimates of mean density. Only 8 days separated the end of the trawl survey from the beginning of ultrasonic tagging in central LFA 25. Thus, it is likely that adult lobster were densely distributed around the release sites of the tagged animals.

Of the 119 animals tagged in central LFA 25, 54 were relocated at least once, giving a recapture rate of 45%. All recaptures were opportunistic, so the number of times each individual was recaptured as well as the way in which it was recaptured differed markedly among animals. New individuals were identified continually throughout the study and the mean number of recaptures for a specific animal was 4 (range 1–19). Almost all animals caught by fishermen were also detected by the VR2 stations (48 individuals, 142 recaptures) while relatively stationary animals

were found only by active tracking (23 individuals, 26 recaptures). Of the 40 individuals released off the coasts of PEI, a total of 15 were recaptured once, 7 in LFA 24 and 8 in northern LFA 25, giving recapture rates of 35% and 40%, respectively. These individuals were recaptured either by harvesters (3 instances) or by active tracking (12 instances).

Although extremely variable, median step length of lobsters during autumn and spring/summer differed significantly from that recorded during winter or from the PEI releases (*c.f.*  $1.9 \pm 2.1$  km and  $1.8 \pm 1.8$  km with  $0.18 \pm 0.63$  km and  $0.14 \pm 0.51$  km, respectively) (Kruskal–Wallis,  $P < 0.001$ ; Fig. 4). Considering only lobsters released in central LFA 25, the

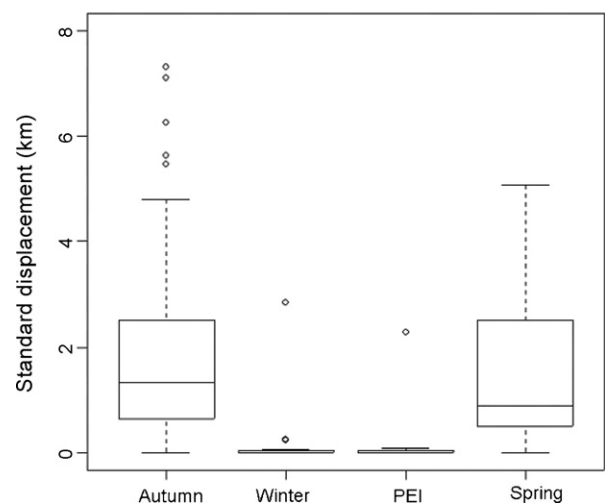


Fig. 4. A boxplot comparing displacement between locations and among seasons (central LFA 25: autumn, winter, spring, and the PEI releases: PEI). Data are pooled for individuals recaptured during autumn (September to November 2004), winter (December 2004 to April 2005), spring (May to August 2005), and PEI (November 2004 to June 2005). Displacement is significantly different between recaptures spanning winter (Winter/PEI) and those in other seasons (autumn/spring) (Kruskal–Wallis,  $P \ll 0.001$ ).

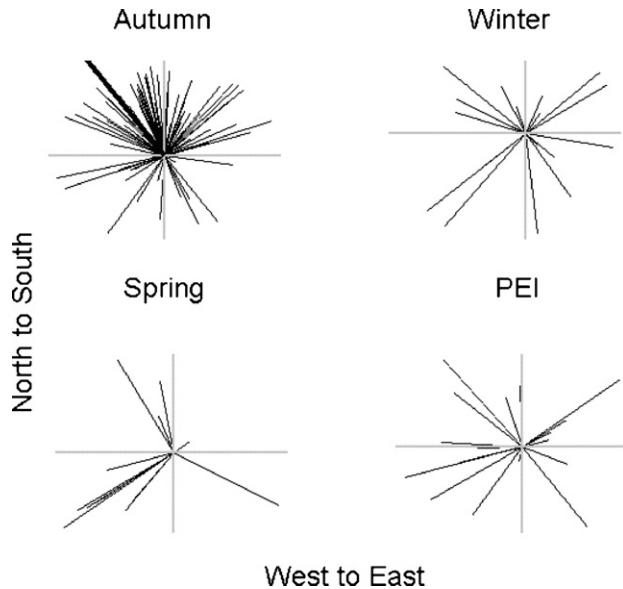


Fig. 5. Distribution of weighted angular vectors from all recorded component moves in autumn, winter, and spring from lobsters released in central LFA 25, and those released off of PEI, pooling data across individuals. During autumn, mean direction is  $122^\circ$  relative to due east (thick black line). There is no preferred direction of movement for lobsters recaptured in winter or spring, or from the PEI releases.

total distance moved by individuals (the sum of all step lengths recorded from recaptures of an individual) averaged 24.3 km (S.D.  $\pm 17.7$  km). The minimum distance traveled by an individual was less than 1 km while the maximum was greater than 85 km. For individuals released off of PEI, mean distance traveled was 2.8 km (S.D.  $\pm 3.3$  km), where the minimum was less than 0.5 km and the maximum was 11.9 km. The direction that lobsters tended to move also differed among seasons as well as between lobsters released in central LFA 25 and those released off of PEI. In autumn, lobsters were not detected in shallower waters to the south of the release sites in central LFA 25 or in nearby estuaries but tended to move northward at a mean trajectory angle of  $122^\circ$  relative to due East (MRT,  $P \ll 0.001$ ; Fig. 5). During the following spring (June and July 2005), the specific individuals recaptured at stationary listening stations had originally been released in central LFA 25 and had been detected moving northward the previous autumn. This suggests that these individuals were returning to central LFA 25 after over-wintering in northern LFA 25, a conclusion supported by the behavioural switching model developed by Bowlby et al., 2007. Lobsters were not detected by the listening stations before the end of May and subsequent detections were relatively consistent during July 2005 (stations were removed in early August). Adult lobster moved in a less directed or coordinated fashion in spring as compared to autumn, as evidenced by the lack of directional preference in trajectory angle (MRT,  $0.5 < P < 0.9$ ; Fig. 5), yet their rate of movement was not significantly lower (Mann–Whitney  $U$ ,  $P = 0.49$ ; Fig. 4). Animals released off of PEI in late autumn were not detected on listening stations in central LFA 25, and showed no evidence of long-distance or persistent movement in any direction (MRT,  $0.1 < P < 0.5$ ; Fig. 5).

There was no difference in the median distance moved between animals tagged in central LFA 25 with those tagged off PEI when movement over analogous time frames (recaptures spanning winter) were compared (Mann–Whitney  $U$ ,  $P = 0.56$ ; Fig. 4). Lobsters tagged in northern LFA 25 were not observed to move laterally across the cold intermediate layer or to immigrate into central LFA 25 in any season. Similarly, no exchange of lobsters across LFA boundaries was observed by any detection method. None of the lobsters tagged in the central Strait or in the northern half of LFA 25 were detected via active tracking outside of LFA 25, nor were any captured in the intensive spring fisheries in LFA 23 or 24. Given that the ‘disperser’ behavioural strategy was much more likely than the ‘resident’ strategy to be captured by the fishery (see below), it is likely that mobile animals were more susceptible to traps and thus should have had a higher probability of detection by harvesters when present.

The rate of lobster movement declined as autumn progressed, from approximately 2.2 km/day in late August to approximately 0.3 km/day by 14th November 2004 (Fig. 6). This reduction in activity is thought to result from declining bottom water temperatures (Aiken and Waddy, 1986; Karnofsky et al., 1989) and presumably compounding energetic constraints (Dieckmann et al., 1999; Bowler and Benton, 2005). In northern latitudes, lobsters remain dormant for winter, exhibiting near-zero activity or movement rates (Lawton and Lavalli, 1995). Assuming that lobster movement declined at a constant rate beyond 14th November 2004, the transition between northward dispersal to over-wintering behaviour would have taken place at the beginning of December, approximately 96 days after release. This timeframe could not be directly identified during autumn data collection, but it is useful for estimating a potential traveling distance of lobsters in a way that is not biased by non-uniform sampling over time (Diamond and Hankin, 1985; Freire and

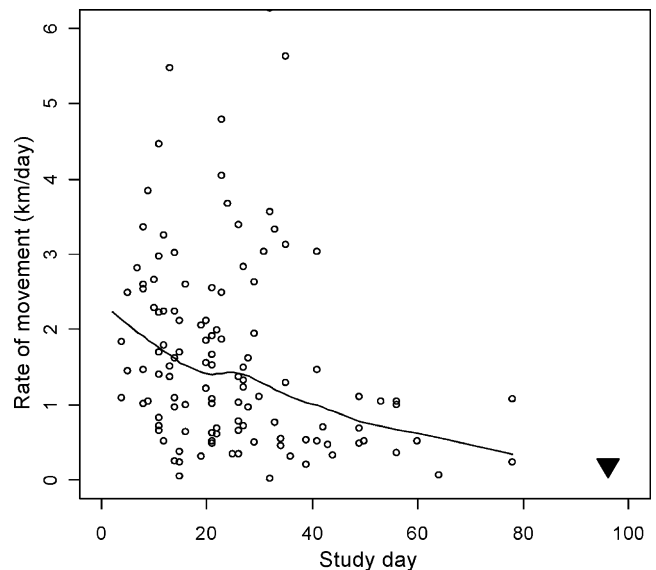


Fig. 6. The distribution of movement rates during autumn, 2004 for lobsters released in central LFA 25 (points), and a lowess smoother describing the change in movement rate over time (line). If the decrease in movement rate during the last 20 days of the study remained constant, negligible movement would be expected after 96 days (solid triangle).

Gonzalez-Gurriaran, 1998). Lobsters released in central LFA 25, northern LFA 25 and western LFA 24 would have had roughly 3, 1.5, and 2 months, respectively, to disperse before winter dormancy. If the daily changes in movement rate described by the lowess smoother are assumed to be representative of the population, adding all step length values from 28 August to estimated dormancy on 2 December suggests a potential traveling distance of approximately 173 km. Adding the daily movement estimates between 20 October and 2 December predicts a traveling distance of approximately 6 km for lobsters released in northern LFA 25, whereas lobsters released in LFA 24 should have been able to travel approximately 60 km between 24 September and 26 November. For lobsters released off of PEI, these estimates incorporate the assumption that all of the study animals have the same ability to move and respond in the same way to environmental variation.

Of the tagged lobsters classified as ‘dispersers’ by Bowlby et al. (2007), 80 recapture events were by harvesters while only 2 were by listening stations, giving a ratio of 40:1. For ‘residents’, only 2 recaptures out of 15 were by harvesters, giving a ratio of 1:7.5. As expected, the proportion of lobsters caught in baited traps was significantly higher for the ‘disperser’ behavioural type than for the ‘resident’ (Fisher’s exact test,  $P \ll 0.001$ ). This suggests that dispersing animals are more likely to encounter and/or enter baited traps, suggesting a correlation between dispersal behaviour and capture by the commercial fishery.

#### 4. Discussion

Tag loss would bias the depiction of lobster movement in two ways. First, movement rates in the spring/summer would be underestimated given that active tracking was most efficient for relocating animals that had moved very little and this was the predominant detection method used during that time period. Second, the incidence of long-distance movements would have been underestimated, given the impossibility of tracking an individual once its tag had detached and the possibility of detecting stationary lost tags. To guard against these biases, the locations where stationary tags were remotely detected were re-sampled approximately 4 months later (May 2005 then August 2005). Since re-sampling failed to detect the tag within a 2 km<sup>2</sup> area approximately half the time, tag retention and localized movement of these animals was considered likely. The probability of detecting lost tags on soft bottom sediment relative to detecting marked animals might be small due to interference with ultrasonic signal transmission caused by the sediment (Pincock and Voegeli, 2002). However, visual confirmation of stationary lobsters was not possible.

Although the magnitude of seasonal lobster movement may have been underestimated because of tag loss, the possibility of substantial movement among fishing areas over the course of a year was not supported by the tag recapture histories or movement patterns of the study animals. Nonetheless, the seasonal movement patterns of lobsters released in central LFA 25 differed from those released off PEI (northern LFA 25 and western LFA 24). From central LFA 25, the majority of lobsters moved substantial distances northward in autumn, exhibited localized

movement in winter, and returned in a less directed fashion in the spring/summer (this manuscript; Bowlby et al., 2007). However, lobsters released off PEI had ample time to disperse during the interval between autumn tagging and estimated winter dormancy, yet would not have been physiologically able to return (due to cold water temperatures) before the spring fishing seasons in LFA 23 and 24 (Chou et al., 2002; Lanteigne et al., 2004; Drinkwater et al., 2006). The observations that no animals originating in northern LFA 25 were detected outside of it either by fishermen or by active tracking, and that animals recaptured in LFA 24 had moved very little, suggests these lobsters were released in suitable over-wintering habitat and exhibited localized movement behaviour throughout autumn and winter. Movement characteristics during winter were consistent among animals released in all locations, and long-distance movement of individuals released off either side of PEI was not recorded in any season. These results are consistent with previous mark-recapture tagging studies that documented more restricted movement by adult lobsters off PEI compared with those in central LFA 25 (Comeau and Savoie, 2002).

If the movement patterns of the study animals were representative of the underlying population, the evolutionary pressures hypothesized to underlie lobster movement patterns can be used to predict plausible seasonal distribution patterns of adult lobster in the absence of year-round abundance sampling. Central LFA 25 is known to provide excellent summer habitat for lobsters (Drinkwater et al., 1996; Comeau et al., 2004) and aggregation of adults in warmer, shallower waters for breeding and molting is well-described and has been linked to enhanced recruitment success (Aiken and Waddy, 1986; Lawton and Lavalli, 1995; Cowan et al., 2001). Resource limitation within LFA 25 during the summer is thought to be very low (Comeau et al., 2004; Lanteigne et al., 2004), so competitive interactions should not prevent animals from reaching high concentrations, as documented by the summer abundance survey. Indeed, the density of adult lobster in 2001 was 1.5 × higher than that measured in 2004 (Comeau et al., 2004). However, lobster movement patterns during autumn indicate that there may be a seasonal redistribution of animals to deeper, more northern, rocky habitats. The variable severity of ice scour and wave action to shallow bottom sediments (Brown et al., 2001) coupled with the minimal activity levels of lobsters in near-zero temperatures would require animals to secure shelter beneath hard-substrate features or in deep water to minimize over-wintering mortality (Ennis, 1984). It seems likely that some adult lobsters would have reached suitable over-wintering sites without ever leaving LFA 25, given that rocky habitat extends partially into Northumberland Strait (Loring and Nota, 1973). Therefore, the seasonal distribution of adult lobster would be predicted to shift from central LFA 25 in summer to northern LFA 25 in winter, a hypothesis supported by the timing, distance and angular trajectories of movement by the study animals. If the distance traveled by an individual lobster was determined by competition, habitat-limitation and density-dependence could have realistically limited dispersal over time (Wahle and Incze, 1997; Fogarty and Idoine, 1986; Bowler and Benton, 2005). In spring, the waters in central LFA 25 warm up more rapidly and attain higher temperatures than waters to the north (Voutier and

Hanson, 2008), so diffusive movements predominantly towards central LFA 25 would tend to concentrate lobsters, as seen during the summer abundance survey.

In autumn, lobsters tagged in central LFA 25 moved from areas of high adult density to low, in a manner relatively consistent with simple diffusive processes (Holt, 1985; Kareiva, 1990). Summer abundance was high in central LFA 25, lower along the NB coast of northern LFA 25, and still lower along the PEI coast of northern LFA 25. However, if autumn dispersal was entirely a result of random diffusion along a density gradient, one would have expected dispersal towards northern PEI, with animals turning right more often than left (Turchin, 1998; Sutherland and Norris, 2002). Given that the observed mean trajectory angle was in a northwest direction, diffusive processes alone cannot structure the behaviour of dispersers. This provides further support that habitat characteristics (substrate composition and bottom topography) influence dispersal behaviour (Bowler and Benton, 2005). In addition to substrate type, water depth could be an additional factor, given that offshore movement during autumn has been well described for American lobster. Movement to deeper water during winter is believed to be related to physiological requirements for egg development (constant 4 °C temperatures) as well as mortality avoidance from ice scour or wave action (Harding et al., 1983; Campbell, 1989; Lawton and Lavalli, 1995).

Despite the differences among areas, movement patterns do not provide substantial evidence for the existence of distinct sub-populations or stocks among adult lobster assemblages in separate LFAs. The greater movement variability among individuals originating in central LFA 25 is consistent with the hypothesis of a slight genetic separation at the population level (de Meeus et al., 1993; McLean and Taylor, 2001), although environmental factors are likely to contribute substantially (or totally) to this difference (Shaklee and Bentzen, 1998). Throughout the range of the American lobster, there is evidence for the existence of sub-populations attributable to morphological differences among geographical regions (Harding et al., 1993; Jones et al., 2003) as well as increased incidences of multiple paternity in heavily fished populations (Gosselin et al., 2005). However, for the Southern Gulf of St. Lawrence, studies of morphology, larval dispersal, allozymes, fishery landing patterns and population genetics all suggest that the lobster population in this region can be considered homogeneous (Tracey et al., 1975; Harding et al., 1997). Pelagic larval mixing throughout the Southern Gulf is thought to be extensive (Harding et al., 1983) and the aggregation of lobsters in central LFA 25 during spring and summer suggests that adult mixing may occur during the breeding season. Connectivity among concentrations of adult lobster in the Southern Gulf would ensure that overall stock size is very large, which would maintain genetic fitness and may contribute to the perceived resilience to exploitation exhibited by this species (Thorpe et al., 2000; Frank and Brickman, 2001).

Based on the temporal and spatial characteristics of the release sites, it is unlikely that lobster movement among LFAs was underestimated in this study (Schwarz and Seber, 1999; Gerber et al., 2003). The straight-line distance between each group of release sites and the nearest LFA boundary is approxi-

mately 73 km for central LFA 25, 19 km for northern LFA 25 and 13 km for western LFA 24. The observed daily movement rates suggest that it would be physiologically possible for lobsters to cross LFA boundaries in autumn, although it would require sustained movement with minimal deviations from a linear trajectory to do so. In an attempt to record such movement, listening stations were deployed along the northern boundary of LFA 25 but had to be removed before winter because of incipient poor weather conditions (severe storms and ice formation). It is possible that these northern listening stations would have detected autumn emigration from LFA 25 if they had remained in the water past the 28th of October 2004. For fishery-dependent data collection, intensive trap-based sampling during autumn (LFA 25) and spring (LFA 23 and 24) by commercial harvesters similarly failed to document any exchange of animals among LFAs. However, these data are believed to accurately reflect lobster movement patterns because of the local interest and participation in data collection generated by the novelty of the ultrasonic tag and the overall importance of the lobster fishery to the economic well-being of the participants (Davis et al., 2004). Fishermen from multiple wharves made reference to marine radio discussions about the tagged lobsters, colloquially dubbed “suitcase lobster” or “suitcases” (personal observation). Such local interest was invaluable for dispensing information to remote wharves or to fishermen with whom we did not work directly. Local participants were effective communicators of the study’s objectives and their interest may have improved overall data quality (Sheil and Lawrence, 2004).

Dispersal behaviour was highly correlated with trap susceptibility, which implies that animals with a greater behavioural tendency to move are more vulnerable to exploitation and make up a greater proportion of the fishery catch than animals with a lesser tendency to move. This is particularly important in LFA 25 where maximum mobility of tagged lobsters was observed concurrent with the autumn fishery. At the population level, selective fishing of individuals with certain behavioural characteristics has been linked to genetic changes and an associated reduction in fitness through artificial selection (Gendron and Gagnon, 2001; Gosselin et al., 2005). Furthermore, it is unlikely that such an effect would be restricted to animals originating in central LFA 25, given that movement patterns provide little evidence of isolated stocks. If the behavioural flexibility exhibited by lobsters is adaptive, care must be taken to limit fishing effort during the times when lobsters are the most mobile.

## Acknowledgements

Special thanks to all of the Lobster Group at the Department of Fisheries and Oceans in Moncton, New Brunswick and to the dedicated members of the Maritime Fishermen’s Union (MFU) and PEI Fisherman’s Association (PEIFA) for field assistance. Thanks to F. Robichaud, J. Cook, O. Duplessis, and B. Comeau for stimulating discussions on resource users’ perceptions of the lobster fishery and fishery research, and to M. Comeau and two anonymous reviewers for helpful comments on the manuscript. This work was done in collaboration with the MFU, PEIFA, Department of Fisheries and Oceans, and Dalhousie



University. Support for this project came from a grant from the Fisheries Science Collaborative Program Fund (Fisheries and Oceans Canada) to J.M. Hanson, an NSERC Canadian Graduate Scholarship to H.D. Bowlby, and an NSERC Discovery Grant to J.A.H.

## References

- Aiken, D.E., Waddy, S.L., 1986. Environmental influence on recruitment of the American lobster, *Homarus americanus*: a perspective. *Can. J. Fish. Aquat. Sci.* 43, 2258–2270.
- Batschelet, E., 1981. *Circular Statistics in Biology*. Academic Press Inc., New York, NY.
- Bell, M.C., Eaton, D.R., Bannister, R.C.A., Addison, J.T., 2003. A mark-recapture approach to estimating population density from continuous trapping data: application to edible crabs, *Cancer pagurus*, on the east coast of England. *Fish. Res.* 65, 361–378.
- Bowlby, H.D., Hanson, J.M., Hutchings, J.A., 2007. Resident and dispersal behavior among individuals within a population of American lobster, *Homarus americanus*. *Mar. Ecol. Prog. Ser.* 331, 207–218.
- Bowler, D.E., Benton, T.E., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev.* 80, 205–225.
- Brown, T.G., Jordaan, I.J., Crossdale, K.R., 2001. A probabilistic approach to analysis of ice loads for the Confederation Bridge. *Can. J. Civ. Eng.* 28, 562–573.
- Campbell, A., 1989. Dispersal of American lobsters, *Homarus americanus*, tagged off southern Nova Scotia. *Can. J. Fish. Aquat. Sci.* 46, 1842–1844.
- Chou, C.L., Paon, L.A., Moffatt, J.D., 2002. Metal contaminants for modeling lobster (*Homarus americanus*) migration patterns in the Inner Bay of Fundy, Atlantic Canada. *Mar. Pollut. Bull.* 44, 134–141.
- Comeau, M., Savoie, F., 2002. Movement of American lobster (*Homarus americanus*) in the southwestern Gulf of St. Lawrence. *Fish. Bull.* 100, 181–192.
- Comeau, M., Hanson, J.M., Mallet, M., Savoie, F., 2004. Stock status of the American Lobster, *Homarus americanus*, in the Lobster Fishing Area 25. *Can. Atl. Fish. Sci. Advis. Comm. Res. Doc.* 04/054, 75p.
- Cowan, D.F., Solow, A.R., Beet, A., 2001. Patterns in abundance and growth of juvenile lobster, *Homarus americanus*. *Mar. Freshwater Res.* 52, 1095–1102.
- Crawley, M.J., 2002. *Statistical Computing: an introduction to data analysis using S-Plus*. John Wiley and Sons, LTD, West Sussex, England.
- Davis, A., Hanson, J.M., Watts, H., MacPherson, H., 2004. Local ecological knowledge and marine fisheries research: the case of white hake predation on juvenile American lobster. *Can. J. Fish. Aquat. Sci.* 61, 1191–1201.
- de Meeus, T., Michalakis, Y., Renaud, F., Olivier, I., 1993. Polymorphism in heterogeneous environments, evolution of habitat selection and sympatric speciation: soft and hard selection models. *Evol. Ecol.* 7, 175–198.
- Diamond, N., Hankin, D.G., 1985. Movements of adult female Dungeness crabs (*Cancer magister*) in northern California based on tag recoveries. *Can. J. Fish. Aquat. Sci.* 42, 919–926.
- Dieckmann, U., O'Hara, B., Weisser, W., 1999. The evolutionary ecology of dispersal. *Trends Ecol. Evol.* 14, 88–90.
- Drinkwater, K.F., Harding, G.C., Mann, K.H., Tanner, N., 1996. Temperature as a possible factor in the increased abundance of American lobster, *Homarus americanus*, during the 1980s and early 1990s. *Fish. Oceanogr.* 5, 176–193.
- Drinkwater, K.F., Tremblay, M.J., Comeau, M., 2006. The influence of wind and temperature on the catch rate of the American lobster (*Homarus americanus*) during spring fisheries off eastern Canada. *Fish. Oceanogr.* 15, 150–165.
- Dunnington, M.J., Wähle, R.A., Bell, M.C., Gerladi, N.R., 2005. Evaluating local population dynamics of the American lobster, *Homarus americanus*, with trap-based mark-recapture methods and seabed mapping. *NZ J. Mar. Freshw. Res.* 39, 1253–1276.
- Ennis, G.P., 1984. Small-scale seasonal movements of the American lobster, *Homarus americanus*. *Trans. Am. Fish. Soc.* 113, 336–338.
- Fisher, J.A.D., Frank, K.T., 2004. Abundance-distribution relationships and conservation of exploited marine fishes. *Mar. Ecol. Prog. Ser.* 279, 201–213.
- Fogarty, M.J., Gendron, L., 2004. Biological reference points for American lobster (*Homarus americanus*) populations: limits to exploitation and the precautionary approach. *Can. J. Fish. Aquat. Sci.* 61, 1392–1403.
- Fogarty, M.J., Idoine, J.S., 1986. Recruitment dynamics in an American lobster (*Homarus americanus*) population. *Can. J. Fish. Aquat. Sci.* 43, 2368–2376.
- Frank, K.T., Brickman, D., 2001. Contemporary management issues confronting fisheries science. *J. Sea. Res.* 45, 173–187.
- Freire, J., Gonzalez-Gurriaran, E., 1998. New approaches to the behavioural ecology of decapod crustaceans using telemetry and electric tags. *Hydrobiol.* 371/372, 123–132.
- French McCay, D.P., Gibson, M., Cobb, J.S., 2003. Scaling restoration of American lobsters: combined demographic and discounting model for an exploited species. *Mar. Ecol. Prog. Ser.* 264, 177–196.
- Gendron, L., Gagnon, P., 2001. Impact of various fishery management measures on egg production per recruit in American lobster (*Homarus americanus*). *Can. Tech. Rep. Fish. Aquat. Sci.* 2369, 31.
- Gerber, L.R., Botsford, L.W., Hastings, A., Possingham, H.P., Gaines, S.D., Palumbi, S.R., Andelman, S., 2003. Population models for marine reserve design: a retrospective and prospective synthesis. *Ecol. Appl.* 13, S47–S64.
- Gosselin, T., Sainte-Marie, B., Bernatchez, L., 2005. Geographic variation of multiple paternity in the American lobster, *Homarus americanus*. *Mol. Ecol.* 14, 1517–1525.
- Haakonsen, H.O., Anoruo, A.O., 1994. Tagging and migration of the American lobster, *Homarus americanus*. *Rev. Fish. Sci.* 2, 79–93.
- Hanson, J.M., Courtenay, S.C., 1996. Seasonal use of estuaries by winter flounder in the southern Gulf of St. Lawrence. *Trans. Am. Fish. Soc.* 125, 705–718.
- Hanson, J.M., Lanteigne, M., 2000. Evaluation of Atlantic cod predation on American lobster in the southern Gulf of St. Lawrence, with comments on other potential fish predators. *Trans. Am. Fish. Soc.* 129, 13–29.
- Harding, G.C., Drinkwater, K.F., Vass, W.P., 1983. Factors influencing the size of American lobster (*Homarus americanus*) stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and Gulf of Maine: a new synthesis. *Can. J. Fish. Aquat. Sci.* 40, 168–184.
- Harding, G.C., Kenchington, E., Zheng, Z., 1993. Morphometrics of American lobster (*Homarus americanus*) larvae in relation to stock determinations in the Maritimes, Canada. *Can. J. Fish. Aquat. Sci.* 50, 43–52.
- Harding, G.C., Kenchington, E.L., Bird, C.J., Pezzack, D.S., Landry, D.C., 1997. Genetic relationships among subpopulations of the American lobster (*Homarus americanus*) as revealed by random amplified polymorphic DNA. *Can. J. Fish. Aquat. Sci.* 54, 1762–1771.
- Harwood, J., Stokes, K., 2003. Coping with uncertainty in ecological advice: lessons from fisheries. *Trend. Ecol. Evol.* 18, 617–622.
- Holt, R.D., 1985. Population dynamics in two-patch environments: some anomalous consequences of an Optimal Habitat Distribution. *Theor. Pop. Biol.* 28, 181–208.
- Hutchings, J.A., Baum, J.K., 2005. Measuring marine fish biodiversity: temporal changes in abundance, life history and demography. *Phil. Trans. R. Soc. B.* 360, 315–338.
- Hutchings, J.A., Reynolds, J.D., 2004. Marine fish population collapses: consequences for recovery and extinction risk. *BioSci.* 54, 297–309.
- Inchausti, P., Weimerskirch, H., 2002. Dispersal and metapopulation dynamics of an oceanic seabird, the wandering albatross, and its consequences for its response to long-line fisheries. *J. Anim. Ecol.* 71, 765–770.
- Jones, M.W., O'Reilly, P.T., McPherson, A.A., McFarland, T.L., Armstrong, D.E., Cox, A.J., Spence, K.R., Kenchington, E.L., Taggart, C.T., Bentzen, P., 2003. Development, characterization, inheritance, and cross-species utility of American lobster (*Homarus americanus*) microsatellite and mtDNA PCR-RFLP markers. *Genome* 46, 59–69.
- Jury, S.H., Howell, H., O'Grady, D.F.O., Watson, W.H., 2001. Lobster trap video: *in situ* video surveillance of the behaviour of *Homarus americanus* in and around traps. *Mar. Freshw. Res.* 52, 1125–1132.
- Kareiva, P., 1990. Population dynamics in spatially complex environments: theory and data. *Phil. Trans. R. Soc. Lond. B.* 330, 175–190.
- Karnofsky, E.B., Atema, J., Elgin, R.H., 1989. Field observations of social behavior, shelter use, and foraging in the lobster, *Homarus americanus*. *Biol. Bull.* 176, 239–246.

- Kelly, S., Scott, D., McDiarmid, A.B., Babcock, R.C., 2000. Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. *Biol. Conserv.* 92, 359–369.
- Kimley, A.P., Voegeli, F., Beavers, S.C., Le Boeuf, B.J., 1998. Automated listening stations for tagged marine fishes. *Mar. Tech. J.* 32, 94–101.
- Lanteigne, M., Comeau, M., Mallet, M., 2004. Stock and fishery status of the American lobster, *Homarus americanus*, in the southern Gulf of St. Lawrence, for 2001 (Lobster Fishing Areas 23, 24, 25, 26A and 26B). *Can. Atl. Fish. Sci. Advis. Comm. Res. Doc.* 04/048, 51.
- Lawton, P., Lavalli, K.L., 1995. Postlarval, Juvenile, Adolescent, and Adult Ecology. The Biology of the Lobster, *Homarus americanus*. Academic Press Inc., New York, NY.
- Loring, D.H., Nota, D.J.G., 1973. Morphology and sediments of the Gulf of St. Lawrence. *Fish. Res. Board. Can. Bull.* 182, 78.
- McLean, J.E., Taylor, E.B., 2001. Resolution of population structure in a species with high gene flow: microsatellite variation in the eulachon (*Osmeridae: Thaleichthys pacificus*). *Mar. Biol.* 139, 411–420.
- Moore, F.R., 1980. A modification of the Rayleigh test for vector data. *Biometrika* 67, 175–180.
- Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Pezzack, D., 1992. A review of lobster landing trends in the Northwest Atlantic: 1947–1986. *J. NW. Atl. Fish. Sci.* 14, 115–127.
- Pincock, D.G., Voegeli, F.A., 2002. Quick Course in Underwater Telemetry Systems. Vemco Manual. Shad Bay, Nova Scotia.
- Pittman, S.J., McAlpine, C.A., 2003. Movement of marine fish and decapod crustaceans: process, theory, and application. *Adv. Mar. Biol.* 44, 205–294.
- Pollock, K.H., Nichols, J.D., Simons, T.R., Farnsworth, G.L., Bailey, L.L., Sauer, J.R., 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* 13, 105–119.
- R Core Development Team, 2004. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Schoener, T.W., 1981. An empirically based estimate of home range. *Theor. Pop. Biol.* 20, 281–325.
- Schwarz, C.J., Seber, G.A.F., 1999. Estimating animal abundance: review III. *Stat. Sci.* 14, 427–456.
- Shaklee, J.B., Bentzen, P., 1998. Genetic identification of stocks of marine fish and shellfish. *Bull. Mar. Sci.* 62, 589–621.
- Sheil, D., Lawrence, A., 2004. Tropical biologists, local people and conservation: new opportunities for collaboration. *Trend. Ecol. Evol.* 99, 634–638.
- Sibert, J., Fournier, D., 2001. Possible models for combining tracking data with conventional tagging data. In: Sibert, J.R., Nielson, J.L. (Eds.), *Electronic Tagging and Tracking in Marine Fisheries*. Kluwer Academic Publishers, Dordrecht, pp. 443–456.
- Smith, M.T., Addison, J.T., 2003. Methods for stock assessment of crustacean fisheries. *Fish. Res.* 65, 231–256.
- Sutherland, W.J., Norris, K., 2002. Behavioural models of population growth rates: implications for conservation and prediction. *Phil. Trans. R. Soc. Lond. B* 357, 1273–1284.
- Thorpe, J.P., Sole-Cava, A.M., Watts, P.C., 2000. Exploited marine invertebrates: genetics and fisheries. *Hydrobiologia* 420, 165–184.
- Tracey, M.L., Nelson, K., Hedgecock, D., Shleser, R.A., Pressick, M.L., 1975. Biochemical genetics of lobsters: genetic variation and the structure of American lobster (*Homarus americanus*) populations. *J. Fish. Res. Board. Can.* 32, 2091–2101.
- Turchin, P., 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates Inc., Sunderland, MA.
- Vecchione, M., Collette, B.B., 1996. Fisheries agencies and marine biodiversity. *Ann. Missouri Bot. Gard.* 83, 29–36.
- Voutier, J.L., Hanson, J.M., 2008. Abundance, distribution, and feeding of lady crab in the southern Gulf of St. Lawrence. *Aquat. Ecol.* 42, 43–60.
- Wahle, R.A., Ince, L.S., 1997. Pre- and post-settlement processes in recruitment of the American lobster. *J. Exp. Mar. Biol. Ecol.* 217, 179–207.
- Zar, J.H., 1999. *Biostatistical analysis*, fourth ed. Prentice-Hall Inc., New Jersey, USA.