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Ontogenetic changes in movement patterns and activity levels of American lobsters (*Homarus americanus*) in Anse-Bleue, southern Gulf of St. Lawrence

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ABSTRACT

In this study, the activity and movements of juvenile, adolescent, and adult American lobsters (*Homarus americanus*) were simultaneously quantified for the first time, using two complementary ultrasonic telemetry tracking systems. Fourteen lobsters measuring 28 to 80.5 mm in carapace length were first tracked for two blocks of 14 days starting in late summer 2011 on a shallow nursery ground in Anse-Bleue, southern Gulf of St. Lawrence, Canada. Tagged lobsters were simultaneously tracked at a fine scale ($\approx 5000\ m^2$) using a VEMCO VRAP ultrasonic telemetry system, and at a larger scale ($\approx 2.5\ km^2$) using an array of 38 VEMCO VR2 receivers. Subsequent monitoring of individuals continued for an additional 58 days (72 total) within the larger VR2 array. Juvenile, adolescent and adult lobsters displayed diurnal activity rhythms, being significantly more active at night than during the day, and they behaved as "central place foragers", undergoing excursions from and to a "central" shelter area. These behaviours were not found to be affected by body size. In contrast, average daily home range increased gradually with increasing body size, and study-length displacements showed a dichotomy between juveniles and adolescents/adults. Most (7/8) adolescent and adult lobsters moved to deeper water as water temperature decreased in the fall, whereas the juveniles (6/6) stayed in shallow water near the VRAP triangle for the duration of the study. This study provides rare empirical data concerning the movement and behavioural ecology of American lobsters on shallow nursery grounds, and it reveals ontogenetic changes in daily and seasonal movements over the juvenile, adolescent and adult life stages.

1. Introduction

The complex ways in which animals move and interact with the environment are fundamental to understanding both basic and applied aspects of their biology (Donaldson et al., 2014). Movement plays a major role in determining the fate of individuals, the structure and dynamics of populations, communities, and ecosystems, as well as the evolution and diversity of life (Nathan et al., 2008). However, because it is difficult to obtain accurate spatial data for most species in the field, our understanding of the lifetime movements expressed by animals in their natural habitat is limited (Morales and Ellner, 2002; Patterson et al., 2007). Historically, studies of individually tagged or banded animals (i.e., mark-recapture studies) have only generated information concerning the tagging location (i.e., usually identified as the starting point of a migration or movement) and the last recapture location of the animal (Petersen, 1896; Bartsch, 1904; Dingle and Drake, 2007).

Mark-recapture studies to quantify movement behaviour of the American lobster (*Homarus americanus*) [hereafter lobster] have been conducted for over a century (Bumpus, 1901). The first tagging study observed lobsters' capability of rapid and sustained movements (one moved 19.3 km in 3d), the uniformity of their movements which suggested a migratory instinct, and the extremely high recapture rate that indicated the high fishing pressure placed upon this commercial species at that time (Bumpus, 1901). Through the use of such mark-recapture studies in collaboration with fishermen, large-scale movements of lobsters have now been documented in many parts of the species' range (e.g., Campbell and Stasko, 1986; Campbell, 1986; Comeau and Savoie, 2002). These studies have shown that lobster movements vary greatly over the species' range, with lobsters in the Bay of Fundy and Gulf of Maine more frequently displaying long-distance movements (10's – 100's km) than conspecifics in the Gulf of St. Lawrence. However, in both regions, and notwithstanding potential bias towards recapturing animals that move less, the majority of lobsters are re-caught within 5 km of their original tagging location, even after a number of years at large (Lawton and Lavalli, 1995 and Comeau and Savoie, 2002). Furthermore, while lobsters undertake seasonal movements in both regions, the magnitude of these movements differs between regions (Lawton and Lavalli, 1995 and Comeau and Savoie, 2002). In the Bay of

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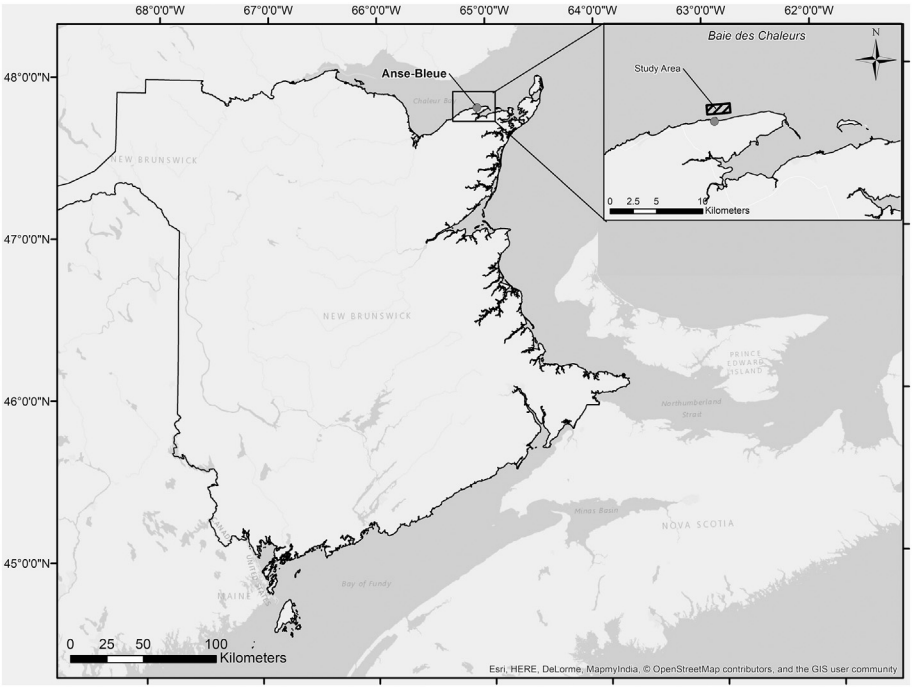

Fig. 1. The location of the 2.5 km^2 study area, just offshore of Anse-Bleue in the Baie des Chaleurs, NB, Canada, in the southern Gulf of St. Lawrence, Northwest Atlantic.

Fundy and Gulf of Maine, adolescent and adult lobsters have been documented to undertake seasonal offshore (fall) inshore (spring) movements, which are thought to help meet physiological requirements of molting, mating, egg extrusion, and embryonic development in areas where the offshore waters are warmer than the surface waters in the winter (Cooper and Uzmann, 1971; Fogarty et al., 1980; Campbell, 1986; Campbell and Stasko, 1986; Pezzack and Duggan, 1986; Pezzack et al., 1992; Lawton and Lavalli, 1995; Estrella and Morrisey, 1997; Cowan et al., 2007). In the Gulf of St. Lawrence, this seasonal shift in temperature difference between shallow inshore and deep offshore areas does not occur, and the seasonal movements lobsters make are thought to be driven by ice scour and below zero surface waters (Ennis, 1984a; Lawton and Lavalli, 1995; Comeau and Savoie, 2002; Bowlby et al., 2007 & Bowlby et al., 2008). While mark-recapture studies on lobsters have provided many valuable insights into their behavioural ecology, due to the nature of the data (i.e., generally only one recapture location, and typically tagging and recapture being constrained in time to the fishing season) the drivers of the movements observed are difficult to elucidate, and no information is captured on the small-scale patterns of activity and movements between tagging and recapture.

Over the past 20 years or so, technological advances in telemetry have enabled researchers to obtain markedly more detailed information on small-scale movements of lobsters (Tremblay et al., 2003; Scopel et al., 2009; McMahan et al., 2013), including most recently for juvenile individuals (Morse and Rochette, 2016). Anchored telemetry positioning systems allow researchers to triangulate the position and construct movement paths of individually tagged animals within the receiver array. The precision of these fixed telemetry systems allows researchers to directly answer questions about foraging behavior that previous studies have been unable to address. These studies suggest that the average daily home range of juvenile lobsters is considerably less ($\approx$27–112 m^2: Morse and Rochette, 2016) than that of adolescents and adults ($\approx$760 m^2: Scopel et al., 2009; $\approx$315–786 m^2: McMahan et al., 2013), providing the first quantitative evidence of a shift in movement behaviour between juveniles and older individuals in nature.

In addition to examinations of lobster movement, acoustic telemetry has been used to quantify diel differences in activity and movement behaviour. Field observations have concluded that juvenile, adolescent and adult lobster display diurnal activity rhythms, being more active at night than during the day (Cooper and Uzmann, 1980; Ennis 1984a, 1984b; Karnofsky et al., 1989), although fine-scale observations of activity using fixed acoustic monitoring systems have shown considerable inter- and intra-individual variability in the daily patterns of activity of adolescents/adults (Golet et al., 2006) and juveniles (Morse and Rochette, 2016). In laboratory studies where activity of lobsters has been best described, activity begins to increase at sunset, peaks within a few hours and then declines towards sunrise (Cobb, 1969; Lawton, 1987; Wahle, 1992; Jury, 1999; O'Grady et al., 2001; Jury et al., 2005), generally aligning with current field observations.

To the best of our knowledge no single study has directly compared movement and activity rhythms of juvenile, adolescent, and adult lobsters in nature. Separate studies have been conducted on juveniles (Morse and Rochette, 2016) and adolescent and adults (Tremblay et al., 2003; Scopel et al., 2009; McMahan et al., 2013), in different regions and years, but there has been no study that has simultaneously tracked juvenile, adolescent and adult lobsters in a same location.

The purpose of this study was to simultaneously quantify small-scale movements and daily activity levels of juvenile, adolescent and adult lobsters in nature, and to determine how these vary with body size. The study consisted of two integrated tracking systems that quantified movements and activity levels of lobsters varying from 28 to 80.5 mm carapace length over two spatial and temporal scales. First, a VRAP (VEMCO Ltd. Nova Scotia, Canada) ultrasonic telemetry system was used to provide a fine-scale spatial examination ($\approx$5000 m^2) for one month. We used this system to: (1) quantify the amount of time lobsters spent actively roaming outside of shelter, (2) determine if there was evidence of diel and tidal cyclicity in lobster activity patterns, and (3) quantify the lobsters' home range. We used the data from these three investigations to test the hypothesis that the frequency and magnitude of movements displayed by lobsters increase with their body size (Wahle, 1992; Wahle and Incze, 1997; Selgrath et al., 2007; Émond et al., 2010; Wahle et al., 2013). A second telemetry array of VR2 (VEMCO Ltd. Nova Scotia, Canada) receivers was anchored outside of the VRAP system, and which allowed data acquisition over a larger area