

MOVEMENT PATTERNS AND MIGRATIONS IN CRABS: TELEMETRY OF JUVENILE AND ADULT BEHAVIOUR IN *CALLINECTES SAPIDUS* AND *MAJA SQUINADO*

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Late stage juveniles and adults of *Callinectes sapidus* in Chesapeake Bay, USA, and *Maja squinado* off the Ría de Arousa, Spain, were compared for ontogenetic changes in movement patterns (speed, distance, orientation) and habitat selection (depth, substrate) using ultrasonic telemetry and published information. After settling in submerged grass beds in the lower Bay, 20-mm juvenile *C. sapidus* disperse long distances into low salinity sub-estuaries to feed and grow to maturity in two years. Within the Rhode River sub-estuary, juvenile *C. sapidus* moved with a mean speed of 12 m h^{-1} in nearshore shallows (1.1 m); whereas adults averaged 24 m h^{-1} in the deeper (2.9 m) channel areas and moved freely in and out of the main estuary. Individuals of both life stages exhibited a pattern of slow meandering (juveniles, 2 m h^{-1} , adults 10 m h^{-1}) within a limited area, alternating with faster, directionally-oriented movement (both stages $>50 \text{ m h}^{-1}$) between meandering sites. Juvenile and adult males over winter in deeper water nearby, while inseminated females migrate long distances into high salinity areas to incubate the eggs. *Callinectes sapidus* completes the migration cycle only once per 2.5-y generation. *Maja squinado* settles on rocks in shallow kelp forests in the coastal zone, where they grow to maturity in 2 y. Juveniles moved slowly (0.5 m h^{-1}) while meandering without directional orientation on shallow (4 m) small patch reefs during summer. After the pubertal moult in summer, adults also meandered slowly (1 m h^{-1}) mostly on rocks at slightly greater depth (7 m). In late summer and autumn, newly mature and older adults moved with directional orientation into deeper (10–40 m) water for the winter, until migrating back to the shallows for the summer; whereas juveniles remained inshore on rocks for the winter. Adult *M. squinado* live several years after puberty and complete the seasonal migratory cycle several times during their lives.

Despite marked differences between the two species in life histories and habitats, their similarities in behaviour and shifts in habitat utilization during ontogeny reflect adaptation to similar selective pressures. For both species, juvenile movement and habitat selection primarily indicates adaptation to intense predation pressure and growth optimization; whereas adult behaviour and migration indicates relaxed predation pressure but optimization of energy needs and site of larval release.

INTRODUCTION

Decapod crustaceans living in coastal environments display major differences in behaviour among life history stages. One of the pivotal events determining these

behavioural changes is the onset of sexual maturity. Ultrasonic telemetry techniques allow analysis of the behaviour and physiology of marine organisms in the field (Wolcott & Hines, 1989a,b; Kasello et al., 1992; O'Dor et al., 1993), including movement patterns and behavioural aspects of habitat selection (Hawkins & Urquhart, 1983; Wolcott & Hines, 1990; Shirley & Wolcott, 1991). However, previous telemetry studies have rarely been used to assess behavioural changes in response to transitions between life history stages, such as maturation.

This paper presents the results of telemetry studies of juveniles approaching maturity and adults of two species of brachyuran crabs which differ greatly in habitat and life history: the blue crab *Callinectes sapidus* Rathbun (Portunidae), and the spider crab *Maja squinado* (Herbst) (Majidae). We review aspects of the life histories of both species, focusing upon ontogenetic changes in orientation behaviour, habitat utilization and migration. Using telemetry, we measured variables of movement (speed, distance and orientation) and habitat utilization (depth, bottom type) of late stage juveniles and adults. Comparison of these behaviours and ontogenetic shifts in movement patterns provides insight into the selective pressures affecting these key life stages in both species.

BLUE CRAB (*CALLINECTES SAPIDUS*) LIFE HISTORY

Habitat. The blue crab is distributed in the western Atlantic from Cape Cod to Brazil, with major fisheries along North American coasts. The best studied population is in Chesapeake Bay, where life history and seasonal migrations are well known (van Engel, 1958; Millikin & Williams, 1984). Long-term descriptive and experimental studies provide background information on population dynamics and predator-prey relations of the blue crab in the Rhode River, Maryland, a mesohaline sub-estuary on the western shore of Chesapeake Bay (Figure 1) (Lipcius & Hines, 1986; Hines et al., 1987, 1990; Shirley et al., 1990; Smith, 1990; Smith & Hines, 1991a,b; Eggleston et al., 1992; Ruiz et al., 1993; Dittel et al., 1995; Hines & Ruiz, 1995). The sub-estuary is shallow (<4 m) with a soft bottom (80% muddy and 20% sandy sediments). There was no submerged aquatic vegetation in the sub-estuary and tidal creeks during the study, but nearshore wood debris was present as an important refuge habitat for epibenthic animals (Everett & Ruiz, 1993). Salinity fluctuated from about 4‰ in spring to 16‰ in fall, and water temperature oscillated seasonally between 1°C in winter and 28°C in summer.

Life history. Megalopae of *Callinectes sapidus* settle during summer and fall in submerged aquatic vegetation beds of the lower Chesapeake Bay (van Montfrans et al., 1991). After growing to 20 mm carapace width (CW), small juveniles move out of submerged aquatic vegetation habitats and disperse 50–250 km into sub-estuaries to feed and grow (van Engel, 1958; Hines et al., 1987; van Montfrans et al., 1991; Pile, 1993). Small crabs (<70 mm) utilize nearshore shallows (<0.7 m deep) in the sub-estuaries as refuge from cannibalistic adults (Ruiz et al., 1993; Dittel et al., 1995; Hines & Ruiz, 1995). Although there is no information on their range of movements, we hypothesize that these small juveniles remain within the sub-estuaries to which they disperse. Medium-sized blue crabs (90–110 mm), like smaller juveniles, utilize the sub-estuaries until the end of their

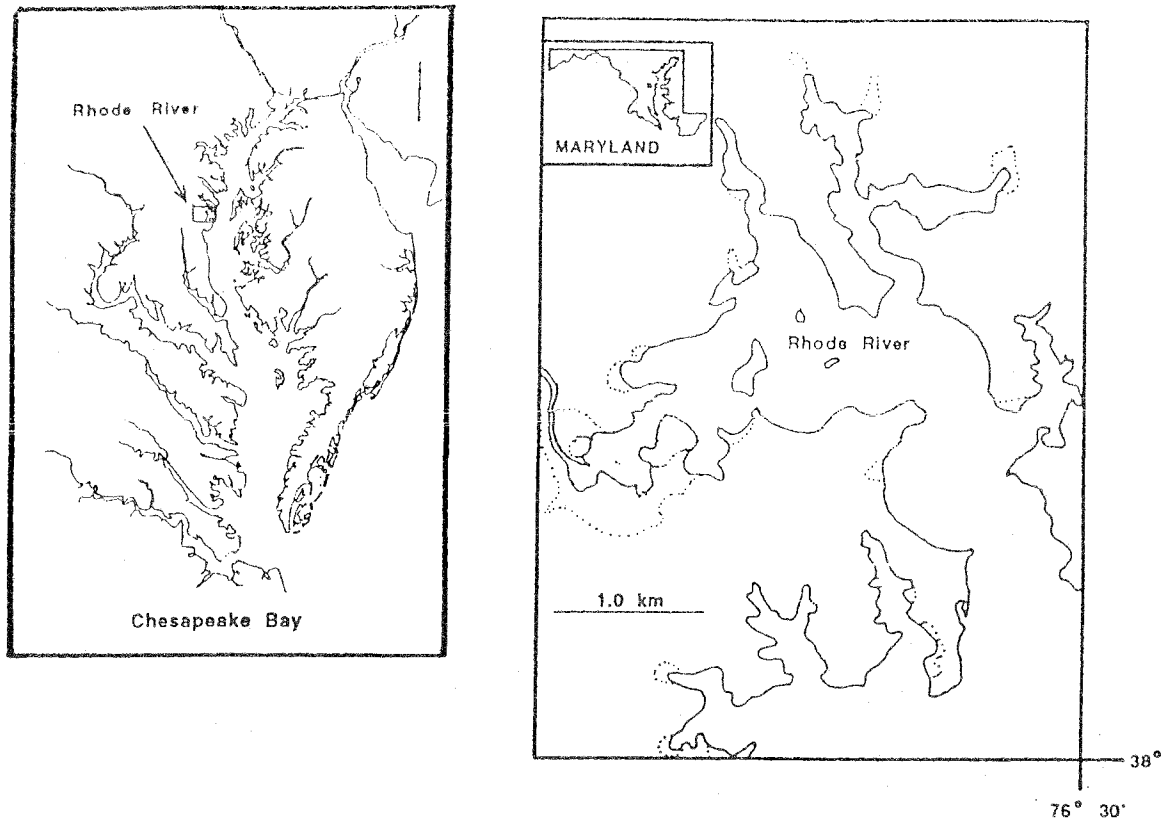


Figure 1. *Callinectes sapidus*. Chesapeake Bay and Rhode River sub-estuary.

first year, when they migrate into nearby deeper water and burrow into the sediment for winter (van Engel, 1958; Hines et al., 1987).

In their second year, blue crabs grow to 120–200 mm and attain sexual maturity. These large individuals move into sub-estuaries to forage, but appear to exchange readily with the Chesapeake main stem and other sub-estuaries. Movement patterns and residence times of large blue crabs in the Rhode River sub-estuary have been measured in detail using ultrasonic telemetry (Nye, 1989; Wolcott & Hines, 1989a,b, 1990; Hines & Wolcott, unpublished data). At the end of their second summer, blue crabs moult to maturity and mate. Inseminated females migrate from the Rhode River 150–200 km back down the estuary to the mouth of Chesapeake Bay to over winter in deep water and brood their eggs during the following spring and summer; whereas adult males over winter in deeper water in the main estuary but do not migrate long distances (Millikin & Williams, 1984; Schaeffner & Díaz, 1988). *Callinectes sapidus* lives about 2.5–3.5 years, so individuals perform this migratory cycle only once per generation.

TELEMETRY OF MOVEMENT AND HABITAT UTILIZATION IN BLUE CRABS

Material and Methods. Tracking of blue crabs was carried out using ultrasonic tags during June and July 1993, which coincided with the summer peak of water temperature (23–28°C) and crab activity (Hines et al., 1987, 1990). We used SONOTRONICS (Tucson, Arizona, USA) equipment, employing 'mini-tags' MT-91-1 to track juveniles and 'standard tags' ST-71-2 for adults. The tags weighed about 1.5 g and 5 g in water,

respectively, which was about 5% of the crabs' body weight. Detailed laboratory observations indicated that the tags did not interfere with normal behaviour and motility, although movement rates determined in this study may be considered conservative estimates due to the possible effect of the tag, and because tracking was non-continuous (see below). The behaviour of tagged and non-tagged crabs did not appear to differ in the laboratory, with tagged crabs exhibiting the full range of movement and behaviour that included burial, walking, swimming, agonistic interactions, mating and moulting (see Wolcott & Hines, 1989a,b, 1990). Speeds and frequencies of movement over short distances in 2-m laboratory tanks did not differ between tagged and non-tagged crabs. Ultrasonic digital receivers and directional hydrophones were used aboard a small boat to locate tagged crabs. See Wolcott & Hines (1989a,b) for details of methods.

Eight juvenile and four adult male intermoult crabs were tagged and released in the upper part of the sub-estuary at 1.5 m depth. Juvenile crabs were tracked until the battery of the transmitter was exhausted or the animal moulted; the length of the battery life (~21 d) corresponded to a large fraction of the juveniles' intermoult period at a warm temperature. Adults were tracked until they moved out of the Rhode River or were caught in traps. Each animal was located and mapped with respect to landmarks approximately twice daily.

Mapped tracks were digitized for computer analysis of distances and directions moved; and these data were combined with field records of the temporal progression of movement and habitat variables (water depth, substrate type) for each mapped location. These data were analysed to determine patterns of movement and habitat utilization.

Results. Juvenile crabs were tracked for an average period of less than two weeks, during which time they remained within the upper and central part of the sub-estuary (Figure 2). For adults, the mean tracking period was less than one week, and all four individuals moved along the axis of the sub-estuary to the mouth area of the Rhode River (Figure 2). This indicated that only adults moved into the main stem of Chesapeake Bay during the study period. Mean speed of adults was more than twice that of juveniles (Table 1). Mean maximum speed for adults (23.7 m h^{-1}) was also nearly twice that for juveniles (12.4 m h^{-1}), but individuals of both juveniles and adults attained maximum speeds of $>50 \text{ m h}^{-1}$, as estimated between successive locations. Juvenile crabs were restricted generally to the nearshore zone $<2 \text{ m}$ deep; whereas adults utilized deeper ($\geq 2 \text{ m}$) areas of the central channel of the sub-estuary (Table 1, Figure 2).

Individual crabs exhibited two basic types of movement: slow meandering within a limited area; and rapid, directional movement between meandering locations (Figure 2). Individuals typically switched between these types once or twice during the tracking period. For juveniles, slow-moving, meandering periods lasted an average of 6.3 d, covering an average gross distance of 242 m in the nearshore zone. During this type of movement, juveniles were located at a mean depth of 1.1 m, and their average speed was only 2 m h^{-1} . During faster, directional movements, juveniles moved at an average speed of 15.5 m h^{-1} for an average time of 4.3 d and total distance of 1470 m. During these periods, juveniles moved across channels (mean depth, 1.7 m) between nearshore

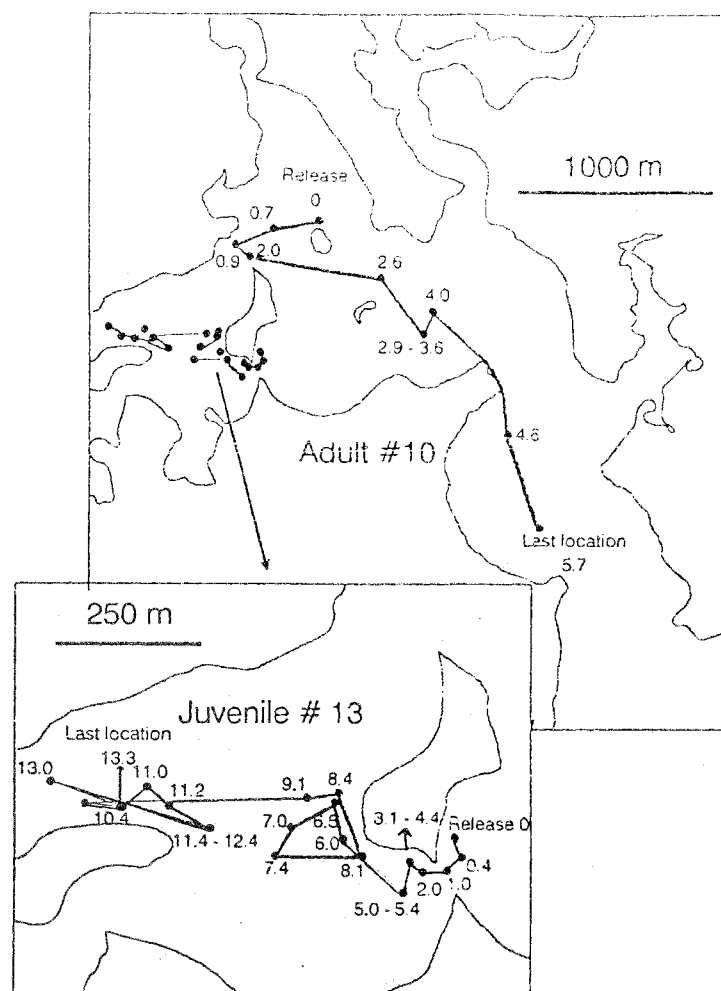


Figure 2. *Callinectes sapidus*. Examples of movements of juvenile and adult crabs tracked in the Rhode River (inset shows a magnified view of juvenile track). Time (d) of each location is indicated (release time=0).

Table 1. *Callinectes sapidus*. Average distance, speed of movement and direction for juveniles and adults calculated from the average of the observations for each crab. Results of t-tests for differences between juvenile and adult parameters are indicated.

	Juveniles	Adults	t-test
Number of crabs	8	4	df=10
Carapace width (mm)	103	142	
Tracking time (d)	12.5	5.8	
Number of observations (1)	23.9	6.8	
Distance (m)	2140	2142	
Speed (m h ⁻¹)	6.98	16.71	3.25**
Depth (m) (1,2)	1.48	2.88	5.65**
Bearing with respect to north (R) (3)	352.0 (0.314)	126.6 (0.962)	
Average R	0.250	0.784	6.09**
Bearing with respect to shoreline (R) (3)	53.4 (0.434)	77.0 (.0966)	
Average R	0.315	0.599	2.96*
Bearing with respect to channel (R) (3)	3.8 (0.104)	7.9 (0.708)	
Average R	0.281	0.766	4.31**

*, $P < 0.05$; **, $P < 0.01$. (1) Excluding observation corresponding to release. (2) Mean depth for each individual, calculated weighting by time at each location. (3) Average bearings calculated from individual angles weighted by parameter R for each individual (in parenthesis, the statistic R obtained for this average angle).

meandering areas. For adults, the meandering periods averaged about 2 d with a speed of about 10 m h^{-1} over a gross distance of about 450 m at depths $>2 \text{ m}$. Periods of rapid, directional movement lasted on average about 1 d at speeds $>50 \text{ m h}^{-1}$ over a distance of about 1 km.

Orientation of blue crab movements was estimated with respect to three different reference directions: north, adjacent shoreline, and the axis of the central channel of the sub-estuary. Mean directionality was calculated as a statistic R , which represents the magnitude of the mean vector, or the concentration of movements around the mean bearing with respect to the reference direction; and Rayleigh tests were used to determine significance of mean directionalities (Batschelet, 1981), testing for each crab the null hypothesis that there was no movement orientation ($R=0$). For each of the three reference directions, R was lower for juveniles than for adults ($P<0.05$; Table 1). For adults, movement with respect both to north and to the channel was always highly directional ($R>0.64$ for individual crabs, $P<0.05$); and R for these two reference directions was greater than that with respect to the shoreline. In contrast, mean directionality of juveniles was highest with respect to the shoreline; but for individual juveniles, R statistics for the three reference directions was always <0.54 and not significantly different from 0 in most cases ($P>0.05$). In a similar contrast of orientation, average bearings (calculated from mean individual angles) indicated highly directional movement in adults ($R=0.71\text{--}0.97$ for all three reference directions), but not in juveniles ($R=0.25\text{--}0.32$). For adults, the mean bearing with respect to north (127°) was similar to the bearing of the long axis of the sub-estuary. However, movements of juveniles were oriented most closely with the bearing of the upper part of the sub-estuary (352°), but this orientation appeared to reflect primarily small-scale movements parallel to the shoreline in the nearshore zone, with larger-scale movements between meandering sites that lacked any orientation with respect to the axis of the sub-estuary.

SPIDER CRAB (*MAJA SQUINADO*) LIFE HISTORY

Habitat. This species of spider crab lives along the coasts of the north-east Atlantic from north Africa to the North Sea and Mediterranean Sea, from tidal level to 90 m. Commercial fisheries exploit this species throughout most of its distribution. Information on the life history of *Maja squinado* (reviewed by Štević, 1967; Kergariou, 1984; and Le Foll, 1993) has been provided from Ireland, southern England and the Atlantic French coast (especially Normano-Breton Gulf) in the northern end of its distribution, and from warmer waters of the Adriatic Sea. In Galician waters (north-western Spain), where the present telemetry study was carried out, information exists on the fishery and life history of the spider crab in the Ría de Arousa and adjacent coastal waters (González-Gurriarán et al., 1993; unpublished data).

Maja squinado is distributed mainly in the outer part of the Ría de Arousa (Figure 3), which provides both a large depth range inhabited by this species (1–60 m), and a mixed hard- and soft-bottom habitat. In shallow areas salinity fluctuates between 33 and 36‰ (during episodes of high rainfall), and temperatures range from 12°C in winter to about

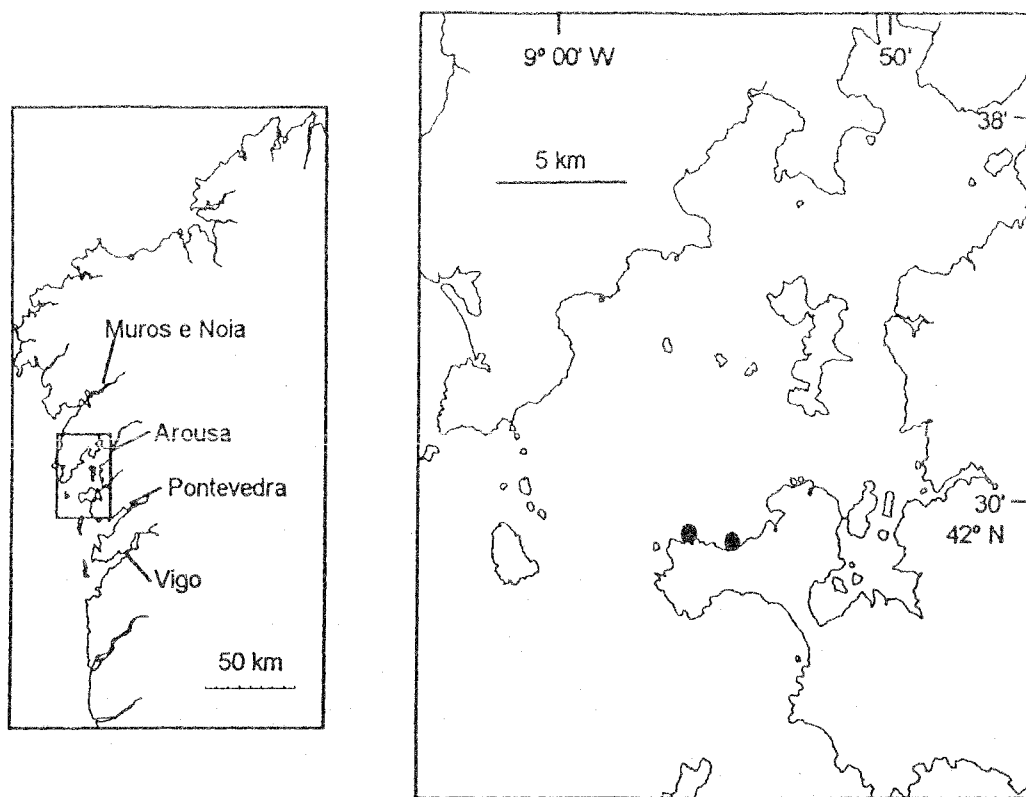


Figure 3. *Maja squinado*. Galician coast (north-west Spain) and Ría de Arousa. Dots indicate shallow areas where crabs with transmitters were released.

18°C in summer; whereas in deeper zones (>30 m) salinity and temperature fluctuations are less marked. The nearshore shallows (<15 m) include rocky substrates dominated by kelp forests mixed with sandy areas; in deeper areas the proportion of soft bottom increases.

Life history. The distribution and abundance of larval stages (Martin, 1980, 1985) indicate that settlement of *M. squinado* probably occurs in summer and autumn in shallow areas similar to the habitat of the juveniles. The spider crab juveniles (10–140 mm carapace length) live in shallow areas (<15 m). In Galician waters immature crabs are abundant in rocky kelp forests and nearby sandy areas; although, in other geographical locations, sandy and seagrass areas are the predominant juvenile habitats (Kergariou, 1984; Le Foll, 1993). Juvenile spider crabs seem to exhibit limited movement while foraging on algal-invertebrate turf during their first two years of life. In the summer of their second year of life, they undergo a terminal moult of sexual maturity in these shallow habitats (González-Gurriarán & Freire, unpublished data).

After the pubertal moult, the crabs occupy juvenile habitat until the adults begin a migration in autumn. Migrations have been studied in different geographical locations using conventional mark-recapture methods (Števčić, 1973; Kergariou, 1976; Edwards, 1980; Camus, 1983; Latrouite & Le Foll, 1989; Le Foll, 1993). Recaptures have been obtained as far as ~200 km from the release point, and mean speeds of 9.6–20.5 km month⁻¹ have been estimated during the migration season (Camus, 1983; Latrouite & Le

Foll, 1989; Le Foll, 1993). During autumn large-scale movements, large spider crabs generally move to deeper waters (40–60 m), and a consistent orientation is evident for crabs migrating from the same area, although average direction of this oriented movement can differ geographically (Latrouite & Le Foll, 1989; Le Foll, 1993). In spring, adults move back to shallow areas from wintering habitats, but it is not clear if individuals return to the zone where they attained sexual maturity. *Maja squinado* lives several years after the terminal moult (Le Foll et al., 1989), so individuals perform the migratory cycle between shallow and deep zones several times per generation (Latrouite & Le Foll, 1989; Le Foll, 1993).

Telemetry of movement and habitat utilization in juvenile and adult spider crabs

Material and Methods. Tracking for *Maja squinado* was carried out in July and August 1993 for juveniles, and from July to December 1993 for adults. Equipment from VEMCO Ltd (Halifax, Canada) was used, employing V2 tags for juveniles and V3 for adults. Comparable temperature transmitters V3T were also used for adults. These tags weighed 3.5 and 17 g, respectively, in water, amounting to less than 5% of the crabs' body weight. Location of crabs with attached transmitters was carried out with a directional hydrophone and digital receiver aboard a small boat, similar to the procedure for blue crabs.

Tagged spider crabs included three juveniles and seven adults, which had recently undergone the pubertal moult to the terminal instar. All tagged spider crabs were released in two shallow kelp forests located in the outer part of the Ría de Arousa (Figure 3). Juveniles were located daily during the battery life of the transmitter (20–25 d), which is equivalent to a large part of the intermoult period for crabs of this size in summer. Four adults were located daily during July and August, and tracks for three of these were continued from late August to December. An additional three adult crabs were tagged and released in October. From late August to December, all animals were located at intervals of 5–11 d until the battery was dead or the crab was lost during long movements in periods of bad weather. Juveniles were located with respect to landmarks (shoreline and rocks) and with a satellite global positioning system (GPS); and the more widely separated locations of adults were determined with GPS.

Results. The range of movement for juvenile *M. squinado* was quite limited during the mid-summer tracking period, with an average speed of $<10 \text{ m d}^{-1}$ (Table 2). Juveniles were restricted to rocky areas with an average depth of $\sim 4 \text{ m}$ (the maximum for an individual location was 9.8 m). Juvenile movement did not indicate any directional orientation, with mean $R=0.19$, which was not significantly different from 0 for all individuals (Rayleigh tests, $P>0.05$) (Table 2; Figure 4).

During the summer and early autumn phase of tracking, adult spider crabs exhibited a movement pattern of slow meandering, similar to that of juveniles (Table 2; Figure 4). Adult speed, although relatively slow, was about twice that of juveniles, but this difference was not significant ($P>0.05$). Like juveniles, adults also remained primarily on a rocky substrate, although they occurred at slightly greater depth than juveniles

Table 2. *Maja squinado*. Average distance, speed of movement and direction for juveniles (using landmark data) and adults (using GPS locations), calculated from the average of the observations for each crab. Average juvenile bearing was not calculated due to the lack of directionality of individual tracks. For adults, two phases of movement are differentiated (see text for details). Results of t-tests for differences between juvenile and first-phase adult parameters, and between first and second phase adult parameters are indicated.

	Juveniles	Adults 1st phase	Adults 2nd phase	Adults Total	t-test	
					Juv- 1st df=6	1st- 2nd df=9
Number of crabs	3	5	6	7		
Carapace length (mm)	123	—	—	151		
Tracking time (d)	23.3	52.9	27.6	61.4		
Number of observations (1)	16.7	14.8	5.0	14.9		
Distance (m)	235	919	1805	2203		
Speed (m d ⁻¹)	9.7	22.1	75.8	51.4	1.52ns	2.27*
Depth (m) (1,2)	4.1	7.3	14.0	10.2	2.46*	2.35*
Bearing, respect to north (R) (3)	—	300.9 (0.540)	318.3 (0.901)	310.6 (0.674)		
Average R	0.190	0.353	0.805	0.584	1.23 ns	3.86**

ns, $P>0.05$; *, $P<0.05$; **, $P<0.01$. (1) Excluding observation corresponding to release. (2) Mean depth for each individual calculated weighting by time each location. (3) Average bearing calculated from individual angles weighted by parameter R of each individual (in parenthesis, the statistic R obtained for this average angle).

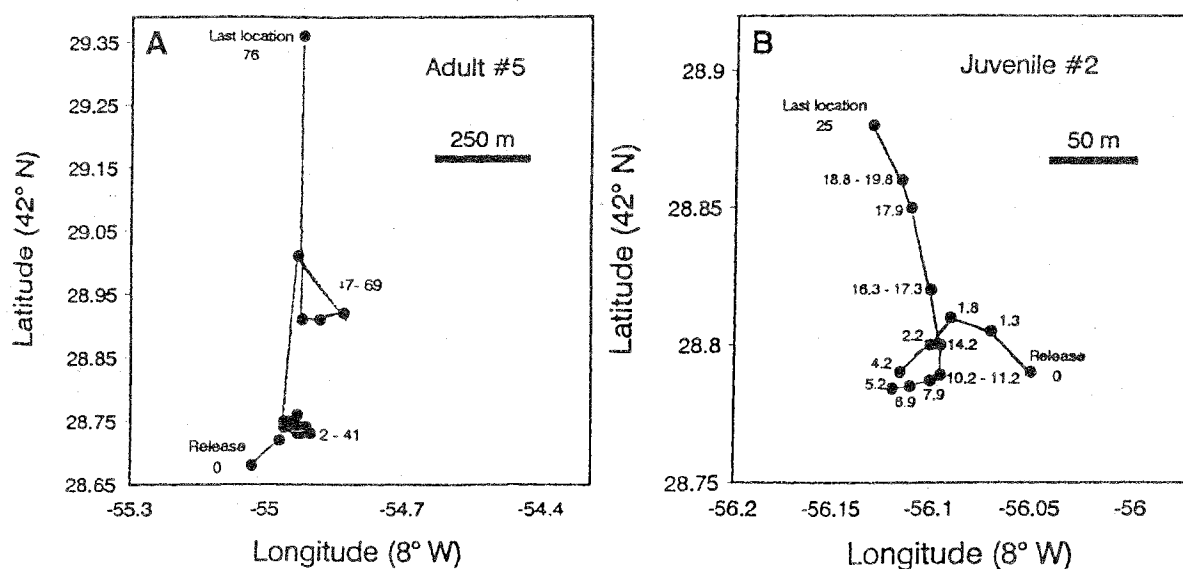


Figure 4. *Maja squinado*. Examples of movements of (A) adult (based on GPS data) and (B) juvenile (based on landmark data) crabs tracked in the Ría de Arousa. Time (d) of each location is indicated (release time=0).

($P<0.05$; maximum, 11.6 m). During this period, adults did not exhibit directionally oriented movement (average $R=0.35$, which is not significantly greater than zero for all crabs except one; $P>0.05$).

The start of the second phase of adult movement was characterized by a much increased scale of movement (>500 m in 5–7 d) into deeper zones (Figure 4). Tagged individual spider crabs initiated this change in movement at varying times from

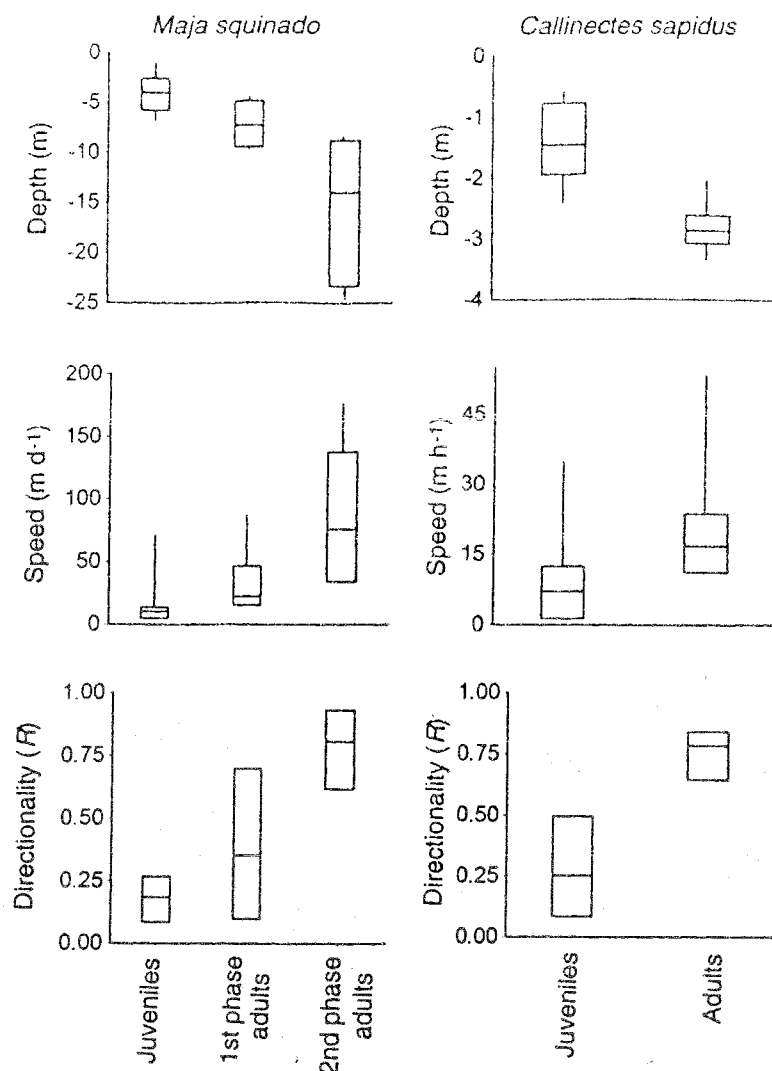


Figure 5. *Callinectes sapidus* and *Maja squinado*. Depth, speed and directionality with respect to north of movements for juvenile and adult crabs. Average of individual means, maximum and minimum individual means and average of maximum and minimum values for individual crabs are indicated.

September to November; and two of the crabs tagged in October began large-scale, directional movement immediately after release. Mean speed increased to about 75 m d⁻¹ (maximum average for one individual was about 138 m d⁻¹), and movement orientation was highly directional (R was >0.61 and significantly greater than zero for all individuals; $P < 0.05$). Mean orientation of movement for individual crabs ranged from 286° to 3° with respect to north, towards deeper areas in the central channel and outer part of the Ría. However, there were also frequent periods of slow, non-directional movements interspersed between large displacements. During this phase, adult crabs underwent approximately an order of magnitude increase in depth. Although we were able to track crabs to a mean depth of 14 m (Table 2), some individuals were tracked to depths of nearly 40 m. In addition, crabs tended to shift their substrate utilization from rocky to predominantly sandy and muddy bottoms.

DISCUSSION

The two studied species have very different life histories and utilize different habitats. *Callinectes sapidus* is predominantly an estuarine species which extensively exploits low salinity zones; whereas *Maja squinado* is predominately a coastal species utilizing oceanic salinities. Juvenile *C. sapidus* disperse widely away from their initial settlement in submerged aquatic vegetation habitat of the Bay mouth to feed and grow in upper sub-estuaries; while juvenile *M. squinado* appear to remain sedentary to feed and grow on algal-invertebrate turf on rocks in their settlement habitat of coastal kelp forests. For *C. sapidus*, juveniles of both sexes and adult males move into deeper water to over winter, and only adult females migrate long distances to the lower Bay for egg incubation; but for *M. squinado*, both male and female adults migrate long distances, while juveniles remain in shallower water over winter. *Callinectes sapidus* is relatively short-lived and completes its migratory cycle only once per generation, in contrast to *M. squinado*, which potentially lives many years after puberty and undergoes seasonal onshore-offshore migration many times during its life span. *Callinectes sapidus* utilizes soft-bottom substrates throughout its life history, while *M. squinado* exploits hard- and soft-bottom substrates alternately during ontogeny and between seasons. Compared to slow-moving *M. squinado*, *C. sapidus* is capable of much greater speed and moves over much longer distances in short intervals.

Despite these marked differences, both species also share similarities in behaviour and habitat utilization during their life cycles (Figure 5). Both species exhibit distinct shifts in behaviour at sexual maturity. *Callinectes sapidus* utilizes progressively deeper water during growth (Ruiz et al., 1993; Hines & Ruiz, 1995; Dittel et al., 1995; Hines & Wolcott, unpublished data). Our telemetry indicates that medium-sized juvenile blue crabs spent most of their time meandering along the shoreline and moved comparatively quickly across deeper water to new nearshore locations within the same sub-estuary; whereas large mature blue crabs utilized primarily deeper channels of the sub-estuary and appeared to exchange rapidly with the main estuary. Similarly, *M. squinado* juveniles meandered in nearshore kelp forests; while mature spider crabs moved into deeper water. The scale of movement and speed increased with size and maturity in both species. Both species shifted their habitat utilization seasonally to occupy primarily deeper water in winter and shallower water in summer, although these migrations differed among life stages for the two species.

These shifts in behaviour and habitat utilization reflect changes in predation pressures during the ontogeny of the two species. The smallest life stages appear to suffer intensive predation and are adapted to exploit habitats where predators are either less abundant or less effective. Larval crabs are subject to predation by high densities of fish in estuaries and the nearshore zone, and are thus released into surface waters which transport these most vulnerable stages off-shore (McConaughy et al., 1983; Morgan, 1987a,b, 1990; Morgan & Christy, 1994). Tiny post-settlement blue crabs gain critical refuge from predators in structurally complex submerged aquatic vegetation beds (Orth & van Montfrans, 1990; Heck & Thoman, 1981). When they disperse from that shelter, they gain refuge from cannibalism in the nearshore shallows (Ruiz et al., 1993;

Hines & Ruiz, 1995; Dittel et al., 1995) and nearshore coarse wood debris (Everett & Ruiz, 1993) of sub-estuaries. Small blue crabs move seasonally into deeper water only after water temperatures have cooled to levels that preclude most predator activity (Hines et al., 1990; Hines & Ruiz, 1995). Similarly, small spider crabs gain refuge from predators in the algal-invertebrate turf of kelp forests (Hines, 1982; González-Gurriarán & Freire, unpublished data) or seagrass and sandy shallow areas (Kergariou, 1984; Le Foll, 1993). However, unlike in Chesapeake Bay, temperatures in deeper waters off Galicia never fall so low as to reduce predator activity enough to allow small spider crabs to move from the complex refuge habitat to deeper water with immunity.

Restriction of juveniles to structurally complex habitats and/or to the shallowest fringes of the nearshore zone appears to relax as the crabs grow and gain increasing immunity from predation by fish and cannibalistic large crabs. Intermediate-sized blue crabs suffer significantly less mortality from intense cannibalism than small crabs (Smith, 1990; Hines & Ruiz, 1995), and our telemetry showed that they are able to utilize deeper water than small crabs. Large blue crabs are essentially immune from (non-human) predation (Smith, 1990), and our telemetry showed that they are thus able to move freely in deep water. Similarly, only after growing to large mature size does *M. squinado* move onto exposed soft bottom and greater depth (Števcic, 1967; Kergariou, 1984; Le Foll, 1993), where large epibenthic fish can prey upon smaller crabs. Since the moult increment of both species is approximately 25–30% of carapace dimension (Drach, 1939; Tagatz, 1969; Le Foll, 1993; González-Gurriarán & Freire, unpublished data), growth of only one or two instars leading up to sexual maturity results in marked differences in vulnerability to size-dependent predation, allowing use of non-refuge habitats.

Larger scale movements and migration of these crabs appear to be adaptive for seasonal cycles in temperature and food availability. In summer, warm productive waters of sub-estuaries (blue crabs) and coastal kelp forests (spider crabs) provide food and elevated temperatures that are optimal for rapid growth in juvenile crabs (van Engel, 1958; Števcic, 1971; Kergariou, 1984; Le Foll, 1993; González-Gurriarán & Freire, unpublished data). In Chesapeake Bay winter temperatures at all depths become cold (1°C) approaching physiological limits, and blue crabs retreat to depths not impacted by ice, and cease activity. Juvenile and mature male blue crabs do not move far for this hibernation (Millikin & Williams, 1984; Schaffner & Diaz, 1988), so they remain close to the optimal summer habitat without expending much energy. While juvenile spider crabs over winter in the refuge of the kelp forest, adults move into deeper waters which are then moderately warmer than the nearshore shallows, and gonad development and incubation are favoured (Števcic, 1971; González-Gurriarán et al., 1993).

Migration also strategically positions mature females of both species for egg incubation and hatching in the spring and summer, when planktonic food resources for larvae increase. Blue crab females move to the Bay mouth, where newly released larvae are transported in the surface waters of the estuarine plume out onto the continental shelf (McConaughy et al., 1983). Spider crab females move off-shore to incubate their eggs (Kergariou, 1984; Le Foll, 1993; González-Gurriarán et al., 1993). For each species, these locations effectively place highly vulnerable larvae off-shore and away from fish

predators in the nearshore zone (Morgan, 1990).

The adaptive significance of these patterns of movement and habitat utilization are similar to those in several species of lobsters and other crabs. *Panulirus argus* settle into structurally complex red algae in shallow inshore habitats as refuges from intense predation, and migrate out to deep coral reef habitats when they approach maturity (Herrnkind & Butler, 1986). Juvenile *Homarus americanus* utilize structurally complex cobble habitat in the nearshore zone to avoid predators (Johns & Mann, 1987; Wahle & Steneck, 1991, 1992); and they begin seasonal on- and off-shore migrations when they grow to maturity, which appears to optimize their temperature regime for reproduction (Campbell, 1986). In *Cancer magister* juveniles settle in shallow estuaries and seek refuge in complex shell substrate and warmer water during early growth, but later migrate out to deeper coastal habitats as they reach maturity (Gutermouth & Armstrong, 1989; Fernández et al., 1993). Juvenile *Chionoecetes opilio* settle to wander in warmer shallow water while growing, but undergo seasonal on- and off-shore migrations after reaching maturity (Watson, 1970; Watson & Wells, 1972; Coulombe et al., 1985; Hooper, 1986). Like these other large decapod crustaceans, *C. sapidus* and *M. squinado* exhibit seasonal and ontogenetic shifts in behaviour and habitat utilization which are adaptive in the size- and energy-dependent trade-offs of predator avoidance, growth, and reproduction.

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