Local population dynamics of estuarine blue crabs: abundance, recruitment and loss

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ABSTRACT: Due to the extensive motility and prolonged reproductive period of the blue crab *Callinectes sapidus*, cohorts may mix and be difficult to differentiate. In such a case, inferences about local population loss and turnover from changes in relative abundance may be tenuous: some form of identification other than size is necessary. We injected coded microwire tags into the musculature of blue crabs ≥ 35 mm carapace width and used the Jolly-Seber (J-S) mark-recapture model to estimate blue crab population size, loss probability, and recruitment over a 2.5 yr period within a 1 km² salt marsh creek system. A separate J-S analysis on juveniles ≤ 80 mm, along with an analysis of the population size structure, enabled us to infer which blue crab size classes were responsible for the changes in population size. Juvenile blue crabs 35 to 80 mm were most common in spring 1985 and from autumn through spring 1986. Their relative abundance index generally decreased from spring through summer, as larger juveniles and adults > 80 mm became more common. Whereas the sex ratio was close to unity when the smallest juveniles were predominant, the ratio became heavily biased towards males when the population size structure shifted toward the larger sizes. Very few juveniles ≤ 80 mm recruited to the population in the autumn-spring of 1986–87 compared to the previous spring and autumn periods. Subsequently, the total population size was lower through the summer of 1987 compared to the prior 2 years. Density peaked in spring 1985 and 1986 (during periods of juvenile abundance) at approximately 0.2 ind. m⁻², expressed as the no. of individuals at low tide throughout the entire subtidal area in the study site. The J-S analysis indicated the existence of time periods when recruitment and loss occurred concurrently. During many spring and summer sampling periods in 1985 and 1986, the probability of loss due to emigration or death was greater than that observed via net changes in the population size. Loss probability during 0.5 mo intervals in March through June 1986 varied from 0.04 ± 0.01 SE to 0.40 ± 0.04 (averaging 0.23) during a period of relatively stable population size of 11 700 to 15 800 individuals. Because of confounding recruitment, the realized rates of gross loss were higher than those discerned from net changes during such time periods. Most of these dynamics involved the juvenile portion of the population: we rarely recaptured large adult crabs, which had a brief residency after attaining adult size. After the adult crabs emigrated from the study area, a commercial crabber captured as many as 50 % of those which we had tagged. Our integration of the J-S mark-recapture model with other population analyses provided a more complete understanding of the population dynamics of the motile blue crab than has previously been possible. Quantification of concurrent recruitment and loss may be important in studies of numerous other estuarine species which have similar life history characteristics.

INTRODUCTION

The blue crab *Callinectes sapidus* is a common decapod crustacean in estuarine and nearshore waters of the Gulf of Mexico and much of the east coast of North America (Williams 1974), where it supports valuable commercial fisheries. Life history patterns may vary somewhat depending on estuarine type and locality, but adult blue crabs reside in estuarine waters of varying depths and salinities where they mate. Mated females (which mate once but may spawn several times) typically migrate to lower estuarine or offshore waters of high, oceanic salinity to spawn and hatch their eggs (Churchill 1919, Tagatz 1968a, Perry 1975). The spawning period is prolonged in their southern range, with gravid females found from spring

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through autumn (Tagatz 1968a, Palmer 1974, Perry 1975, Archambault et al. 1990). While mechanisms for larval/postlarval recruitment to (or retention within) the estuary are debated (Epifanio 1988, McConaugha 1988), small juveniles usually develop in shallow water habitats (Tagatz 1968a, Dudley & Judy 1973, Perry 1975, Orth & van Montfrans 1987). The blue crab's *in situ* growth rate and longevity is not known precisely because there are no reliable aging techniques, although in southern regions adult size can be attained approximately 1 yr after hatching (Tagatz 1968b).

Obtaining estimates of population parameters for blue crabs is complex due to this motile animal's life history strategy and patterns of habitat utilization. A prolonged reproductive period makes identification of separate cohorts difficult in southern regions, the same habitat may be used by crabs of different ages, and migrations further mask size structure patterns via mixing of cohorts. These are fundamental considerations in the study of a number of migrant consumers found within the salt marsh estuary, but are often difficult to address due to methodological and logistical difficulties. There have been numerous population studies of juvenile and adult blue crabs which described changes in relative abundance through periodic sampling (e.g. Darnell 1959, Tagatz 1968a, Dudley & Judy 1973, Miller et al. 1975, Perry 1975, Heck & Thoman 1984, Zimmerman & Minello 1984, Hines et al. 1987, Orth & van Montfrans 1987). Some of these studies attempted to infer general trends regarding growth or movement of perceived cohorts, but given the potential for false conclusions (Darnell 1959), such inferences may be viewed with caution depending on the extent to which cohorts can be easily discerned.

Where cohorts are difficult to distinguish, quantification of population parameters such as emigration or turnover requires some form of identification, of individuals or groups of individuals, other than age (size). Adult blue crabs, which no longer molt or do so with very low frequency, have been tracked individually in several regions by mark-recapture studies using tags that are visible externally. These studies (see Millikin & Williams 1984 for a synopsis) provided information on short and long distance movements, much of which is related to reproductive behavior. However, the lack of a suitable marking system for immature instars of blue crabs, which molt frequently and lose external marks, has until recently precluded studies in which the fate of juveniles can be discerned.

In a recent study by van Montfrans et al. (1991) in Chesapeake Bay, coded microwire tags (Jefferts et al. 1963) were injected into juvenile and adult blue crabs for an analysis of short term (2 mo) changes in abundance. However, the single-release mark-recapture

model that they used limited the extent to which they could address some issues of population turnover and loss (see 'Discussion'). As part of a project to determine the blue crab's influence on ecosystem dynamics in a Georgia (USA) salt marsh estuary, we report the local population dynamics of both juveniles and adults over a 2.5 yr period. In our study, we used the internal, coded microwire tags to permanently mark batches of juveniles and adults ≥ 35 mm carapace width, and used the multiple-release Jolly-Seber mark-recapture model (Jolly 1965, Seber 1965) to estimate local population size, number of recruits, and probability of loss (emigrating or dying). We also used analyses of the population size structure and of losses to the commercial fishery to complement the Jolly-Seber model, providing a detailed synthesis of local dynamics. Such an analysis not only provided estimates of crab abundance, but also of the loss from and recruitment to the local population in spite of confounding migrations which size structure analysis alone could not discern accurately. Such quantification of concurrent recruitment and loss allows better estimates of gross loss rates and of residency within the local area, providing the basis for evaluating the extent to which blue crabs may be a vector of biomass export from a salt marsh habitat.

METHODS

Population sampling. The local population under study was within a 1 km² salt marsh creek system located in the upper reaches of the Duplin River along Sapelo Island, Georgia, USA (Fig. 1). The intertidal vegetation is dominated by *Spartina alterniflora*, while the muddy subtidal areas have no submerged aquatic vegetation. The river is actually a large tidal slough, where tidal heights range from 1.5 to 3 m above mean low water and the only direct freshwater input to the upper river is from local runoff. The salinity of the lower Doboy Sound and surrounding area (including the lower Duplin River) is influenced by freshwater outflow from the Altamaha River to the south; a detailed hydrological study of the Duplin River system can be found in Imberger et al. (1983).

We used trawl tows to sample blue crabs ranging from small juveniles to adults in the subtidal areas. The 5 m wide otter trawl had a 19 mm square mesh in the body with a 6 mm mesh cod end liner and was rigged with a tickler chain. The distance of each 10 min tow defined 1 of 4 adjoining segments of the river, starting at the uppermost point from which a tow was possible and ending approximately 1.4 km downriver near the confluence of another tidal creek of similar size. Segment 1 was furthest upriver and shallowest, with an average mid-river depth at mean low water of
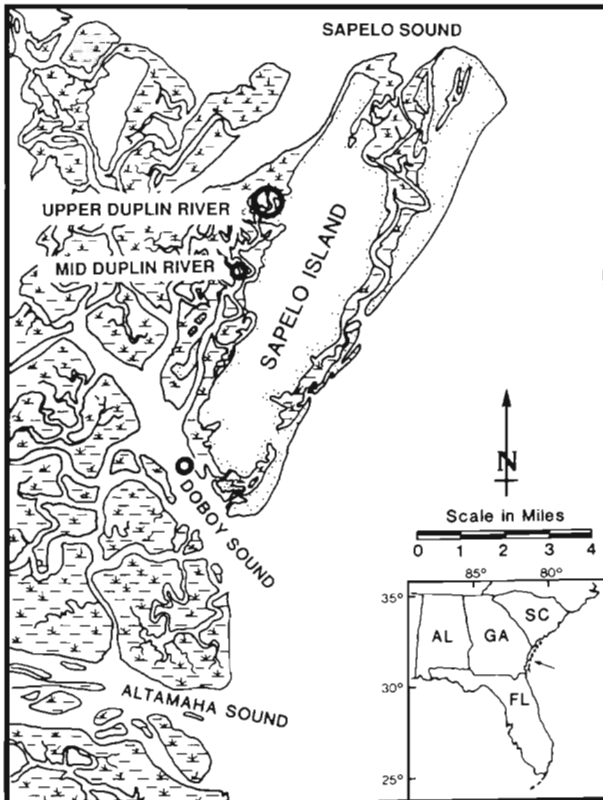
Fig. 1 Sampling sites in the Duplin River and Doboy Sound. The primary crab tagging site is within the circle labeled Upper Duplin River, comprised of trawling segments 1 to 4. The mid-river sampling site is a shallow mud bank within the circle labeled Mid Duplin River

approximately 1.5 m. The other segments (2 through 4) had gradually increasing depths, averaging from 3 to 3.5 m. While much of the sampling was along relatively shallow river banks, these latter segments also traversed comparatively deep basins at sharp turns in the river.

We sampled either semi-monthly or monthly, from April 1985 through August 1987. Because of the sampling intensity required for the mark-recapture program, each sampling period usually lasted 5 d; the end of 1 period to the start of the next was separated by at least 10 d. On most sampling days, we conducted trawl tows in Segments 1 through 4, repeated Segments 4 through 1, then repeated Segment 1. All trawl tows were made between 2 h before and 2 h after the daytime slack low tide. Captured crabs were grouped by approximate size and placed in a compartmented holding box filled with water. Though physiological stress was minimized, aggression between captured crabs resulted in occasional injuries. If a crab had a significant carapace wound and/or loss of pereiopods that were obviously recent, it was not tagged and was

considered removed from the population. The minimum sized crab that we considered was 35 mm in carapace width between the tips of the lateral spines, a criterion established due to (1) the ineffectiveness of the mesh size of the body of the trawl net in capturing and retaining smaller juveniles and (2) the lower size limit of our tagging system. Each crab was measured to the nearest mm and its sex determined. Starting in 1986 females were also recorded as being either mature or pubertal, the latter being within approximately 6 d of molting into the mature form (Van Engel 1958).

Coded microwire tags, which are completely internal within the organism and are detected magnetically (Jefferts et al. 1963), have been used primarily for fish marking (see Emery & Wydoski 1987), but recently have been shown to be retained effectively by juvenile blue crabs without affecting growth or mortality (van Montfrans et al. 1986, Fitz & Wiegert 1991a). Crabs were marked with a stainless steel, coded microwire tag injected into the basal muscle of the fifth pereiopod, the 'backfin muscle'. An automated injection system (Northwest Marine Technology, Shaw Island, WA 98286, USA) cut a 2.1 mm long tag from a spool of 0.36 mm diameter wire (which had previously been etched with a binary code) and inserted the tag into the musculature of the crab via a hypodermic needle.

In addition to the internal microwire tags, we fastened individually-numbered plastic tags bearing a return address onto the carapace of crabs ≥ 120 mm, using wire wrapped around the lateral spines of the carapace (Cronin 1949). Crabs of this size were susceptible to commercial harvest, being slightly less than the minimum legal size. Although these external tags were shed if the crabs molted, individuals of that general size have a prolonged intermolt period averaging at least 40 d (Tagatz 1968b), while many do not molt again. All crabs were released immediately after being tagged.

All crabs captured in our sampling were passed across a sensitive magnetic moment detector (Northwest Marine Technology) that allowed us to identify recaptured crabs bearing only a microwire tag. These recaptures were not released but brought to the lab for dissection and identification of the tag's code. We used a different spool of coded microwire tags for each sampling period, each spool being stamped with a different, continuously repeating binary code. Thus this was a batch release program in that recaptures were identified by the period of release, but not by information on the individual. Externally tagged recaptures were the exception in that they were identified individually and were released again as a 'newly' tagged individual.

The fate of externally tagged individuals after emigration from the study area was monitored by tag return information from commercial crabbers and the general public. Flyers requesting cooperation in reporting tagged captures were posted in public areas and in crab processing houses. Most importantly, we gained extensive cooperation in tag returns from the single commercial crabber operating within the Duplin River and Doboy Sound near the mouth of the river.

For a qualitative comparison of crab abundance among areas within the river system, we also conducted a limited number of standardized trawl tows at locations downriver of the primary crab tagging site of the upper Duplin River. All of the sites had similar depths as the primary site and were located in small creeks and along the river bank. Preliminary sampling in October and November 1984 indicated relatively low crab abundance at these locations compared to the primary site, particularly in the smaller size classes. We chose 1 site along a river bank located approximately midway (3.5 km) downriver to sample most frequently (Fig. 1). That station was sampled at times other than the tagging periods, using identical trawling methods immediately after sampling trawl Segment 1 of the primary site.

Mark-recapture analysis. We defined the study population as those crabs that were present in the drainage area of the relatively isolated creek system of the primary sampling site. At low tide, the water drained the marsh and most small creeks adjacent to the trawled segment of the river, thus concentrating the blue crabs within that main portion of the creek system.

The stochastic Jolly-Seber (J-S) model for an open population was used in a continuous mark-recapture program to estimate several population parameters: population size, the probabilities of survival and loss, and the numbers of individuals which recruited to the population. This model allows for the removal of recaptured crabs from the population as necessitated by our tagging system. We followed the basic notation of Jolly (1965) and added a loss parameter that is the complement of the survival probability. While ϕ_i is the estimate of probability of survival (not emigrating or dying) between the midpoints of sampling periods i and $i+1$, the probability of loss during that period is $PL_i = 1.0 - \phi_i$.

Crabs could be tagged and recaptured during the same sampling period i because of the multiple samples taken over a 4 to 5 d period ($d = 1$ to 5). Such a same-code-recapture, $scr_{d,i}$, did not contribute useful information to the standard J-S analysis and was treated in either of 2 ways depending on whether it remained in the population: (1) all $scr_{d,i}$ without external tags were removed from the population for identification, thus

were counted in the number captured during sample i (n_i) only once (for the initial capture) but were not counted at all in the number tagged and released (s_i); (2) externally tagged (and individually identified) $scr_{d,i}$ were released and counted once in n_i and once in s_i (for the initial capture and tagging).

We developed a FORTRAN program to manage the raw data and calculate the bias-corrected (Seber 1973) J-S parameter estimates. These estimates included population size at i (N_i), the no. of individuals recruited to a catchable size between i and $i+1$ (B_i), and the survival (ϕ_i) and loss (PL_i) probabilities. The associated standard errors of the N_i, ϕ_i (and PL_i), and B_i estimates were derived from the variances representing only the sampling variation, or 'error of estimation' given by Jolly (1965).

To determine the effectiveness of our sampling intensity, several additional statistics were tabulated by the program. One, the recapture proportion (RP_i) for each sampling period, provided a basic comparative measure of the proportion of the population that had been tagged and subsequently recaptured during the period i: $RP_i = m_i/n_i$, where m_i = the no. of n_i that had a tag. Similar to that was the frequently used statistic of the probability of capture, $P_i = m_i/M_i$, where M_i = the J-S estimate of the no. of tagged crabs alive in the population at i (as opposed to the observed random variable n_i). Somewhat unique to our sampling regime was a third statistic concerning the proportion of the population that was tagged during sampling period i: $SAT_{d,i} = scr_{d,i}/nn_{d,i}$, where $nn_{d,i}$ = total no. of crabs captured on the dth day of i. Note that $\sum nn_{d,i} \geq n_i$ ($d = 1,5$) because the number of crabs caught on each sampling day may have included same-code-recaptures, which by definition are counted only once in the n_i of a sampling period. Over a multi-day sampling period i, $SAT_{d,i}$ provided a comparative indication of the extent to which we marked the population that was present during the sampling period.

We also used the program JOLLY developed by J. Hines (7 Oct 1988 version, U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD 20708, USA), based on observed and expected recaptures, to analyze the chi-square goodness-of-fit of the data to the general J-S model (Pollock et al. 1985). This goodness-of-fit test provided an omnibus test of the extent to which some model assumptions were met.

The J-S model makes the following assumptions: (1) tags are permanent and their codes are identified correctly upon recapture; (2) every crab within the population, regardless of tag presence, age, etc., has the same probability of capture; (3) every crab has the same probability of survival between i and $i+1$ provided it is present (and alive) immediately after i; (4) the corollary to (2) and (3) above – emigration is

permanent; and (5) the sampling time is small compared to the interval between samples. Aspects of some of these assumptions could be addressed *a priori*, but we reserve discussion of all of them for the 'Discussion' section.

Relative abundance analysis. We analyzed blue crab relative abundance (a relational abundance index derived from numbers captured per trawl tow) to complement the J-S analysis. The Duplin River within the study area varied substantially in depth and width, and we observed differences in blue crab abundance among the trawling segments. For analyses of temporal changes in relative abundance within 1 homogeneous habitat, we chose to focus on trawling Segment 1 of the upper river. That segment was the most homogeneous in depth profile compared to the other segments which encompassed deep basins. In order to capture more individuals for mark-recapture, Segment 1 was sampled as many as 3 times on each day, with the third overlapping the area of the second. Only the first 2 were used in the relative abundance analysis because of that overlap (dependence) of samples within the confines of the river segment.

RESULTS

Relative abundance

Juvenile crabs ≤ 80 mm were most common during spring 1985 and from late autumn through early spring 1986 due to an influx of small juveniles to the population during these times. Throughout the summer of both years, there was a gradual shift in population size structure towards larger juveniles and adults as total population abundance generally decreased (Fig. 2). However, very few juveniles recruited to the population during the period from autumn through spring 1986–87, and total population abundance was low through the remainder of 1987.

Males generally dominated the population during the study. The male:female sex ratio ranged from slightly over 1:1 to almost 3:1 in a variable manner during 1985. The sex ratio then decreased to near 1:1 in the winter of that year through spring 1986 (Fig. 3), when juveniles were abundant. The ratio then gradually increased to high levels of male dominance by autumn as larger crabs predominated, and fluctuated
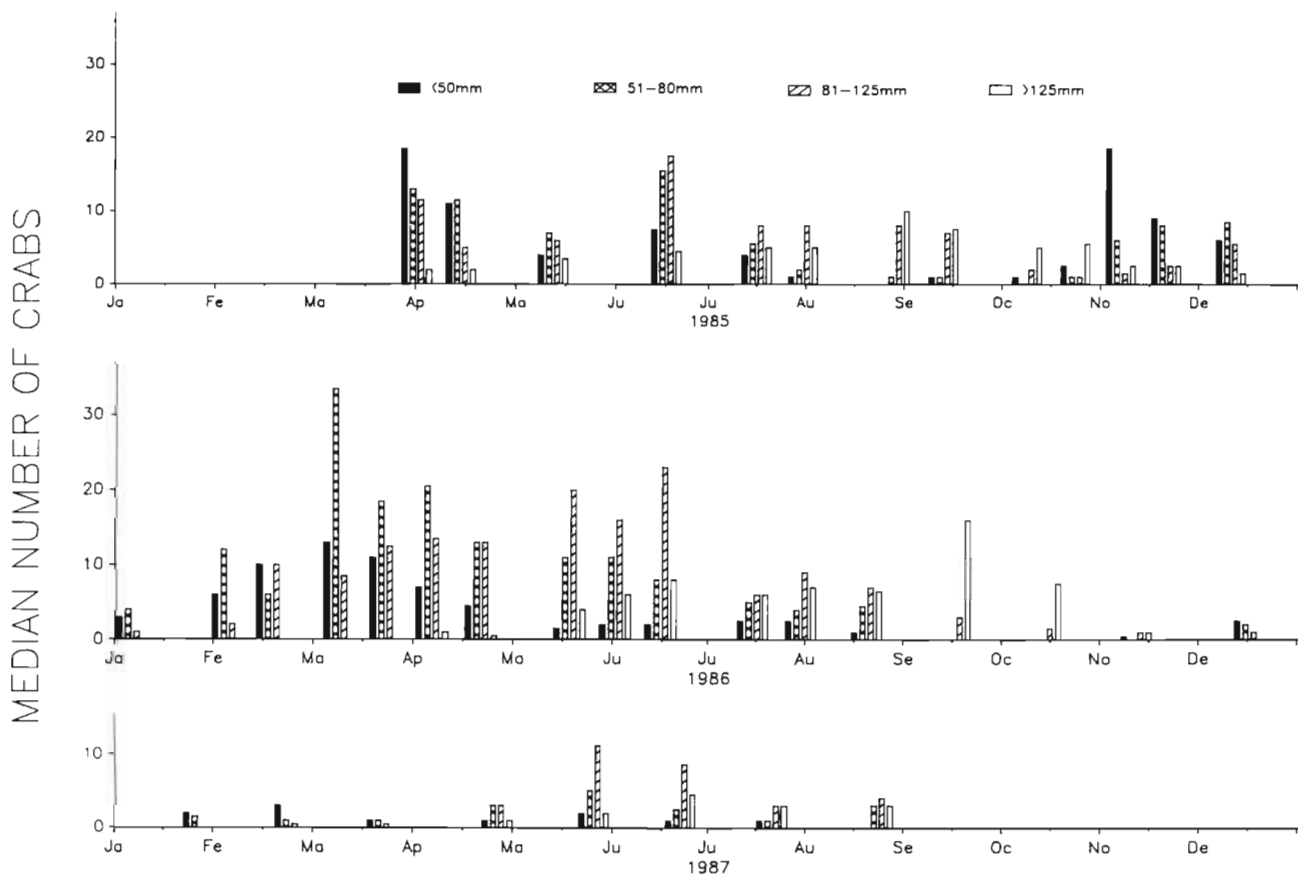

Fig. 2. *Callinectes sapidus*. Relative abundance of 4 size classes of blue crabs at trawling Segment 1 within the upper Duplin River. Each cluster of bars is centered over the date of the midpoint of a sampling period
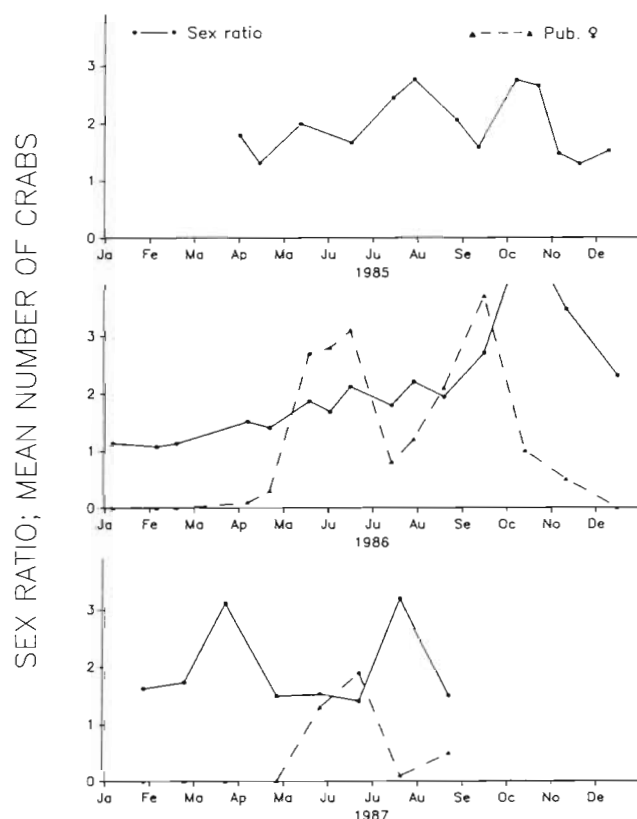
Fig. 3. *Callinectes sapidus*. Sex ratio and no. of pubertal females at trawling Segment 1 of the upper Duplin River The sex ratio is calculated as the no. of males to females captured during each sampling period; the mean no. of pubertal females captured per trawl sample is indicated by the same scale along the vertical axis

through the rest of the study. Mature females were uncommon in the study area, reaching brief maxima in late June and July in 1986 and 1987, when they approached 4 to 6 % of the mean total number of crabs per sample. More commonly found was the penultimate female instar; numbers of pubertal females peaked in May through June of both 1986 and 1987, with a second peak in August through September 1986 (Fig. 3).

Jolly-Seber model fit and precision

A total of 20 220 crabs were captured ($\sum n_i, i = 1,35$) for the mark-recapture program; of those, 17 546 crabs were given a tag ($\sum s_i, i = 1,35$) for the mark-recapture statistics, though more were tagged and sacrificed as same-code-recaptures. Because sampling effort remained constant, the numbers of crabs that were marked during each sampling period varied considerably depending on their abundance, ranging from an

extreme low of 98 in March 1987 to 1056 in early March 1986. Appendix 1 provides the matrix of captures, recaptures, and probability of capture for each sampling period.

The chi-square goodness of fit test of program JOLLY showed no significant departure from the J-S model for the sampling periods $i = 1,30$ (p = 0.14), an indication that the standard J-S model was appropriate for our data. Sampling periods after $i = 30$ were not included in the analysis because the program JOLLY was limited to 30 periods and the later samples had very poor precision and little utility (see below). Based on a simpler mark-recapture model, Seber (1973) indicated that small sample bias may be introduced into the J-S model when m_i is less than approximately 10, while Arnason & Mills (1981) determined through simulation that m_i and r_i should both be greater than 5 for the J-S model to avoid this bias. Some of the sampling periods in 1985 and all from October 1986 ($i = 25$) and later had m_i and/or r_i less than 10, in some cases much lower. A very good model fit (chi-square, p = 0.50) was found when we reduced the analysis to only include 1 yr of sampling periods $i = 10,24$; conservatively, this range of i contained no m_i or r_i which were below 10 and had the largest numbers of captures and recaptures of the study. This period had the best model fit, good precision (see below), and was free from small sample bias in any of the estimates.

The coefficient of variation (CV = SE/estimate) was used as a measure of the precision of an estimate. The CV of N_i from October 1985 through September 1986 ($i = 10,24$) ranged from 0.14 to 0.43 (mean = 0.24), whereas the precision of the estimates prior to that period averaged 0.44 (Fig. 4). The precision of virtually all of the estimates from late 1986 until the end of the study was very poor and we will not analyze that period with any rigor, except to indicate that the population was very small and that the J-S model was of little utility for that period. The most precise estimates, with the CV below 0.25 in early 1986, were usually associated with RP_i that were relatively high (up to 13 ‰) (Fig. 4). However, some relatively precise estimates corresponded with low RP_i, such as in March 1986 with $RP_i = 3$ % and the CV of $N_i = 0.20$. This was due to the presence of tagged specimens within the population that were captured at some other period, modifying the population size estimate and increasing precision. The probability of capture, P_i, which is most frequently reported in the literature, accounted for such marked crabs. P_i followed a trend similar to RP_i, but indicated some unrealistically high values (Appendix 1) when population estimates were poor. This appears to be primarily the result of P_i being dependent on the estimate of M_i, the number of tagged crabs in the population at i, whereas RP_i is determined directly from observed variables.
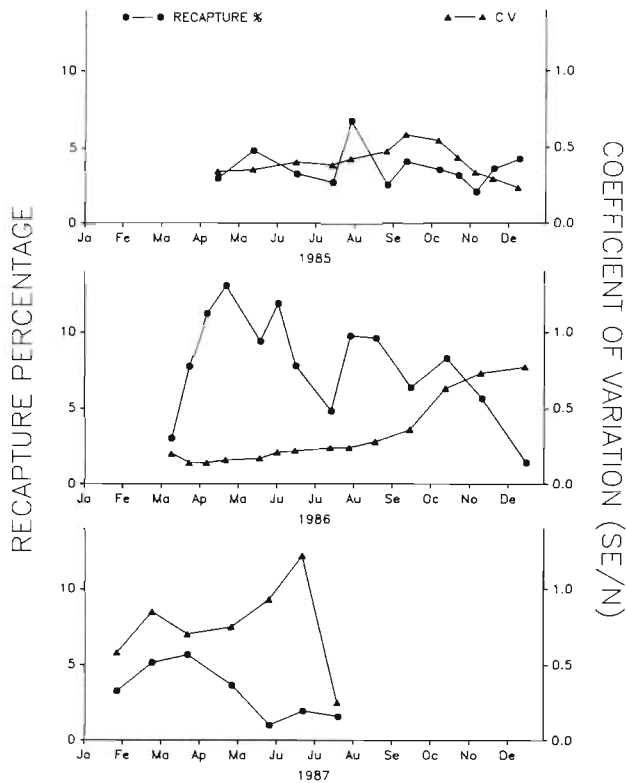
Fig. 4. *Callinectes sapidus*. Percent of crabs caught during each sampling period that were recaptures from a previous release ($RP_i \times 100$) compared with the precision (coefficient of variation) of the population size estimate N_i

The proportion of the population that was tagged during a sampling period ($SAT_{d,i}$) was variable, but generally increased through the fifth day (Fig. 5). During the dramatic overall decline of the population in 1987, we had very little success in marking a significant proportion of the population, while sampling effort remained constant. The proportion that was tagged by the fifth sampling day averaged 0.063 ± 0.042 SD during all sampling periods, with a maximum of 0.137 in March 1986; the average tagged proportion during sampling periods $i = 10,24$ was 0.082 ± 0.035 SD.

Population size and density

The pattern of J-S estimates of population size was very similar to that indicated by the changes in relative abundance because the no. of crabs captured during each sampling period was incorporated into the population size estimate. From October 1985 to September 1986, local population size reached a maximum of 15 000 to 20 000 crabs during November and March, while the minimum was approximately 1000 individuals in October (Fig. 6).

From digitized aerial photographs, the drainage area of the study marsh was estimated to be 112 ha. This represented the surface area of *Spartina* marsh bounded by land, a high marsh line, and an imaginary boundary in the Duplin River at the confluence of the trawled area and an adjacent tributary creek. The area of the river and creek beds which remain flooded at low tide was 9.3 ha. Error of estimation in the multiple digitized calculations is relatively small, (ca 1 % of the estimate), but error in delineation of the surfaces may have been present. If the blue crabs distributed themselves evenly across the entire subtidal plus intertidal area at high tide, their density reached a maximum on the order of 0.02 m^{-2}. If the crab distribution is taken to be that within all subtidal areas during low tide, maximum density at low tide was an order of magnitude higher, approximately 0.2 m^{-2}. These estimates are conservative in that they include area that may not be utilized by blue crabs, but they are unaffected by the (unknown) sampling
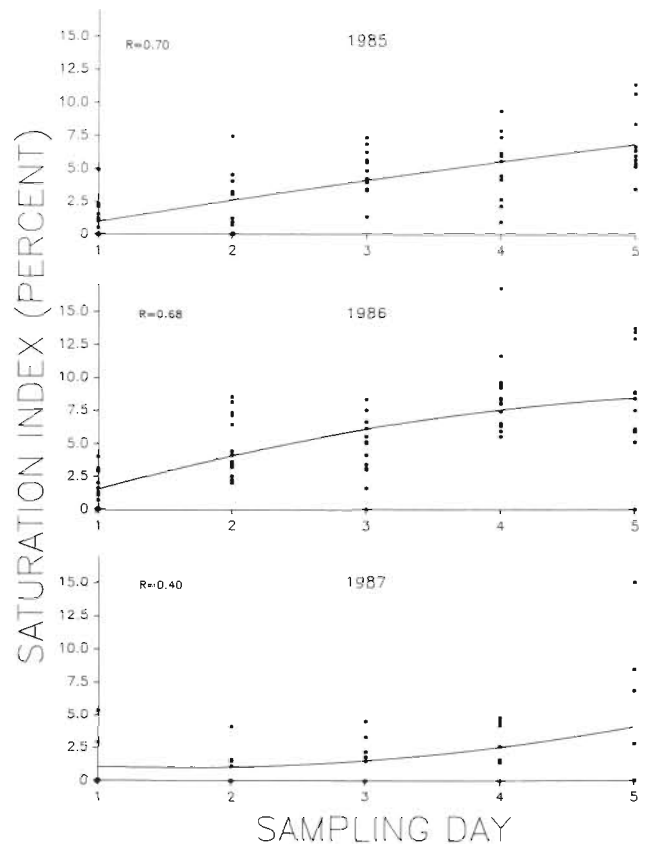
Fig. 5. *Callinectes sapidus*. Tag saturation index during the 5 d sampling periods for each year of the study. Each point represents $SAT_{d,i} \times 100$, which is the percent of captured crabs during each day d of a sampling period i that had been tagged and released with code i during that same sampling period. Curves are of the best second order polynomial fit to each year's data, indicating the regression coefficient R
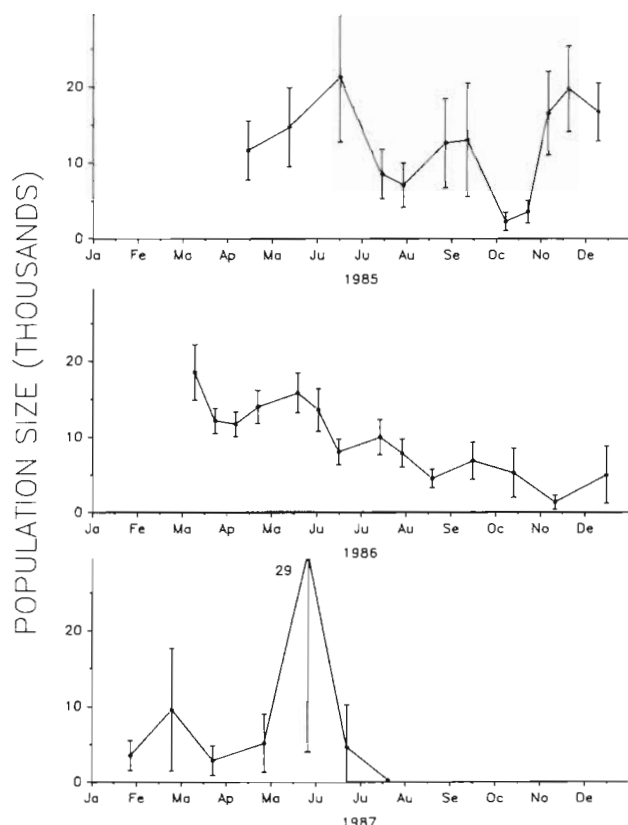
Fig. 6. *Callinectes sapidus*. J-S estimates of total population size during each sampling period, indicating the estimate ± 1 SE

efficiency of the trawl net and are applicable to the broadly defined subtidal+intertidal or subtidal areas of this salt marsh estuary.

Recruitment and loss

The J-S results indicated that recruitment of crabs into the population (B_i) occurred at intervals throughout much of the spring and late summer in 1985 (Fig. 7). As seen from the relative abundance (Fig. 2) and J-S analyses (Fig. 7), large pulses of recruitment of juveniles then occurred in late fall 1985 and spring 1986. However, many of these periods of recruitment were concurrent with losses of large proportions of the population (Fig 7). Loss probabilities $(PL_i \pm 1\ SE)$ were between 0.4 ± 0.1 and 0.6 ± 0.3 during several periods in 1985 when substantial recruitment to the population had also occurred. Populations sampled from November 1985 through March 1986 had PL_i varying from 0.30 ± 0.07 (SE) to 0.62 ± 0.09, during the period of high juvenile recruitment. From late March through early June 1986, when population size was relatively stable, the losses continued with PL_i averag-

ing 0.23 per 0.5 mo intersample period (range 0.04 ± 0.01 to 0.40 ± 0.04). As particularly evident in the relatively precise estimates from late 1985 through mid-1986, losses that were concurrent with recruitment were not discerned by net changes in abundance.

Smallest size classes

To analyze recruitment and losses solely within the smallest size classes of the population, the J-S model was used for the subpopulation of juveniles ≤ 80 mm. The chi-square goodness-of-fit (of program JOLLY) indicated highly significant departure from the model $(p = 0.0007)$ for $i = 1,30$. However, when we analyzed only sampling periods during high abundance and with sufficient numbers of recaptures to avoid small sample bias (November 1985 through June 1986,
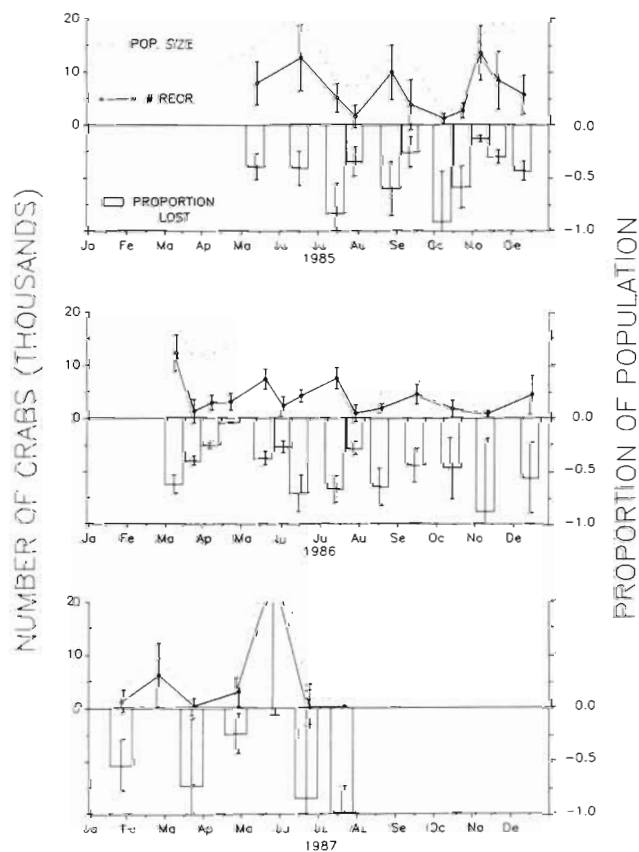
Fig. 7 *Callinectes sapidus*. J-S estimates of the no. of individuals in the total population at each sampling period i (N_i), the no. of crabs recruited to (B_i) and the proportion lost from (PL_i) the population between $i-1$ and i. J-S estimates of recruitment (B_i) and loss (PL_i) are plotted against the date of $i+1$ in order to indicate the gains and losses between $i-1$ and i which result in the population size N_i. Error bars are ± 1 SE. Lack of an estimate either indicates a zero value or model failure in calculation
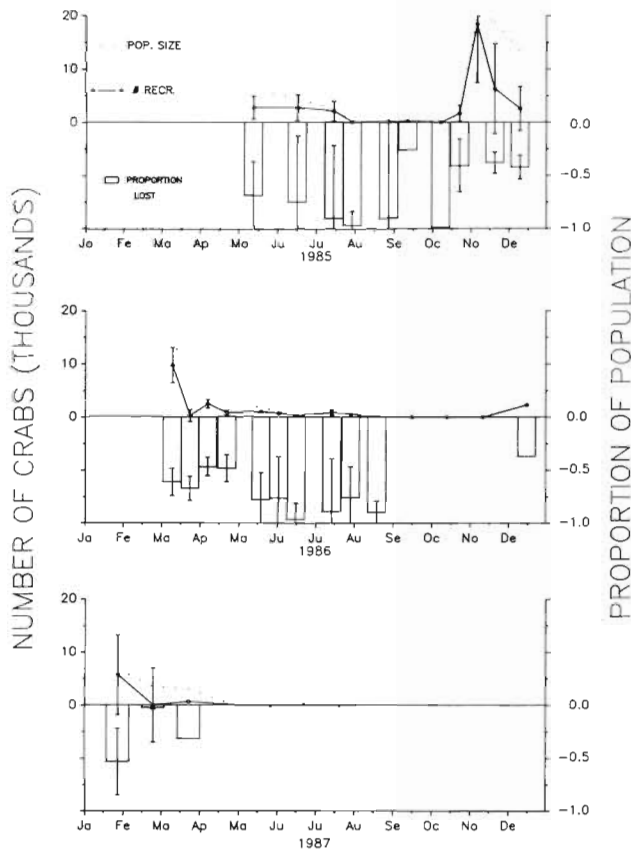
Fig. 8. *Callinectes sapidus*. J-S estimates of the no. of individuals in the smallest size classes (≤ 80 mm) of the population at each sampling period i (N_i for these classes), the no. of crabs recruited to and the proportion lost from these size classes (B_i and PL_i respectively) between $i-1$ and i. J-S estimates of recruitment (B_i) and loss (PL_i) are plotted against the date of $i+1$ in order to indicate the gains and losses between $i-1$ and i which result in the population size N_i. Error bars are ± 1 SE. Lack of an estimate indicates either a zero value or model failure in calculation

$i = 11,20$), we found a very good fit to the model with no significant departure from expectation (p = 0.48). Appendix 2 provides the capture and recapture data for the subpopulation of juveniles ≤ 80 mm.

The model lacked precision when juveniles were uncommon. However, during the period of good J-S model fit, the analysis showed that recruitment of crabs into that juvenile subpopulation occurred in fall and early spring, with overwintering (J-S) losses from that portion of the population (Fig. 8). Losses from the total population before April 1986 were due primarily to juvenile (≤ 80 mm) mortality and emigration, with evidence of loss from the juvenile subpopulation due to growth into the larger size classes (Figs. 7 & 8). After May 1986, relatively few crabs in the smallest size classes were evident in the J-S analysis of the juvenile subpopulation, indicating that the overall population changes through that late spring and summer were mostly due to changes in the larger (> 80 mm) size classes (Figs. 7 & 8).

Externally tagged crabs

The extent to which large (≥ 120 mm) emigrating crabs were exploited commercially was determined only for 1986 because returns of external tags during other periods were known to be incomplete. We were ensured of the return of all tags from crabs released during April through August 1986 that were caught by the commercial crabber. Of the 923 crabs that were tagged externally during that time, 36 % were subsequently captured by the crabber in the Duplin River (downriver of the release site), while an additional 1 % were captured in the Doboy Sound. The proportion captured increased through the season, with no returns of 40 tagged crabs in late April to a peak return of 52 % of 218 tagged crabs in late July (Table 1). The number of tags returned by other commercial crabbers and the general public outside the Duplin River were comparatively few (16 during the entire study) and considered potentially incomplete, preventing an analysis of movements from the Duplin River system.

It was not possible to determine accurate rates of exploitation due to inadequate information on the exact date of the commercial capture, but, of crabs tagged in April and May, all returns were within 2 mo. Of those tagged in June, at least 86 % of the returns were within 1.5 mo; at least 80 % of the crabs tagged in middle and late July were returned within 1 and 1.5 mo, respectively; all returns of those tagged in August were within 2 mo.

Table 1. *Callinectes sapidus*. Tagged blue crabs captured by a commercial crabber in the Duplin River and Doboy Sound after they emigrated from the primary sampling site. No. tagged is the no. of externally-tagged crabs that were released during the given sampling period; dates represent the midpoint of a sampling period

Period of release	No. tagged	Crabs captured Duplin River No.	Crabs captured Duplin River %	Crabs captured Duplin & Doboy No.	Crabs captured Duplin & Doboy %
9 Apr 1986	28	1	3.6	1	3.6
24 Apr 1986	40	0	0.0	0	0.0
21 May 1986	57	5	8.8	6	10.5
4 Jun 1986	86	22	25.6	23	26.7
18 Jun 1986	108	32	29.6	34	31.5
16 Jul 1986	212	91	42.9	92	43.4
31 Jul 1986	218	108	49.5	114	52.3
20 Aug 1986	174	69	39.7	69	39.7
Total:	923	328	35.5	339	36.7

We recaptured comparatively few large crabs in the release site: during the April through August 1986 period analyzed above, we recaptured (and re-released) 5.2 % of the crabs that had been tagged externally. Of those recaptures, 56 % were caught in the sampling period following that in which they had been tagged, while 85 % were caught by the second sampling period after being tagged. Because inter-sample periods varied between 0.5 to 1 mo, these data represent 35 % recaptured within approximately 0.5 mo, 69 % within 1 mo, and 83 % within 1.5 mo. Multiple recaptures (i.e. tagged externally and recaptured more than once) were rare: 3 of the 3153 individuals tagged externally. In those 3 cases, a total of 29, 61, and 77 d elapsed from the tagging date and the second recapture (the maximum no. of times an individual was recaptured). These data indicated the relatively short period during which the largest individuals resided within the study area creek.

Downriver sampling

During the first year of sampling there were a total of 8 additional periods during which we sampled both Segment 1 of the primary sampling site and the mid-river site, for a total of 72 samples. All crabs were checked for tag presence, but no crabs were recaptured in any of the samples outside of the release area, (including 39 other samples taken at opportunistic times at other locations in the upper/middle Duplin River and the Doboy Sound). The mid-river site had substantially lower crab abundance than the upriver Segment 1 (Fig. 9), and particularly fewer crabs in the smaller size classes. Other locations downriver of the primary sampling site generally had lower abundances than the mid-river site but were potentially of similar magnitude. This limited sampling provided some qualitative evidence that the smaller juveniles were found in greatest abundance within the upper reaches of the Duplin River and did not appear to move downriver until they attained larger sizes.

DISCUSSION

The blue crab population that we studied fluctuated in abundance on both seasonal and interannual scales. However, these changes in relative abundance did not reveal a more interesting feature of this population. Losses of substantial proportions of the population occurred during periods of little net change in abundance, apparently due to turnover associated with concurrent loss from, and recruitment to, the population. The microwire tagging system that we used with the
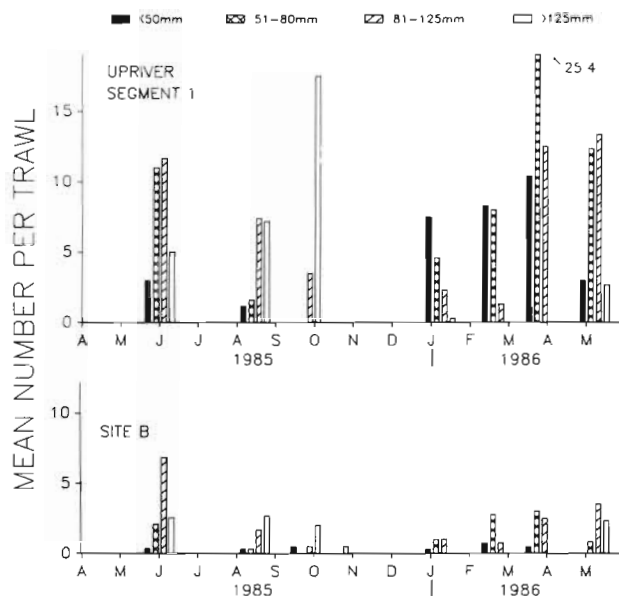
Fig. 9. *Callinectes sapidus*. Mean no. of crabs per trawl sample at the primary site (Segment 1) in the upper Duplin River and the mean no. per sample at the mid-river site. Each cluster of bars is centered over the date of the midpoint of a sampling period

J-S mark-recapture model provided an effective means of identifying components of a migrant estuarine population and determining losses and turnover over a prolonged period.

Relative abundance

Our 2.5 yr study was of sufficient duration that some general patterns of blue crab abundance could be discerned. Small juveniles recruited to the local population in the late fall and early spring of the first 2 yr of the study, overwintering to some extent in the shallow estuary. Subsequently, larger juveniles and adults predominated through the summer as the demographics indicated apparent growth of individuals within the population. In general, trends in abundance and size structure of the blue crab population in this shallow Georgia estuary were similar to those found other studies where blue crabs are found in the USA [e.g Perry (1975) in the Gulf Coast region, Tagatz (1968a) in Florida, Archambault et al. (1990) in South Carolina, Dudley & Judy (1973) in North Carolina, and Hines et al. (1987) in Chesapeake Bay], with differences in timing of development and extent of overwintering depending on the location.

During the summertime progression in size structure that we observed, the sex ratio became skewed toward male dominance. Periods of abundance of pubertal

females in early summer were indicative of probable mating activity, but mature females were never common in the study area as they apparently emigrated downriver. Although the 1986 adult population that would produce a new autumn cohort did not appear to be low compared to the prior year (Fig. 2), juvenile recruitment to the population was dramatically lower in fall/spring 1986/1987. Drought conditions occurred during the summer of 1986, as was somewhat evident locally in that salinity in the study area was generally elevated by several ppt in late summer (Fitz 1990). Although an understanding of specific causal mechanisms is lacking, it appears that some factor associated with that summer's weather and drought (such as reduced freshwater riverine input to the nearshore region or altered wind/water circulation) produced unfavorable conditions for larval/postlarval survival and recruitment.

Precision of J-S estimates

A principal component of our population study was the J-S mark-recapture model, which required a determination of the efficacy of the model in portraying the population dynamics. The proportion of the population tagged was important to the precision of the J-S estimates. Nichols et al. (1981) provided guidelines for the expected precision of J-S estimates given different probabilities of capture (P_i), showing that P_i should be greater than 0.10 to 0.20 for good precision, and that precision increased with population size. However, they analyzed only hypothetical populations with 100 to 1000 individuals. This was the lower range of abundance of our blue crab population, which had a maximum size of ca 20 000 individuals. Simulations by Hightower & Gilbert (1984) showed that precision can be acceptable for some purposes when studying populations in the tens of thousands of individuals when capture probabilities are extremely low $(P_i \ll 0.10)$. We used P_i, the recapture proportion (RP_i), and the tag saturation index $(SAT_{d,i})$ to estimate the extent to which we had tagged the population. These indices, using different observed random variables and/or parameter estimates, all indicated that the proportion of the population that we marked was generally not large and averaged less than 0.10. Nevertheless, because the population size was larger than most studied with the J-S analysis, the no. of tagged crabs and recaptures were often large enough to provide precision that was adequate for our objectives (i.e. CV in the range of 0.15 to 0.30).

The precision of the population size estimate (N_i) was usually similar to that of the loss probability (PL_i) (and survival probability ϕ_i), although the recruitment estimate (B_i) was always less precise than either of those parameters due to its dependence on both the population size and survival probability estimates. Most population estimates through summer 1985 were without small sample bias and had adequate precision to discern real occurrences of recruitment and loss, yet not on a consistent basis throughout the period. A potential cause for the lower precision may have been commercial crabbing. Four or five traps were set daily within the study area until the end of the 1985 season and, because the crabber did not understand that we desired such local information, he removed large numbers of tagged crabs from the area which were not reported. Such losses were a part of the J-S estimates of loss, but represented a substantial cost in terms of the size of the tagged population. Thus the precision of the estimates was most likely reduced during periods of heavy fishing pressure. Subsequent to 1985, commercial crabbing was not conducted in the study area and the commercial catches of tagged crabs occurred after emigration from the site. The J-S model performed best with data during the year starting in late 1985, but then precision was poor from fall 1986 through the end of the study, when, after a season of drought, comparatively few crabs were captured and recaptures were few.

Assumptions of J-S model

Scrutinizing the assumptions of the J-S model and the extent to which the data met these criteria was an integral aspect of ensuring an unbiased analysis. While some assumptions could be addressed a priori, others could not necessarily be tested directly. We now consider the various assumptions (given in 'Methods') in light of our data results, the blue crab population characteristics, and simulations and analyses of the J-S model robustness from the literature. Basically, the assumptions call for a permanent tag having no effect on the individuals in the population, along with homogeneity in capture and survival probabilities among members of the population. Natural populations will never be completely homogeneous in all respects, and thus one question is whether the model is adequately robust to the degree of heterogeneity within the blue crab population data.

The tagging system was critical to the study because a number of assumptions revolve around the tag status of the animal. The first assumption and aspects of the second and third concern retention of the tag and its effect on crab survival and growth rates. In a laboratory experiment (Fitz & Wiegert 1991a), microwire tags were retained effectively (96 to 98 % minimum) through multiple molts by crabs of the smallest size

used in our field study, and tag presence had no effect on growth or survival rates over an 80 d period. It follows from those experimental results that tags could be considered permanent and the presence of a tag did not affect growth or survival rates in the field situation.

Tag presence/absence most likely did not affect the probability of capture because: (1) trawl sampling does not influence the future probability of recapture in any behavioral sense such as a 'trap response' (see Pollock et al. 1990); (2) the capture efficiency of the trawl net is independent of tag presence; and (3) at least 20 tidal cycles (10 d) intervened between sampling periods to allow adequate mixing of the tagged and untagged members of the population such that the probabilities of capturing tagged and untagged crabs are equivalent (see Jolly 1965; Seber 1973, p. 211). Adequate mixing of tagged and untagged crabs was evident over intervals of only several days: the $SAT_{d,i}$ index did not increase rapidly during the sampling periods and was similar to the estimated capture probability (P_i) and recapture proportion (RP_i). If mixing had not been relatively rapid, $SAT_{d,i}$ would have increased more rapidly to higher levels during the daily releases, as tagged crabs concentrated within the areas sampled.

Homogeneous capture probability among blue crabs of varying sizes is also assumed. Although the actual sampling efficiency need not be known for the J-S model, a large sample size is generally needed for mark-recapture studies, necessitating an effective sampling device for capturing all sizes of organisms that are targeted for study. Based on crab and net dimensions, the body mesh size of our trawl net was considered sufficient to capture juvenile crabs ≥ 35 mm, while the smaller cod end liner retained them. The sampling efficiency of the trawl net, which we estimated (below) to have been relatively low, should nevertheless have been similar for all crabs that we considered (but inefficient in capturing smaller juveniles). There is evidence that very small juveniles are found at high densities in the shallowest habitats (< 1 m) of estuarine waters of most geographic regions, (e.g. Zimmerman & Minello 1984, Orth & van Montfrans 1987, Mense & Wenner 1989, Wilson et al. 1990). However, those studies (using drop nets or cylinders) found very few crabs of the size (≥ 35 mm) that we sampled with the trawl net, and crabs of such size were usually ignored in their studies. Our sampling included some areas with depths slightly less than 1 m, but habitats shallower than that were not sampled. While there is a substantial area of very shallow water that was not accessible to our trawl sampling, it appeared likely that most of the juvenile blue crabs in that habitat were small juveniles that had not attained the size to be considered recruits to the catchable population. If heterogeneity was present in capture probability, N_i

would be negatively biased while M_i and ϕ_i (and PL_i) have very little bias, or are asymptotically unbiased (Cormack 1972, Carothers 1973). However, the arguments given above, and importantly, the goodness of fit test (discussed below) indicated that such heterogeneity was not present in our population data to the extent that it could have influenced the results in a significant manner.

Survival (not dying or emigrating) is assumed to be equivalent for all members of the population during any intersampling period (but may vary among periods). However, mortality rates of crabs under field conditions are unknown. Juvenile blue crabs do molt more frequently than their larger counterparts and, while in the soft postmolt stage, they are vulnerable to predation. Therefore, survival may increase with age to some extent. Conversely, the well-known migrations of adult male and female blue crabs (Cargo 1958, Judy & Dudley 1970, Oesterling & Adams 1982, and this study) reduce the 'survival' of that size class upon emigration from the study area. The J-S analysis of the juvenile subpopulation ≤ 80 mm (Fig. 8) showed that the changes in the total population (Fig. 7) were predominately associated with this small size class only during late fall through spring, with results between the 2 analyses in good agreement during that time. Population changes after March/April were evidently due to larger crabs. Though there was some overlap in the presence of crabs in the 2 broad classes of ≤ 80 mm and > 80 mm in late spring, the extremes in sizes of crabs within the total population were generally separated in time. Importantly, the smallest (≤ 50 mm) and largest (> 125 mm) sizes of crabs were not abundant simultaneously (Fig. 2), thus there was unlikely to be a strong effect of size (age) on the total population analysis.

Cormack (1972) and Seber (1973, p. 232) showed that the J-S method will not be greatly affected by age-dependent mortality (or emigration) if intersample survival is independent of tag status and if probability of capture is independent of age, both of which we have previously indicated to be reasonable assumptions within our sampling regime. Although simulations of Manly (1970) showed that some positive bias can be introduced in N_i and ϕ_i if survival is lower for younger individuals, those simulations indicated that the J-S model 'can reasonably be used whenever mortality rates are not strongly affected by age' As with heterogeneity in capture probability, the goodness of fit test (below) provided a more quantitative test, with the results indicating that heterogeneity in survival probability did not appear to bias our results.

Emigration was assumed to be permanent, in that if crabs left the area after being tagged, they were absent during a later sampling period and did not

return subsequently. While there is no explicit test for this assumption, it appears reasonable in our data considering the below factors. We recaptured very few crabs bearing external tags, while more than half of those recaptures occurred during the sampling period following their release, and 85 % by the next sample. This indicated a brief residency, with few crabs returning to the system after emigration. Juvenile movements could not be monitored directly, but the rarity of smaller juvenile crabs in the lower river sites (Fig 9) and the trends in recapture data (Appendices 1 & 2) indicated that temporary emigration could be considered to be minimal within the context of the J-S model. If temporary emigration were a significant problem in the data for this population, it would be most severe if a given marked cohort remained within the general (sampled and unsampled) area for prolonged periods and had high capture probabilities. After the initial recapture, subsequent recaptures of a given code decreased rapidly in number with little variation in pattern (Appendices 1 & 2); heterogeneity in patterns of recapture would be a potential indicator of some types of temporary emigration. Thus, recapture of individuals that may have emigrated temporarily appears unlikely to have severely influenced the J-S parameter estimates.

The length of the sampling periods was at least half that of the intersample periods, and the tagged and untagged proportions of the population were assumed to have been adequately mixed by that time interval (as implied by the assumption of a sampling period sufficiently short compared to the intersample period). We previously indicated that mixing within the population was rapid, such that tagged and untagged crabs were adequately mixed well within a 10 d period, and thus the estimates of the population parameters (N_i, ϕ_i, etc.) were those of averages during a given sampling period.

The above discussion of the various assumptions provided evidence that the standard J-S model was appropriate for our population analysis, but the goodness-of-fit test provided a general quantitative test of homogeneity of the population data. There were 2 components to this test in the program JOLLY (Pollock et al. 1985), the second being that which was applicable to our mark-recapture data. This test showed that, with marginal confidence (chi-square test, $p = 0.14$), the data met the general assumptions for the first 30 sampling periods. However, the power of the test may be questioned when capture probabilities are relatively low (Pollock et al. 1985). It is plausible that, at this probability level, the model was accepted falsely in the presence of heterogeneity, but the year from October 1985 through September 1986 had a substantially lower probability of false acceptance of the

model (with a higher $p = 0.50$). Using simulations, Pollock et al. (1985) found that the power of the test increased with N_i; the average N_i in our study during the year analyzed was 13 600, while they analyzed populations no greater than 1000 in size. Given all of the logical arguments, model robustness and the very good model fit, we believe that our J-S estimates were sufficiently unbiased through late 1986, and in particular, during the year from autumn 1985 through autumn 1986.

Jolly-Seber analysis

Unbiased sampling of all habitats available to the blue crabs is difficult due to differences in efficiency and selectivity of sampling gear depending on the habitat. The mark-recapture population size estimate alleviated these problems to a large degree in that knowledge of the capture efficiency was not required for J-S estimates. Based on the population size and approximate area estimates, if blue crabs dispersed uniformly throughout the entire subtidal area of our study site at low tide, their maximum density was approximately 0.2 crabs m^{-2} in the late fall and early spring when small juveniles were common. Density determined in this manner provided a conservative estimate for the generalized subtidal creek habitat.

Blue crab density estimates are rare in the literature due to methodological obstacles. The sampling efficiency of trawl tows (i.e. the percentage of organisms in the towed path that are captured) is invariably low and is dependent on the organism, season, towing speed, and width of substrate actually covered by the trawl. Although there are no estimates of the catch efficiency for the blue crab, published efficiency estimates for fishes range from 6 % (*Leiostomus xanthurus*: Loesch et al. 1976) to 49 % (*Lagodon rhomboides*: Kjelson & Johnson 1978), while 45 % efficiency was reported for brown shrimp (*Penaeus aztecus*: Loesch et al. 1976). In a period of peak abundance during March 1986 of our study, a density estimate based on the mean number of crabs per trawl tow, uncorrected for efficiency, was approximately 0.03 m^{-2}. Using our J-S estimate of 0.2 crabs m^{-2} as the basis for comparison, the catch efficiency of our trawl net for blue crabs ≥ 35 mm would be approximately 15 %. Since the actual density in the area covered by the trawl may have been greater than 0.2 m^{-2}, our trawl sampling efficiency appeared to be less than 15 %.

In Chesapeake Bay, Hines et al. (1987) used a 22 % trawl efficiency estimate and reported similar densities to our study (< 1 blue crab m^{-2}), whereas Miller et al. (1975) reported peak density estimates approaching

4 crabs m⁻². However, the latter study did not state how densities were derived from trawl samples. Using seining techniques in a shallow North Carolina marsh creek, Weinstein (1979) reported maximum densities of ca $0.2 \, m^{-2}$ in November/December of one year, similar to the maximum that we estimated here. Other density estimates for blue crabs used various forms of drop nets or cylinders (Zimmerman & Minello 1984, Orth & van Montfrans 1987, Mense & Wenner 1989, Wilson et al. 1990) which appeared to target juveniles smaller than found in our study, and thus could not be suitably compared.

While density and changes in density are fundamental parameters of population analysis, also important in an open system are concurrent inputs and losses which are not indicated by net changes in population abundance. The J-S mark-recapture model is one of the few statistical methods that can estimate such dynamics without explicit observations of individuals immigrating, emigrating, and dying. Although net losses were quantified using both the relative abundance index and the J-S analysis, the latter analysis indicated that significant losses also occurred during some periods when the population size increased or remained relatively unchanged. Such dynamics were particularly apparent in the spring and early summer periods before the population structure was dominated by the largest crabs. While a proportion of the losses was due to death, mortality on the order of 40 % or more of the population in 2 to 4 wk appears high, particularly considering the fluctuations in the losses. The loss probability during the intersample period in mid-April 1986 was 0.04 ± 0.01 in 2 wk. If this lower value is taken to be an approximate mortality rate of the juveniles during the springtime period, much of the loss from the population during such periods appears to be due to emigration from the study area.

Quantifying such dynamics has been difficult to achieve for motile estuarine organisms. Weinstein (1983) provided some estimates of fish (*Leiostomus xanthurus*) losses from a Virginia salt marsh, but was hindered by very low recapture rates and a model which could not explicitly account for dilution of tagged fish by immigration of untagged fish to the system. More recently, van Montfrans et al. (1991) used similar methodology in a study of blue crabs in an intertidal salt marsh creek in Chesapeake Bay, but employed a slightly different model that attempted to circumvent the problem of immigration. While their model was an improvement over that of Weinstein (1983), some assumptions associated with their model necessarily restrict the conclusions. In that single-release model, immigration and emigration were assumed to be constant during the 2 mo study, which the present study indicates may not necessarily hold at all

times. Moreover, samples taken 2, 4, and 8 d after release were used in the analysis by van Montfrans et al. (1991), but it was unclear whether the tagged crabs were mixed randomly in the population within that relatively brief period (and would thus be biased towards capture of tagged crabs). If the assumption of homogeneous capture probability was not met, part of the observed decrease in numbers of recaptures with time would have been a sampling artifact. Efficiency of the capture system was also a necessary statistic for their model. This was directly measured at the end of the study, and a linear regression of tag decay was used to extrapolate an efficiency estimate at the beginning of the study (and then was used again to estimate loss of crabs from the population). The different efficiency estimates (13.8 vs 40.4 %) were assumed to represent a linear increase in catch efficiency with time, but without explanation as to a possible mechanism. Assuming constantly increasing catch efficiency, they concluded that the population decreased (by half) after 1 mo and then increased back to the original size. However, the population size estimate increases more or less continuously if a constant 40 % capture efficiency is assumed [pop. size = (11.9505 × day) + 561.172, $r^2 = 0.86$]. Nevertheless, their 65 d tag decay data indicated that about 5 % (4.5 % assuming constant 40 % efficiency, 5.7 % assuming varying efficiency) of the population was lost from the local area each day. Although difficult to directly compare because of the intertidal vs subtidal habitats, we found loss rates of similar magnitude in this study.

Observations of net changes in abundance have been appropriate for many objectives in population study of marine animals, including analyzing an impact of a predator on community trophic dynamics. However, the ultimate fate of local production is partly determined by the movements of macrofaunal species from the local system after their assimilation of biomass and growth within the area. Upon emigrating, the distance that the crabs traveled is not known, but the movement from the study area appears to have been permanent as discussed above. Whereas a specific, possibly unchanging number of crabs consumed resources and grew during residency within a local habitat, emigration that was concurrent with influx of new individuals represented a higher rate of gross loss than was evident purely from relative changes in population size. In a study of intertidal marsh utilization, individual blue crabs foraged within and returned to a specific Georgia intertidal marsh over a period of ca 2 wk or less (Fitz & Wiegert 1991b). A similar intertidal study (van Montfrans et al. 1991) also indicated residency of less than 2 wk within a Chesapeake Bay intertidal creek system. Results of these studies indicate that blue crabs have a relatively short residency

within a local habitat, and their effect as a vector of carbon export appears to be greater than would be evident if the turnover of the local population was not considered.

IMPLICATIONS

The residency of motile macrofauna within a local estuarine habitat has been difficult to discern due to the confounding effect of migrations to and from a population. These dynamics associated with concurrent recruitment and loss likely operate in local populations of other macrofaunal species which are motile and which have indistinct cohorts. Thus, tagging and mark-recapture techniques are tools that should be considered when attempting to infer growth within or movements from such a population.

A tagging study such as this is costly in terms of time involved to tag an adequate number of organisms so that recapture probabilities are large enough for usefully precise and unbiased estimates. Moreover, if the duration of the intersample period is excessively long and the organism's residency short, the recaptures will be few and estimates poor. Related to this is the spatial scale over which the organisms can be effectively sampled. If the release area has few boundaries and the organisms can rapidly disperse in numerous directions within that unbounded region, it may be difficult to adequately recapture sufficient numbers to provide useful precision. We chose the upper reaches of the Duplin River in this study as an area that provided several boundaries that tended to hinder widespread dispersal, except to and from the downriver direction. We found that the local blue crab abundance varied such that the J-S model fit the data very poorly during a year of reduced abundance, yet the analysis provided useful estimates during 2 other seasons.

Promising for future research is the availability of individually coded microwire tags, with which growth of individuals can be measured. Thus, it would be possible to estimate the probability of loss from the population during a period, in addition to growth while in the local habit. Quantitative information on both residency and *in situ* growth would a significant advance in population studies of such species within the broader context of community or ecosystem dynamics.

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Appendix 1. *Callinectes sapidus*. Matrix of capture and recapture data during each sampling period i for the J-S analysis of the total population, also providing calculations of the probability of capture. Date: midpoint of each sampling period i; s_i: no. of crabs that were tagged and released during i; n_i: no. of crabs captured during i; m_i: no. of n_i that were recaptures from any previous release; z_i: no. of s_i that were recaptured after i, but not captured at i; r_i: no. of crabs captured and tagged before i, not captured at i, but recaptured after i; P_i: estimate of the probability of capture during i. (*) Failure of the model in calculating P_i from the available data

Date	i	s_i	n_i	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	m_i	z_i	P_i
3 Apr '85	1	780	877	28																																		28	14	0.079
17 Apr '85	2	880	952	10	16																																	26	25	0.036
15 May '85	3	503	545	1	16	11																															28	14	0.039
18 Jun '85	4	782	864	1	1	3	10																														15	14	0.062
17 Jul '85	5	517	561	1	2	3	3	23																													32	13	0.066
31 Jul '85	6	417	477	0	1	0	1	5	4																											11	13	0.032
28 Aug '85	7	410	436	1	1	0	0	1	6	11																										20	8	0.036
13 Sep '85	8	464	494	1	1	0	0	1	4	0	1																									8	6	0.090
9 Oct '85	9	213	228	0	0	0	0	0	1	0	2	7																								10	11	0.082
24 Oct '85	10	304	317	0	0	0	0	0	0	0	3	4	9																							16	24	0.044
7 Nov '85	11	718	775	0	0	0	0	0	0	0	0	2	6	14																						22	51	0.030
21 Nov '85	12	563	611	0	0	0	0	0	0	0	0	1	8	12	18																					39	51	0.054
11 Dec '85	13	830	922	0	0	0	0	0	0	0	0	0	0	9	6	21																				37	75	0.065
12 Mar '86	14	1056	1227	0	0	0	0	0	0	0	0	0	1	1	3	13	68																			90	132	0.095
26 Mar '86	15	917	1161	0	0	0	0	0	0	0	0	0	1	4	3	10	31	53																		101	171	0.076
9 Apr '86	16	700	899	0	0	0	0	0	0	0	0	0	0	1	3	3	6	38	46																	116	152	0.063
24 Apr '86	17	701	888	0	0	0	0	0	0	0	0	0	1	2	1	1	6	18	21	30																99	114	0.066
21 May '86	18	835	1054	0	0	0	0	0	0	0	0	0	1	1	5	2	6	24	21	9	38															95	86	0.058
4 Jun '86	19	623	799	0	0	0	0	0	0	0	0	0	1	1	1	1	2	7	9	15	21	30														91	29	0.144
18 Jun '86	20	965	1170	0	0	0	0	0	0	0	0	0	0	2	1	3	4	9	12	3	1	1	25													35	45	0.071
16 Jul '86	21	630	728	0	0	0	0	0	0	0	0	0	0	2	0	0	2	3	2	1	1	3	15	34												63	43	0.081
31 Jul '86	22	547	646	0	0	0	0	0	0	0	0	0	0	0	1	0	3	3	1	0	4	0	3	18	22											51	24	0.116
20 Aug '86	23	419	531	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	0	0	8	7	16										33	16	0.074
17 Sep '86	24	439	519	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	3	6	6	2	12									24	8	0.054
15 Oct '86	25	264	290	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	6	2	4								9	3	0.111
12 Nov '86	26	143	160	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2						3	5	0.032
17 Dec '86	27	197	211	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	4					6	9	0.046
28 Jan '87	28	167	183	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5				7	13	0.013
25 Feb '87	29	126	136	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	1			6	9	0.033
25 Mar '87	30	98	106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	2		8	5	0.038
29 Apr '87	31	200	219	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2		3	6	0.007
28 May '87	32	270	294	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	5	8	1	0.079
24 Jun '87	33	371	406	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	0	4	0	*
22 Jul '87	34	233	252	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	3	0	
24 Aug '87	35	264	282	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	3
r_i				42	37	17	15	31	11	15	6	15	29	49	39	61	147	140	97	61	67	34	51	61	32	25	16	4	5	10	11	2	4	4	3	3	3			

Sampling period i of release of recaptured crabs

Appendix 2. *Callinectes sapidus.* Matrix of capture and recapture data during each sampling period i for the J-S analysis of the subpopulation of juveniles ≤ 80 mm, also providing calculations of the probability of capture. Date: midpoint of each sampling period i; s_i: no. of crabs that were tagged and released during i; n_i: no. of crabs captured during i; m_i: no. of n_i that were recaptures from any previous release; z_i: no. of crabs captured and tagged before i, not captured at i, but recaptured after i; r_i: no. of s_i that were recaptured after i; and P_i: estimate of the probability of capture during i. (·) Failure of the model in calculating P_i from the available data

Date	i	s_i	n_i	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	m_i	z_i	P_i
3 Apr '85	1	578	642	21																																			21	8	0.068
17 Apr '85	2	683	740	6	11																																		17	9	0.055
15 May '85	3	321	352	1	7	8																																	16	2	0.102
18 Jun '85	4	420	466	1	0	0	4																																5	2	0.091
17 Jul '85	5	250	275	0	0	1	1	9																															11	0	·
31 Jul '85	6	127	155	0	0	0	0	0	2																														2	1	0.157
28 Aug '85	7	42	47	0	0	0	0	0	1	2																													3	0	0.077
13 Sep '85	8	35	39	0	0	0	0	0	0	1	0																											1	0	·
9 Oct '85	9	59	63	0	0	0	0	0	0	0	0	2																											2	3	0.057
24 Oct '85	10	142	147	0	0	0	0	0	0	0	0	1	4																										5	10	0.026
7 Nov '85	11	590	638	0	0	0	0	0	0	0	0	1	1	10																									12	29	0.025
21 Nov '85	12	467	508	0	0	0	0	0	0	0	0	0	5	8	15																								28	29	0.052
12 Dec '85	13	652	719	0	0	0	0	0	0	0	0	0	1	5	8	16																							30	35	0.066
12 Mar '86	14	880	1021	0	0	0	0	0	0	0	0	0	0	3	5	11	49																						68	39	0.159
26 Mar '86	15	653	820	0	0	0	0	0	0	0	0	0	0	2	0	6	15	37																					60	49	0.111
9 Apr '86	16	450	575	0	0	0	0	0	0	0	0	0	0	3	0	3	6	25	30																				69	25	0.144
24 Apr '86	17	378	484	0	0	0	0	0	0	0	0	0	0	0	0	0	2	8	11	16																			37	10	0.212
21 May '86	18	287	374	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	6	17																		27	3	0.270
4 Jun '86	19	243	302	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	9																	12	0	·
18 Jun '86	20	309	359	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9																	9	2	0.266
16 Jul '86	21	235	267	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	13																15	5	0.240
31 Jul '86	22	151	184	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	15														20	0	·
20 Aug '86	23	117	156	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3													3	0	·
17 Sep '86	24	7	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0												0	0	·
15 Oct '86	25	3	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0											0	0	·
12 Nov '86	26	43	54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1									1	1	0.037
17 Dec '86	27	156	168	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0								1	5	0.012
28 Jan '87	28	150	158	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5								7	6	0.031
25 Feb '87	29	110	120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	1							5	3	0.022
25 Mar '87	30	73	79	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0						3	0	·
29 Apr '87	31	120	126	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					0	0	·
28 May '87	32	130	132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				0	0	·
24 Jun '87	33	136	144	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1			1	0	·
22 Jul '87	34	77	82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	·
24 Aug '87	35	88	94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	·
r_i				29	18	9	5	9	3	3	0	5	12	31	28	36	72	70	45	22	20	9	11	18	15	3	0	0	2	5	8	2	0	3	0	1	0			

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