A combined telemetry – tag return approach to estimate fishing and natural mortality rates of an estuarine fish

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Abstract: A joint analysis of tag return and telemetry data should improve estimates of mortality rates for exploited fishes; however, the combined approach has thus far only been tested in terrestrial systems. We tagged subadult red drum *Sciaenops ocellatus* with conventional tags and ultrasonic transmitters over three years in coastal North Carolina, USA, to test the efficacy of the combined telemetry – tag return approach. There was a strong seasonal pattern to monthly fishing mortality rate (*F*) estimates from both conventional and telemetry tags; highest *F* occurred in fall months and lowest levels occurred during winter. Although monthly *F*s were similar in pattern and magnitude between conventional tagging and telemetry, information on the estimate of *F* came primarily from conventional tagging. The natural mortality rate (*M*) in the combined model was low (estimated annual rate ± SE: 0.04 ± 0.04) and was based primarily upon the telemetry approach. Using high-reward tagging, we estimated significantly different tag reporting rates for state agency and university tagging programs. The combined tag return – telemetry approach can be an effective approach for estimating *F* and *M* as long as several key assumptions of the model are met.

Keywords: *Sciaenops ocellatus*, survival, mark-recapture, tagging, tag reporting rate

Introduction

Obtaining accurate estimates of the fishing and natural mortality rates experienced by fish stocks is a central goal of fisheries stock assessment. Regulation of the fishing mortality rate (*F*) is commonly used to generate sustainable harvest levels of fish stocks with recreational or commercial importance (Hilborn and Walters 1992). Overestimates of *F* would result in lost harvest, while underestimates can result in unsustainable exploitation rates.

Natural mortality rate (*M*) is important because it helps to determine the productivity of a population. Whereas estimates of *F* are typically produced internally in stock assessment models, *M* is often estimated externally and included in models as a fixed parameter (Vetter 1988). Changes in *M* (e.g., 0.05 – 0.20) have been shown to result in very different harvest recommendations (Zheng et al. 1997; Clark 1999; Williams 2002). It is difficult to estimate *M* because natural deaths are rarely observed (Quinn and Deriso 1999). Moreover, it is hard to separate the effects of *M*, *F*, and recruitment on the population dynamics of fish stocks (Hilborn and Walters 1992; Quinn and Deriso 1999). Given the difficulty of estimating *M*, methods that use life history parameters are often used to develop predictive regression relationships with *M* (Vetter 1988). These methods usually require minimal data; however, the precision of these estimates is unknown (Vetter 1988; Pascual and Iribarne 1993) and *M* is often required to be constant among ages, seasons, or years (Hightower et al. 2001).

The unknown accuracy of life history methods and other techniques to estimate *M*, combined with the need for improved estimates of *F*, have prompted recent developments using tag-return methods to estimate mortality rates of fish stocks (Hoenig et al. 1998*a*, 1998*b*; Latour et al. 2001). Tag-return models can be considered special extensions of capture-recapture models (Seber 1982), except that tagged fish are harvested and tags are returned by the fishery

(Brownie et al. 1985; Pine et al. 2003). Rates of *F* and *M* can be determined using tag-return models if the tag reporting rate (λ) can be reliably estimated with a high-reward tagging study or other methods (Pollock et al. 1991, 2001, 2002).

An alternative approach used to separately estimate *F* and *M* for fish populations that has received recent attention is telemetry. Telemetry methods have been used by wildlife researchers to estimate the survival rates of terrestrial animals (White and Garrott 1990; Pollock et al. 1995), but only recently have these methods been applied to aquatic organisms (Hightower et al. 2001; Heupel and Simpfendorfer 2002; Waters et al. 2005). Pollock et al. (1995) developed a method to estimate survival of telemetered animals when the probability of relocation is less than one, and Hightower et al. (2001) extended this approach to estimate *F* and *M* for fish populations in an aquatic setting. The general methodology is to release a sample of telemetered animals, then locate each individual at fixed time periods until the animal has died, emigrated from the study area, has been harvested, or until the transmitter battery fails. Natural mortalities are inferred from transmitters that stop moving over successive relocation periods, and fishing mortalities are inferred from the disappearance of transmitters from the study system.

A novel approach for estimating *F* and *M* is to combine the use of tag-return and telemetry data in joint analyses. Combined analyses were first developed for terrestrial animals to estimate total mortality (Catchpole et al. 1998; Powell et al. 2000; Nasution et al. 2001), but recent simulations have shown that combining the two techniques may be useful in aquatic systems as well (Pollock et al. 2004). In theory, the combined tag-return and telemetry approach improves estimates of *F* and *M* compared to either method independently by drawing on the strengths of each (Pollock et al. 2004). Specifically, telemetry methods provide direct information about natural mortalities from transmitters that stop moving, while tag-return methods provide direct information about fishery harvests from returned tags (Pollock et al. 2004). Another benefit of combining two independent methods to estimate mortality rates is that if the separate estimates do not agree, the two (independent) methods might help to identify the possible assumption violations that are causing the disparity.

This field test of the combined telemetry and tag return approach used red drum (*Sciaenops ocellatus*) as a model species. Aspects of the biology and management of subadult red drum (i.e., ages 1 to 3) make this species and size class amenable to a combined tag-return and telemetry approach. First, subadult red drum are thought to have particularly strong site fidelity (Collins et al. 2002; Dresser and Kneib 2007), allowing for a long-term analysis of telemetered fish in an estuary. Second, subadult red drum in North Carolina are exploited by both commercial and recreational fishers within a slot limit, but estimated *F*s come from tag-return studies (Ross et al. 1995; Bacheler et al. 2008) and uncertain assessment results (Takade and Paramore 2007). Last, estimates of *M* of subadult red drum in the most recent stock assessment come from a life history method (Boudreau and Dickie 1989) that has unknown accuracy and precision.

Here, we provide the first field test of a combined tag return – telemetry approach for a fish species. Estimates of *F* and *M* from the combined model were compared to the estimates from the tag return and telemetry models separately to assess potential improvements in precision when combining the independent approaches. Results of our study document the ways tag return and telemetry data can be combined to inform the interpretations of the two independent approaches and increase the precision of mortality rate estimates.

Materials and methods

Four sources of data were used in this study: (1) low-reward external tags released by North Carolina State University (NCSU), (2) low-reward external tags released by North Carolina Division of Marine Fisheries (NCDMF), (3) high-reward external tags released by NCSU, and (4) ultrasonic telemetry tagging by NCSU. Methods for each data source are described below.

Tag return approach

NCSU low-reward tagging

Fig.1

Tagging was performed by NCSU within the Neuse River Estuary (NRE), the major southern tributary of North Carolina's Pamlico Sound (Fig.1). The NRE is a shallow, mesohaline estuary with a watershed of 16,000 km^2. The NRE is relatively large in size, with a length of over 70 km and an average width of 6.5 km (Buzzelli et al. 2001).

Table 1

In the winter and spring of 2005 – 2007, approximately 400 red drum (300 – 500 mm total length, TL) were externally tagged each year in the NRE (Table 1). Most red drum were captured using the "strike net" method, whereby a 200-m gill net with 102-mm stretch mesh was set in an arc along the shoreline. A 7.2-m research vessel was then driven between the net and shoreline, scaring fish into the net. The net was then immediately retrieved, and when red drum were captured, the monofilament netting was cut in order to prevent injury to the fish. In the rare case where a red drum was injured, it was released without a tag. Electrofishing was also used periodically to catch red drum for tagging. Healthy fish were placed in 140-L aerated round tanks on board until all fish were ready for tagging. Fish were then removed from tanks and measured (TL; mm).

Fish were tagged with wire core internal anchor tags (Floy® FM-95W)[1]. Internal anchor tags were yellow in color and stated "REWARD FOR TAG," and were additionally labeled with a tag number, a toll-free phone number, and "NCSU." A t-shirt, hat, or US$5 check was given to fishers reporting low-reward tags. During the telephone interview, fishers were asked for the tag number, location and date of capture, whether they were a commercial or recreational fisher, fate of the fish and tag (i.e., whether the fish was kept or released and whether the tag was cut off or left on if released), and length of fish.

We used a six month age-length key to convert total length of fish at tagging to an estimated age based on a January 1 birthday. The age-length key was based on 17 years of North Carolina red drum ageing data (Ross et al. 1995). A six month age-length key (January - June and July - December) was used because of rapid summer growth rates that subadult red drum experience in North Carolina (Ross et al. 1995). The six month age-length key reliably separates the age-2 red drum used in this study from other age classes.

NCDMF low-reward tagging

The NCDMF tagged between 356 and 1,555 age-2 red drum annually in 2005 – 2007 (Table 1). Tagging was done year-round at sites throughout North Carolina but concentrated in the eastern and western Pamlico Sound. Fish were collected primarily using electrofishing and strike netting, and fish were tagged with Floy® FM-95W internal anchor tags. All tags were labeled with "NCDMF," a unique tag number, "REWARD" message, a mailing address to send the tag, and a toll-free phone number. The NCDMF tags were blue or yellow in color. The

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[1] The use of trade, product, industry or firm names or products or software or models, whether commercially available or not, is for informative purposes only and does not constitute an endorsement by the U.S. Government or the U.S. Geological Survey.

NCDMF asked each fisher about the fate of the fish and tag, gear used, total length, and date and location of capture. A hat or US$5 check was given to fishers returning NCDMF tags.

NCSU high-reward tagging and reporting rate estimation

In order to partition total mortality (Z) into F and M, we estimated λ using high-reward tagging (Hoenig et al. 1998*a*, 1998*b*; Pollock et al. 2001). High reward tags were red in color and stated "$100 REWARD FOR TAG," in addition to all other information provided on NCSU low-reward tags. Approximately 75 red drum were tagged each March (2005 – 2007) with high-reward tags, and high-reward tagging occurred simultaneously with low-reward tagging by NCSU in the Neuse River (i.e., for every six fish tagged and released with NCSU low reward tags, one was released with an NCSU high-reward tag). In early April of 2006, an additional 150 NCSU high-reward tags were released simultaneously with 850 low-reward NCDMF tags in eastern Pamlico Sound. Laminated advertisements describing the high reward study were placed in local tackle shops, boat ramps, and fish houses, and advertisements were posted at many popular fishing websites in North Carolina. Tag reporting rates were estimated separately for NCSU and NCDMF low-reward tags.

Mortality rate estimation using tag-return data

We estimated monthly F and M, as well as λ for NCSU and NCDMF tags separately, using a modified instantaneous rates formulation of the Brownie tag return model similar to Jiang et al. (2007) and Bacheler et al. (2008). The NCSU tagging was assumed to occur at the beginning of April each year, while NCDMF tagging was assumed to occur at the beginning of each month throughout the year. Harvest was assumed to occur continuously throughout the year. Since the slot limit is centered directly on age-2 red drum, maximum selectivity occurs on this age class (Bacheler et al. 2008). Recoveries were only used for age-2 fish; once a fish turned age 3, it was censored due to the low sample size of age-3 fish in our study. Thus, F and M only apply to age-2 red drum in our study.

Jiang et al.'s (2007) tag return model accounts for fish either being harvested or caught and released by separating the "death" of a tag from the death of a fish. We treated tags reported from fish caught and released with tag intact as though tags were cut off; the few subsequent captures of those fish were ignored (see Bacheler et al. 2008). By treating released fish the same whether or not their tags were left intact upon release, we were able to account for catch and release mortality more accurately than if these recoveries were ignored. The expected number of low-reward tags returned, R, from fish tagged at age 2 and released in month i, and harvested in month j, is:

(1) $$E[R_{ij}] = N_i\, P_{ij},$$

where

(2) $$P_{ij} = \begin{cases} \left(\prod_{v=i}^{j-1} S_v\right)(1-S_j)\dfrac{F_j}{F'_j + F_j + M}\lambda_x & (when\ j > i) \\ (1-S_j)\dfrac{F_j}{F'_j + F_j + M}\lambda_x & (when\ j = i) \end{cases}$$

in which $S_{ij} = \exp\left[-\left(F_j + F'_j\right) - M\right]$. Here, R_{ij} is tag returns due to harvest, N_i is the number of fish tagged in month i, P is the probability of recovery, S is the monthly survival rate, F'_j represents the instantaneous fishing mortality rate for tags of fish caught and released in month j, and λ_x is the tag reporting rate (i.e., lambda), with subscript x referring to the source of tags (i.e., NCSU or NCDMF tags). The expected number of low-reward tag returns from fish tagged and released in month i, then caught and released in month j, is:

(3) $E[R'_{ij}] = N_i P'_{ij}$,

where

(4) $$P_{ij}' = \begin{cases} \left(\prod_{v=i}^{j-1} S_v\right)(1-S_j)\dfrac{F'_j}{F'_j+F_j+M}\lambda_x & (when\ j>i) \\ (1-S_j)\dfrac{F'_j}{F'_j+F_j+M}\lambda_x. & (when\ j=i) \end{cases}$$

The same equations above were used for the expected number of high-reward tag returns, except that λ was removed because we assumed 100% reporting of high-reward tags. This method also assumes that reporting rate was equal for harvested and released fish. It is unlikely that fishers would not detect tags on harvested fish. There is a chance that some tags may not have been detected if, for instance, a red drum was caught and released at night by fishers without lights. If a fish is caught and released without the angler noticing (and clipping) the tag, then for practical purposes the fish was not seen and no death of fish or tag is assumed. This situation would only cause a problem when trying to account for mortality associated with catch-and-release, which is low in our study (see below).

Following Jiang et al. (2007), the tag returns due to harvest (R_{ij}) and catch-and-release (R_{ij}') from N_i tagged fish follow a multinomial distribution. The likelihood function then is:

(5)
$$L = \prod_{i=1}^{I} \binom{N_i}{R_{ii}, R_{ii+1}, \ldots R_{iJ}, R_{ii}', R_{ii+1}', \ldots R_{iJ}', N_i - \sum_{j=i}^{J} (R_{ij} + R_{ij}')} \times \left(\prod_{j=i}^{J} P_{ij}^{R_{ij}} P_{ij}'^{R_{ij}'} \right) \left(1 - \sum_{v=i}^{J} (P_{iv} + P_{iv}') \right)^{N_i - \sum_{v=i}^{J} (R_{iv} + R_{iv}')} .$$

Maximum likelihood estimates of the model parameters were obtained using program SURVIV (White 1983), which permits coding of the multinomial cell probabilities P_{ij}.

To account for catch-and-release mortality, we adjusted F upward using a previously estimated catch-and-release mortality (δ) for red drum (10%; Jordan 1990) and F' using the following equation (Jiang et al. 2007):

(6)
$$\hat{F}_{j,adjusted} = \hat{F}_j + \delta \hat{F}_j' .$$

Our full tag return model was then compared to various reduced models using the Akaike information criteria (see below).

Assumptions of the tag-return approach:

(1) *The tagged sample is representative of the target population or the tagged animals are mixed thoroughly with the untagged ones.*

Based on telemetry and recapture locations, movement rates of red drum appeared to be high enough that tagged fish mixed well with untagged fish. Also, only 57 out of 409 fishers (14%) reported more than one tag, and the majority of these fishers catching multiple tagged fish caught them on separate fishing trips. We constructed models allowing for non-mixing (Hoenig et al. 1998*b*) for time periods of 1 and 3 months, and estimates of *F* and *M* were nearly identical to the model assuming mixing; AIC selected our original model over either non-mixing model, so non-mixing model results are not reported.

(2) *There is no tag loss, or the rate is reliably known and can be adjusted for.*

Based on a double-tagging study and holding tank experiments with subadult red drum, chronic tag loss of internal anchor tags was minimal (6 of 272 fish [2.2%] lost an internal anchor tag over 14 months; Latour et al. 2001). Therefore, no adjustment was made for tag loss.

(3) *Survival rates are not affected by tagging.*

Tag-induced mortality was not observed for age-2 red drum based on a holding tank study at various water temperatures (Latour et al. 2001).

(4) *The fate of each tagged fish is independent of the fate of other tagged fish.*

This assumption may be violated because subadult red drum are thought to aggregate, but the extent of aggregation is not known. Violations of this assumption make the precision appear lower than it really is, but violations do not cause bias (Pollock et al. 2004).

(5) *The month of tag recovery is correctly tabulated.*

We assumed that fishers correctly tabulated the date of tag recovery.

(6) *All tagged fish, within an identifiable class, have the same survival and recovery probabilities.*

As fish were tagged over a narrow size range, we assumed all red drum had the same survival and recovery probabilities.

Ultrasonic telemetry methodology

Study sites for telemetry

Telemetry occurred in five tributaries along the southern shoreline of the NRE: Slocum Creek, Hancock Creek, Clubfoot Creek, Adams Creek, and South River (Fig. 1). These are long and narrow embayments with average depths of 1 – 3 m. Each tributary has a narrow mouth that can be monitored with an acoustic receiver array to determine timing of emigration by telemetered red drum out of the study site (see below). These tributaries were chosen instead of tributaries on the northern shoreline of the NRE because of accessibility. Since tidal influence in each system is minimal, all habitats were accessible by boat at all times making telemetry feasible. Slocum and Hancock Creeks are designated as nursery areas, and are thus closed to commercial fishing but are open to recreational harvest (1 $\text{fish}\cdot\text{d}^{-1}$ bag limit). The other three tributaries are open to both commercial (7 $\text{fish}\cdot\text{d}^{-1}$ bag limit) and recreational fishing.

Transmitter implantation

In total, 180 age-2 red drum were implanted with transmitters in various tributaries of the NRE in 2005 – 2007 (Table 1). Surgical procedures can be found in Bacheler (2008). Fish were surgically implanted with ultrasonic transmitters (VEMCO, Ltd., Nova Scotia, Canada; V16 4H, 10 g in water; 10 mm wide; 65 mm long), and were released once swimming behavior returned to normal (approximately 10 min). The transmitters operated on a frequency of 69 kHz, and were programmed to be active for a period of 641 d. External tags were not placed on telemetered fish so that a fisher's decision to retain or release a captured red drum was not influenced by the external tag (Hightower et al 2001).

Telemetry relocations

Telemetered red drum were manually relocated monthly to determine location using a VEMCO VR100 receiver and hydrophone. The research vessel was stopped approximately every 150 m along the shoreline of each creek to listen for telemetered red drum, resulting in 30 – 80 listening locations in each creek. Upon relocation of a telemetered fish, the latitude and longitude coordinates were recorded. The first two weeks of data after surgery were censored for all fish to account for post-surgery deaths that may otherwise appear as natural mortalities.

Submersible VR2 VEMCO receivers were used at the mouths of each tributary to document emigration events, since unaccounted-for emigration from the tributaries would bias estimates of F. For example, a fish that swam undetected out of the study estuary would be incorrectly considered a fishery removal. Previous studies have found relatively high site fidelity for subadult red drum (Collins et al. 2002; Dresser and Kneib 2007), but there has tended to be an increased probability of emigration from estuaries with increasing size (Daniel 1998). In preliminary work, VR2 receivers detected nearly 100% of pulses from V16 tags at 400 m in our study systems. Therefore, submersible receivers were placed a conservative distance of 600 m apart from one another and within 250 m of shoreline. If a fish emigrated from a tributary, it was censored from the mortality analyses. Approximately 300,000 detections can be stored in a single VR2 receiver, so data were downloaded every 1 – 5 mo to avoid filling the memory. Telemetered fish missed by manual relocation during a monthly search were recorded as present in that month if they were detected by a submersible receiver.

Another potential form of bias was if a predator consumed a telemetered red drum and subsequently emigrated from the estuary. Heupel and Simpfendorfer (2002) were able to determine likely predation events upon two telemetered blacktip sharks in Florida by unusual movement patterns of transmitters through an array of stationary receivers. In our study, average swimming speeds were calculated for pods of bottlenose dolphins *Tursiops truncatus* observed opportunistically in our study systems, because subadult red drum composed a small proportion of bottlenose dolphin diets in North Carolina (Gannon 2003). The exact locations of telemetered red drum was not known, so we used the continuous transmitter pings to assign fish to a given submersible receiver location. Swimming speed was then calculated for each telemetered red drum as the total time the fish was detected continuously within a receiver array, divided by the distance between the first and last lines of receivers. Bottlenose dolphin swimming speeds were compared to the speed at which transmitters exited our study systems. If no overlap was observed, it would suggest that bias from emigrating predators having a telemetered red drum in its stomach was negligible.

Transmitter retention and post-surgical survival experiments

A laboratory study was initiated in 2004 to estimate transmitter retention and post-surgical survival. Six fish (*n*=6) were captured using hook-and-line (only jaw-hooked fish were retained) and one was captured using a 30 m beach seine. All fish were transported back to the laboratory in plastic tubs filled with 100 L of aerated water. Each fish was released into a separate flow-through holding tank (1.2 m diameter, 1 m deep, filled with 0.7 m deep water) with a continuous air supply. Approximately 38 L of water flowed into (and out of) each tank per hour. Water temperature (°C), salinity (psu), and dissolved oxygen ($mg \cdot L^{-1}$) were recorded each day. Fish were fed daily to satiation with a variety of frozen fish and invertebrates. Seven fish were implanted on November 18, 2004, with “dummy” V16 transmitters of the exact size and shape as used in the field study, using the same surgical procedure as described above. Due to the death of one fish on November 28, 2004, from jumping out of the tank, an additional subadult red drum was caught by hook-and-line on November 30 to replace the dead fish; this fish was surgically implanted on December 14, 2004. Fish were checked daily for loss of transmitter or death, and in the instance where deaths did occur, necropsies were performed by doctors of veterinary medicine to identify the cause of death.

Mortality rate estimation using telemetry

Telemetry data were interpreted according to the criteria described in Hightower et al. (2001). A fish was assumed to be alive if it moved between searches and was dead from natural mortality if a fish was located in the same location after repeated searches. As red drum were fairly mobile in our study, dead fish were obvious within a few monthly relocation periods and mortality was applied to the period immediately preceding the relocation of the fish when first found at that location. If a fish was not located after repeated searches and was not detected by submersible receivers as having emigrated, it was assumed that the fish was harvested. Our estimates of M may be positively biased if hook-and-release or discard mortality was occurring. Transmitter failure would appear as a fishery removal, positively biasing F, but the likelihood was small given that transmitters from all dead fish in the systems ($n = 4$) and returned transmitters ($n = 7$) remained audible through the end of their suggested battery life. Osprey *Pandion haliaetus* predation could also appear as a fishery harvest, but the sizes of telemetered red drum in this study are beyond the upper limit of previously observed fish prey sizes for osprey (Carss and Godfrey 1996), so avian predation on age-2 red drum is unlikely. Furthermore, most surgeries occurred during winter months when osprey were not present in the NRE.

Monthly F and M values were estimated from telemetry data using the Pollock et al. (1995) general capture-recapture model, with the modification of Hightower et al. (2001).

Relocations of dead fish were used as a direct estimate of M, while F was estimated indirectly from the disappearance of telemetered fish over successive months. Relocation probabilities were estimated for each relocation period based on the number of fish missed during one relocation period but found during a later period.

Parameter estimation during each relocation period was based on the expected probabilities of each of the above outcomes for all fish released at time i (Hightower et al. 2001). All fish relocated at time $i - 1$, as well as all newly tagged fish, become part of the new "virtual" release R_i at time i. Following Hightower et al. (2001), the expected number of fish in release R_i that are first relocated at time $i + 1$ was determined as the product of the number released (R_i), the survival rate from time i to $i + 1$ ($S_i = \exp[- F_i - M_i]$), and the probability of relocating an individual during search $i + 1$ (p_{i+1}):

$$(7) \qquad R_i \times \exp(-F_i - M_i) \times p_{i+1}$$

where F_i is the instantaneous rate of fishing mortality and M_i is the instantaneous rate of natural mortality at time i. The expected number of fish first relocated at time $i + 2$ following release R_i would then be

$$(8) \qquad R_i \times \exp(-F_i - M_i) \times (1 - p_{i+1}) \times \exp(-F_{i+1} - M_{i+1}) \times p_{i+2}$$

where $(1 - p_{i+1})$ is the probability of a tagged fish not being relocated at time $i + 1$. The expected number of natural deaths from release R_i first relocated at time $i + 1$ would be

$$(9) \qquad R_i \times M_i \times \frac{1-\exp(-F_i - M_i)}{(F_i + M_i)} \times p_{i+1}.$$

The expected number of natural deaths from release R_i first relocated at time $i + 2$ would be

$$(10) \qquad R_i \times \exp(-F_i - M_i) \times (1 - p_{i+1}) \times M_{i+1} \times \frac{1-\exp(-F_{i+1} - M_{i+1})}{(F_{i+1} + M_{i+1})} \times p_{i+2.}$$

We used program RELEASE (Burnham et al. 1987) to convert the relocation history into a summary table of relocations for each release. The summary table of relocations (i.e., full-m array) was then used by program SURVIV (White 1983) to estimate model parameters on monthly time intervals. The Akaike information criteria (AIC; Burnham and Anderson 2002) was then used to compare our full model to various reduced models (see below).

Assumptions of telemetry method

(1) *All marked fish present in the study area at time i (whether alive or dead of non-harvest causes) have the same probability (p_i) of being relocated.*

The tributaries were small enough to be searched thoroughly so that live and dead fish should have been found with equally high probability.

(2) *All marked fish alive in the study area at time i have the same survival rate to the next time i+1.*

Because we tagged fish over a relatively narrow size range, we assumed all telemetered fish had similar survival rates.

(3) *The probability of transmitter failure or of a transmitter being shed is negligible.*

Hightower et al. (2001) and Heupel and Simpfendorfer (2002) used VEMCO V16 transmitters and neither study found evidence of premature transmitter failure. In our study, seven transmitters were returned from the fishery and four transmitters from dead fish were relocated monthly, and all functioned for at least the minimum guaranteed battery life. Tag retention was 100% in our holding tank study (see *Results*).

(4) *Marked and unmarked fish have the same survival rates.*

There were no surgery-related deaths in subadult red drum implanted with dummy transmitters in the laboratory holding study (see *Results*).

(5) *All fish behave independently with respect to capture and survival.*

See conventional tag assumption #4.

(6) *Movement patterns can be used to determine whether a tagged fish remains alive or has died due to non-harvest causes (possibly including catch-and-release or discard mortality).*

Movement patterns have commonly been used to identify the fate of individual telemetered fish (Jepsen et al. 2000; Heupel and Simpfendorfer 2002; Waters et al. 2005). Red drum movement rates were high enough that natural mortalities were not difficult to detect after a few monthly relocations. We also found no evidence of bottlenose dolphin predation by comparing swimming speeds of emigrating transmitters to emigrating bottlenose dolphins (see *Results*).

(7) *Natural mortality occurs immediately prior to the first relocation.*

By sampling monthly and maintaining high relocation probabilities, the timing of natural mortalities was assumed to occur in the period previous to when it stopped moving.

(8) *There is no emigration out of the study area, or emigrating fish can be detected and censored from the analysis.*

Emigrating fish were detected with a submersible receiver array and censored from the analysis.

Combined methodology and model selection

The methodology for the combined telemetry-conventional tag-return approach was described in Pollock et al. (2004). Monthly estimates were obtained using maximum likelihood methods, where the overall likelihood function (L) was the product of the likelihood functions for the tag-return (L_{tag}) and telemetry data sets (L_{tel}) because the two sets of data are independent:

$$(11) \qquad L = L_{tag} \times L_{tel}.$$

Tag returns and relocations of live and dead telemetered fish were both assumed to follow multinomial distributions.

We used the Akaike information criterion (AIC), corrected for overdispersion and including a second order bias correction (QAIC$_c$), to evaluate the likelihood of our full models (separately for tag return alone, telemetry alone, or combined data) compared to various reduced models (Burnham and Anderson 2002). The QAIC$_c$ method provides a benefit for model fit and a penalty for adding parameters, resulting in models that produce the best trade-off between bias and variance (Burnham and Anderson 2002). The QAIC$_c$ is:

$$(12) \qquad \mathrm{QAIC_c} = -2\log\left[l\left(\underset{-}{\hat{\theta}} \middle| y \right) \right] / \hat{c} + 2K + \frac{2K(K+1)}{n-K-1},$$

where $\log\left[l\left(\hat{\underline{\theta}}\middle|y\right)\right]$ is the log likelihood function evaluated at the MLEs $\hat{\underline{\theta}}$ given the data y, K is the number of parameters, and $\hat{c}$ is a variance inflation factor. The variance inflation factor can be calculated as:

(13) $\hat{c} = \chi^2 / df,$

where χ^2 and df correspond to the value of the Pearson goodness-of-fit test of the most general model in the model set and its degrees of freedom (Burnham and Anderson 2002). The number of parameters of each model was augmented by one to account for the estimation of $\hat{c}$, and we inflated all SEs in this paper by the square root of $\hat{c}$ (conventional tagging = 2.04; telemetry = 1.18; combined = 1.89). Both of these modifications are recommended by Burnham and Anderson (2002). We then computed simple differences (Δ_i) between the best model (QAICc_{min}) and the i^{th} model (QAICc_i) as

(14) $\Delta_i = \text{QAICc}_i - \text{QAICc}_{min}.$

For each approach (tag return alone, telemetry alone, and combined), *F* was allowed to vary in six ways: by month, month and year, quarter, quarter and year, year, or it was held constant. Natural mortality rate and relocation probability were allowed to vary by month, year, or be constant. In addition, parameter estimates were model averaged based on QAIC_c to account for uncertainty in model selection (see Burnham and Anderson 2002 for a full description).

The spatial coverage of the telemetry and tag return components of this study did not completely overlap, since the telemetry component occurred in Neuse River tributaries while the tag return study occurred throughout North Carolina. We tested the assumption of a spatially-explicit F and M by comparing the QAIC$_c$ values of four separate models: (1) a spatially-invariant F and M (i.e., $F_{tel} = F_{tag}$ and $M_{tel} = M_{tag}$), (2) a spatial-invariant F and an M that varied by space ($F_{tel} = F_{tag}$ and $M_{tel} \neq M_{tag}$), (3) an F that varied by space and a spatially-invariant M ($F_{tel} \neq F_{tag}$ and $M_{tel} = M_{tag}$), and (4) an F and M that both varied by space ($F_{tel} \neq F_{tag}$ and $M_{tel} \neq M_{tag}$). In each of these models, an F was estimated that varied by quarter and year and M was held constant.

Results

External tags were applied to 4,776 red drum, with a larger percentage (68%) receiving NCDMF tags (Table 1). Eight percent of external tags released were high-reward tags.

Overall, there were 116 recoveries of NCSU high-reward tags (33% return rate), 299 recoveries of NCSU low-reward tags (26% return rate), and 512 recoveries of NCDMF low-reward tags (16% return rate) within their first year. Both NCSU and NCDMF tags were recovered throughout the estuarine and coastal waters of North Carolina, including the Neuse and Pamlico Rivers, Pamlico Sound, Core Sound, all major northern inlets, and coastal beaches from the northern Outer Banks all the way south to Wilmington (Fig. 2). Fig.2

Eight red drum were surgically implanted with dummy transmitters and held in the laboratory for 9 months. Fish resumed eating within 0 – 2 d after surgery, and surviving fish healed completely and were healthy at the end of the study. Each red drum in the study retained its transmitter. Three fish died over the course of the holding tank study, but none were judged by veterinarians to have died from the surgery process: one died from jumping out of the tank, one died from a fishing hook found in its stomach during necropsy, and one died from a storm-related poor water quality event affecting the entire laboratory.

Ultrasonic transmitters were surgically implanted in 180 age-2 red drum (mean TL ± SE = 457.9 ± 1.9 mm; mean weight = 950.7 ± 11.2 g). All fish were large enough that the transmitter never weighed more than 1.25% in water of the fish's weight out of water, as recommended by Winter (1996). Telemetered fish were only released into Hancock Creek (*n* = 105), South River (*n* = 46), and Slocum Creek (*n* = 30); thus, detections in Clubfoot and Adams creeks would represent fish migrating from their tagging location. The number of red drum present in all tributaries each month (i.e., new releases plus virtual releases of relocated fish) ranged from 0 to 44 (mean = 13.5; Table 1).

Relocations within the first two weeks after tagging were censored to account for surgery-related effects. This resulted in the exclusion of 32 telemetered fish from our model. During the first two weeks, there were 2 apparent surgery deaths and 4 harvests along with 26 confirmed emigrations. Of the remaining 148 telemetered red drum that were included in the model, 19 were harvested, 1 died of natural mortality, 112 emigrated, and 16 were alive until they reached age 3 and were excluded from the study. Harvest was verified in four of nineteen cases of presumed harvest by returned transmitters from fishers.

Submersible receiver detections were used to document emigration events from the tributaries over the three years of this study. Overall, 30 submersible receivers recorded 1,522,843 detections from telemetered red drum. Most detections came from Hancock Creek (*n* = 980,000), while the least came from Adams Creek (*n* = 17, 223). The residence time of fish

Fig.3

ultimately emigrating was 3.8 ± 0.3 months (Fig. 3). Weight at tagging for fish ultimately emigrating was not different than the mean weight of all telemetered red drum in total ($P = 0.34$).

There was strong evidence that F did not vary spatially (Table 2), justifying the combination of telemetry and tag return Fs in subsequent models. The spatially-invariant M model, however, only received slightly more support from the data than the model allowing M to vary spatially (Table 2). Because all additional parameter estimates were nearly identical between these two models, only the results of the spatially-invariant M model are presented below. The implications of each model are described in the *Discussion*.

Table 2

Preliminary modeling using $QAIC_c$ showed that constant M and yearly P parameters outperformed all other forms of these parameters, so these were used in all models. The best model using external tagging data alone according to $QAIC_c$ was one that had 28 parameters and allowed F to vary by quarter and year, with a constant M (Table 3). The best model using telemetry data alone estimated 9 parameters and allowed F to vary by quarter, M to be constant, and relocation probability to vary by year (Table 3).

Table 3

The best model chosen for the combined tag return and telemetry data was the model that estimated 31 parameters and allowed F to vary by quarter and year, M to be constant, and relocation probability to vary by year (Table 3).

The tag return model estimated monthly Fs that ranged from 0 – 0.08, and monthly relative standard errors (RSE; $SE \cdot estimate^{-1} \cdot 100$) of 15 – 101%. Fs were generally low in winter and spring months, increased in summer months, and peaked in the fall (Fig. 4A). Fs were also variable among years, with highest F in 2006 and lowest in 2007. The mortality rate experienced by tags (F') varied between 0 and 0.04 (RSE = 14 – 101%) and showed a seasonal pattern, being low in winter months and highest in summer months (Fig. 4A).

Fig.4

The telemetry model estimated monthly *F*s that were low in winter, spring, and summer months (ranging from 0.01 – 0.03) and highest in fall (0.14). Relative standard errors of monthly estimates ranged from 33 to 107%, similar to RSEs from the tag return model. Monthly *F*s from the telemetry approach mirrored the seasonal pattern observed in the tag return results, with the exception of higher magnitude in fall months (Fig. 4B).

Monthly *F*s in the combined model ranged from 0.01 to 0.07, with RSEs of 11 - 102% (Fig. 4C). The magnitude and seasonal pattern of monthly *F*s in the combined model closely mirrored estimates from the tag return data alone, being low in winter and spring, increasing in summer months, and peaking in the fall. Fishing mortality was also highest in 2006 and lowest in 2007. In addition, *F*' varied between 0 and 0.04 (RSE = 13 – 101%), and showed a seasonal pattern of being low during the winter months and highest in the summer (Fig. 4C).

Annual estimates of *F* from the combined model were partitioned into recreational and commercial components based on the returns of high-reward tags from harvested fish. Commercial *F* varied from 0.07 in 2007 to 0.13 in 2005 and 2006, while recreational *F* was generally higher and varied from 0.11 in 2007 to 0.22 in 2006 (Fig. 5). The recreational sector made up between 50 and 64% of the total *F* among the three years of the study, with the commercial sector making up the remainder.

Fig. 5

Monthly *M* from the tag return model was estimated to be 0.03 ± 0.02. Considerably lower estimates were obtained for the telemetry-only model (0.002 ± 0.002) and the combined model (0.003 ± 0.003). Therefore, annual estimates of *M* were 0.38 (tag return), 0.03 (telemetry) and 0.04 (combined model).

It did not appear that predation upon telemetered red drum by bottlenose dolphins in our systems was frequent, since there was nearly complete separation between the speed of

Fig.6

emigrating transmitters and the range of observed speeds of bottlenose dolphins (Fig. 6). The single red drum that emigrated from South River at an unusually high rate of speed (8.2 km·h^{-1}) may have been consumed by a predator such as a bottlenose dolphin. Since possible predation occurred on this fish within the two-week censor period, it was not included in the analysis.

In the tag return model, λ was estimated at 0.82 ± 0.08 for NCSU low-reward tags, but was much lower for NCDMF low-reward tags (0.53 ± 0.05). The estimates changed slightly in the combined model, resulting in lower reporting rates for both NCSU (0.76 ± 0.07) and NCDMF (0.49 ± 0.04) low reward tags. Based on the relative returns of NCSU low and high-reward tags by sector over the entire study, we calculated reporting rates of 0.77 for the recreational sector and 0.44 for the commercial sector.

Relocation probability of telemetered fish was high for all years of the study, varying from 0.87 ± 0.05 in 2005 to 1.00 ± 0.07 in 2007 in the telemetry model and 0.84 ± 0.05 in 2005 to 1.00 ± 0.08 in 2007 in the combined model.

Discussion

By combining telemetry and tag return data into one joint analysis, we estimated seasonal *F*s and annual *M*s for an estuarine fish. Our work provides the first field test of the simulations by Pollock et al. (2004), who suggested that a combined telemetry and tag return approach could provide precise and unbiased estimates of *F*, *M*, and λ. The strength of the telemetry method is estimating *M*, while the tag return method is better at estimating *F* (Pollock et al. 2004). The combination of these two approaches takes advantage of the relative strengths of each and provided more precise estimates of *F* and *M* than either independent approach alone.

Recent work has highlighted the benefits of combining different techniques and data sources to estimate mortality rates of organisms. For instance, improved estimates of mortality have been acquired using multiyear fishery tagging models combined with catch data (Polacheck et al. 2006) or catch-at-age and observer data (Eveson et al. 2007). Coggins et al. (2006) used catches of marked and unmarked fish in a fisheries stock assessment model to estimate capture probabilities, survival, abundance, and recruitment. Likewise, previous work from terrestrial systems has shown that combining mark-recapture techniques with telemetry resulted in improved models that allowed estimation of additional parameters and assessment of assumptions (Barker 1997; Powell et al. 2000; Nasution et al. 2001). For example, Nasution et al. (2001) estimated precise monthly survival rates of snail kites (*Rostrhamus sociabilis*) in Florida when combining a Cormack-Jolly-Seber mark-resight model with Kaplan-Meier radio telemetry analyses. Our combined model provided the same benefits in a fisheries context, but has gone further by being able to partition total mortality into F and M with good precision.

The combined tag return – telemetry model estimated relatively precise monthly Fs. We attribute the good precision to four factors: (1) a large number of red drum were tagged and telemetered each month (with the exception of telemetered fish in fall months), (2) the annual exploitation rate of red drum while in the slot limit was high (e.g., 0.30 in our study in 2006), (3) λ was high, and (4) relocation probability of telemetered red drum was high (≥ 0.80). Large monthly sample sizes of tagged, recovered, and telemetered fish permitted us to use a monthly model, which clearly demonstrated the strong seasonality in F that peaked in the fall months, but was different among years. Unlike most stock assessments that only produce an annual F, information about the seasonality of F estimated by our combined model could be used by managers to employ seasonal closures that would have maximum impact. For subadult red drum in North Carolina, fishing effort could be reduced or restricted in fall months to reduce F most substantially.

There are additional benefits of using a monthly time step. Although fish are often tagged continuously over time in tagging studies, many applications of tag return models assume that tagging only occurs at the beginning of each annual time step. Monthly time steps reduce potential problems associated with continuous tagging. It was also encouraging that monthly estimates of *F* from the tag return and telemetry approaches were similar in seasonal pattern, especially considering their independence. The apparent differences in magnitude of *F* during the fall months between the tag return and telemetry approaches were not substantial; differences may have been real if *F* was higher in NRE tributaries compared to the rest of the state. However, models testing for separate *F*s did not fit as well as the combined *F*s. Our results suggest that, although the tag return data drove estimates of *F* in the combined model, both the tag return and telemetry approaches can be used to estimate monthly mortality rates with reasonable precision given large sample sizes.

Natural mortality is notoriously difficult to estimate because natural deaths are rarely seen and it is often confounded with other parameters in population models (Quinn and Deriso 1999). Our annual estimate of *M* (0.04) is consistent with recent telemetry research that suggests *M* may be lower than previously thought for many fish species. For instance, estimates of *M* ranging from 0.10 to 0.16 have been determined for adult striped bass *Morone saxatilis* in North Carolina reservoirs using telemetry (Hightower et al. 2001; Thompson et al. 2007). Likewise, our estimate of *M* is substantially lower than previous estimates for subadult red drum. Latour et al. (2001) estimated an annual *M* of 0.83 – 1.37 for age-2 red drum in South Carolina based on tagging, but the authors noted that these estimates were likely positively biased due to emigration from the study area towards the coast. The rarity of observed natural mortalities in our telemetry study ($n = 1$) made it difficult to compare a constant *M* model to one that allowed *M* to vary by shorter time steps such as months or years. In cases where natural deaths are more common, it will likely be possible to estimate season- or yearly-specific *M* using the telemetry approach (e.g., Waters et al. 2005).

It is unlikely that our estimate of *M* was biased low because of unaccounted-for predation. By using submersible receivers to quantify emigration rates of transmitters and quantifying the average swimming speed of bottlenose dolphin in our systems, we were able to show that in only one instance did a transmitter emigrate at a speed suggestive of a bottlenose dolphin. That particular fish was ultimately censored from our analyses because it emigrated within the two week censor period. Other predators capable of consuming a 2-kg red drum were very rare or absent in these oligohaline tributaries. Future studies using the telemetry approach on small fish in open systems must be able to separate live emigrating fish from those emigrating while in the stomach of a predator. Given that the separate *M* and shared *M* models performed equally well, it remains unknown whether *M* experienced by subadult red drum in tributaries of the NRE are reflective of rates elsewhere. The value of *M* estimated using tag return data alone was much higher but it was not a precise estimate, likely because natural deaths are estimated indirectly with this approach.

It is not necessary to assume that all tags are reported to separate *F* and *M* in a tag return study, but λ must be known or estimable. There are many methods available to estimate λ, including high-reward tagging (Pollock et al. 2001), planted tags (Hearn et al. 2003), observers in multi-component fisheries (Hearn et al. 1999), and tagging studies with pre- and post-fishing season tagging (Hearn et al. 1998). For recreational species like red drum, high-reward tagging has become the primary method used to estimate λ. There are some important assumptions of the high-reward method that must be considered before conducting a high-reward tagging study (reviewed in Pollock et al. 2001). Most importantly, high- and low-reward tagging must be spread over a large area to avoid changing the behavior of the fishery and to reduce the chance that individual fishers will catch multiple tags. Furthermore, the high-reward tagging study must be widely advertised and high-reward tags must be obvious in color and message so that fishers recognize high-reward tags when caught. If not, the critical assumption of 100% reporting of high-reward tags will likely not be met, which will cause the λ of low-reward tags to be positively biased (Conroy and Williams 1981). By spreading tagging over a large area, advertising the tagging project widely, and using a unique tag color with an obvious $100 reward message, we believe our estimates of λ for NCSU and NCDMF tags are accurate.

We estimated λ for NCDMF and NCSU external tags separately. Our λ estimates (0.49 and 0.76) are consistent with previous work on red drum, which have estimated λ ranging from 0.36 to 0.63 (Green et al. 1983; Denson et al. 2002). We also showed that λ varied substantially between the two sources of released tags. The 0.27 difference in λ could be due to some fishers being less likely to report tags to a management agency compared to an academic institution. For instance, some fishers may be reluctant to return tags to a management organization because of a perceived risk of additional regulations, but they may not have the same fears of returning tags to an academic institution. It is unknown if differences in λ of low-reward tags between a university and a management agency would translate to unequal reporting of high-reward tags from different sources. Future high-reward tagging studies, especially those conducted by management agencies, must consider this possibility.

Another advantage of using a tagging approach with high-reward tags to estimate mortality rates for fish species is that F can be decomposed into recreational and commercial components. Assuming both sectors reported 100% of all high-reward tags from harvested fish, we found that recreational fishers accounted for 50 – 64% of *F* in North Carolina from 2005 to 2007. Our results are consistent with estimates of landings in North Carolina that suggest recreational fishers have harvested approximately 56% of the total red drum harvest in the state since 1999 (Takade and Paramore 2007). Furthermore, the observed increase in *F* from 2005 to 2006 appeared to be due entirely to an increase in recreational *F*, while the commercial *F* stayed constant over the same time period. The factors contributing to variability in the magnitude of sector-specific *F*s for red drum requires more research attention.

We estimated mortality rates of one age class of red drum only because sufficient sample sizes were lacking for other age classes and we were particularly interested in slot-limit (legal) fish in this study. The combined approach can easily be adapted to an age-dependent analysis, however. The model structure for conventional tagging analyses of multiple age classes has been described in Jiang et al. (2007) and Bacheler et al. (2008); it would be straightforward to combine these analyses with age-dependent telemetry data to produce an age-dependent combined model.

The potential benefit of adding a telemetry component to an on-going tag return study is substantial, as long as it is possible to detect emigration from the study area. For instance, telemetry can also be used to estimate mixing or emigration rates; this is important because emigration is often confounded with mortality in most tagging models (Pollock et al. 1990). Given variable fishing effort over space, movement and habitat use data can be biased in traditional tagging studies. Telemetry provides much more accurate information about movement and habitat use because it does not rely on the spatial and temporal patterns of the fishery for returns. The telemetry approach also avoids problems associated with tag reporting rate and tag loss common in traditional tagging studies.

The telemetry mortality approach is most easily used in closed systems such as lakes, reservoirs, or rivers blocked by dams. The telemetry approach can be adapted to open systems, however, by using submersible receivers as gateways through which telemetered fish enter and exit the study system or area. We staggered the release of 180 telemetered red drum over the course of our 34 month study in an attempt to maintain an adequate monthly sample size. Had movement rates of subadult red drum been lower, many fewer transmitters would have been required to maintain adequate monthly sample sizes, but the downside would have been that mixing rates of conventional tagged fish would have been much lower. In our study, it appeared that movement rates of subadult red drum were high enough that substantial mixing of conventionally tagged fish occurred, but it also resulted in a high emigration rate of telemetered fish from Neuse River tributaries.

The use of both tag return and telemetry techniques may ultimately be a cheaper alternative than traditional stock assessment approaches to control exploitation rates of managed fish populations (Martell and Walters 2002; Walters and Martell 2004). Traditional stock assessment approaches typically rely on fishery landings and survey data, which are only linearly related to true biomass if catchability (*q*) remains constant over time (Hilborn and Walters 1992). Variability in *q* arising from technological advances, range contractions, or any number of other reasons has famously resulted in erroneous stock assessments of many species (see Walters and Martell 2004 for a review). The combined tag return – telemetry approach may be a viable alternative that can be used to directly estimate *F* and *M*, as long as several key assumptions (discussed above) are met and benchmarks could be established. Tagging thousands of fish annually with high- and low-reward tags as well as releasing a modest number of transmitters may appear to be an expensive way to estimate mortality rates. In many situations, however, this approach may be much less risky and expensive than collecting and analyzing survey and aging data needed for traditional stock assessment approaches (Walters and Martell 2004).

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Table 1. Monthly sample sizes of external tagged and telemetered age-2 red drum in North Carolina from April 2005 to December 2007.

Month	External tagging			Telemetry
	NCSU low-reward	NCDMF low-reward	NCSU high-reward	Virtual releases
Apr. 2005	391	149	74	44
May 2005	0	27	0	33
June 2005	0	86	0	31
July 2005	0	23	0	25
Aug. 2005	0	29	0	17
Sept. 2005	0	11	0	3
Oct. 2005	0	25	0	4
Nov. 2005	0	4	0	1
Dec. 2005	0	2	0	29
Jan. 2005	0	55	0	32
Feb. 2006	0	256	0	31
Mar. 2006	0	502	0	23
Apr. 2006	391	463	211	24
May 2006	0	43	0	19
June 2006	0	41	0	26
July 2006	0	19	0	17
Aug. 2006	0	66	0	12
Sept. 2006	0	61	0	10
Oct. 2006	0	40	0	3
Nov. 2006	0	6	0	0
Dec. 2006	0	3	0	0
Jan. 2007	0	0	0	0
Feb. 2007	0	323	0	0
Mar. 2007	0	323	0	2
Apr. 2007	388	114	67	1
May 2007	0	326	0	0
June 2007	0	94	0	0
July 2007	0	10	0	12
Aug. 2007	0	8	0	8
Sept. 2007	0	12	0	8
Oct. 2007	0	7	0	10
Nov. 2007	0	45	0	11
Dec. 2007	0	81	0	10
Total	1 170	3 254	352	581

Table 2. Candidate models allowing fishing and natural mortality rates to vary or be constant across space using program SURVIV.

Model	Parameters	Log likelihood	AIC	$QAIC_c$	$\Delta QAIC_c$
$F_{\boldsymbol{.}}M_{\boldsymbol{.}}$	30	-719.9	1 499.8	772.9	0.0
$F_{\boldsymbol{.}}M_{space}$	31	-718.3	1 498.6	773.3	0.4
$F_{space}M_{\boldsymbol{.}}$	41	-712.3	1 506.6	787.6	14.8
$F_{space}M_{space}$	42	-711.6	1 507.2	789.0	16.1

Note: Fishing (*F*) and natural mortality rate (*M*) was allowed to vary by space (*space*) or be constant (**.**).

Table 3. Candidate models fitted to tag return data alone, telemetry data alone, or combined tag return and telemetry data with program SURVIV.

Model	Parameters	Log likelihood	AIC	$QAIC_c$	$\Delta QAIC_c$
Tag return					
$F_{qy}M.$	28	-672.7	1 401.4	661.3	0.0
$F_mM.$	28	-700.7	1 457.4	686.5	25.2
$F_qM.$	12	-738.6	1 501.2	688.3	27.0
$F_{my}M.$	70	-616.0	1 372.0	696.1	34.8
$F_yM.$	10	-887.5	1 795.0	818.2	156.7
$F.M.$	6	-918.8	1 849.6	838.3	177.0
Telemetry					
$F_qM.P_y$	9	-62.6	143.3	88.8	0.0
$F_{qy}M.P_y$	17	-50.6	135.3	92.1	3.3
$F.M.P_y$	6	-72.2	156.5	93.4	4.6
$F_yM.P_y$	8	-71.5	159.1	96.7	7.9
$F_mM.P_y$	17	-55.5	145.0	97.5	8.7
$F_{my}M.P_y$	37	-43.0	160.0	127.7	38.9
Combined					
$F_{qy}M.$	31	-745.4	1 552.8	831.7	0.0
$F_{my}M.$	73	-691.7	1 529.4	861.9	30.2
$F_mM.$	31	-774.9	1 611.8	862.1	30.4
$F_qM.$	15	-809.7	1 649.4	865.7	34.0
$F_yM.$	13	-965.6	1 957.2	1 022.6	190.9
$F.M.$	9	-994.6	2 007.2	1 044.5	212.8

Note: Fishing mortality (*F*) was allowed to vary by month (*m*), month and year (*my*), quarter (*q*), quarter and year (*qy*), year (*y*), or be constant (**.**). Natural mortality rate (*M*) was held constant and relocation probability (*P*) was allowed to vary yearly based on preliminary modeling.

Figure captions

Fig. 1. Map of study area, showing North Carolina and neighboring states (a), and an enlarged view of the Neuse River Estuary (b). The conventional tagging took place throughout Pamlico Sound and associated rivers. The telemetry component of the study was conducted exclusively within the five labeled creeks in the Neuse River, and stars indicate location of submersible receiver arrays.

Fig. 2. Tagging (gray circles) and recovery sites (black circles) for red drum tagged and released by NCSU (A – C) and NCDMF (D – F) in 2005 – 2007.

Fig. 3. Proportion of telemetered red drum emigrating from Neuse River tributaries in various monthly intervals after initial release, 2005 – 2007. Emigration events were documented with submersible receiver arrays at the mouth of each tributary.

Fig. 4. Monthly fishing mortality rate (solid line; ± SE) for subadult red drum from April 2005 – December 2007. Fishing mortality rates were estimated by the tag return model alone (A), the telemetry model alone (B), or the combined tag return – telemetry model (C). The mortality rate experienced by tags (*F*', for caught-and-released fish only) is shown by the dotted line.

Fig. 5. Annual fishing mortality rate of age-2 North Carolina red drum attributed to recreational (black bars) and commercial fishing sectors (gray bars), estimated by the yearly returns of high-reward tags from harvested fish.

Fig. 6. Proportion of emigrating transmitters (black bars) and bottlenose dolphins (white bars) based on estimated swimming speed from detections in the receiver arrays.

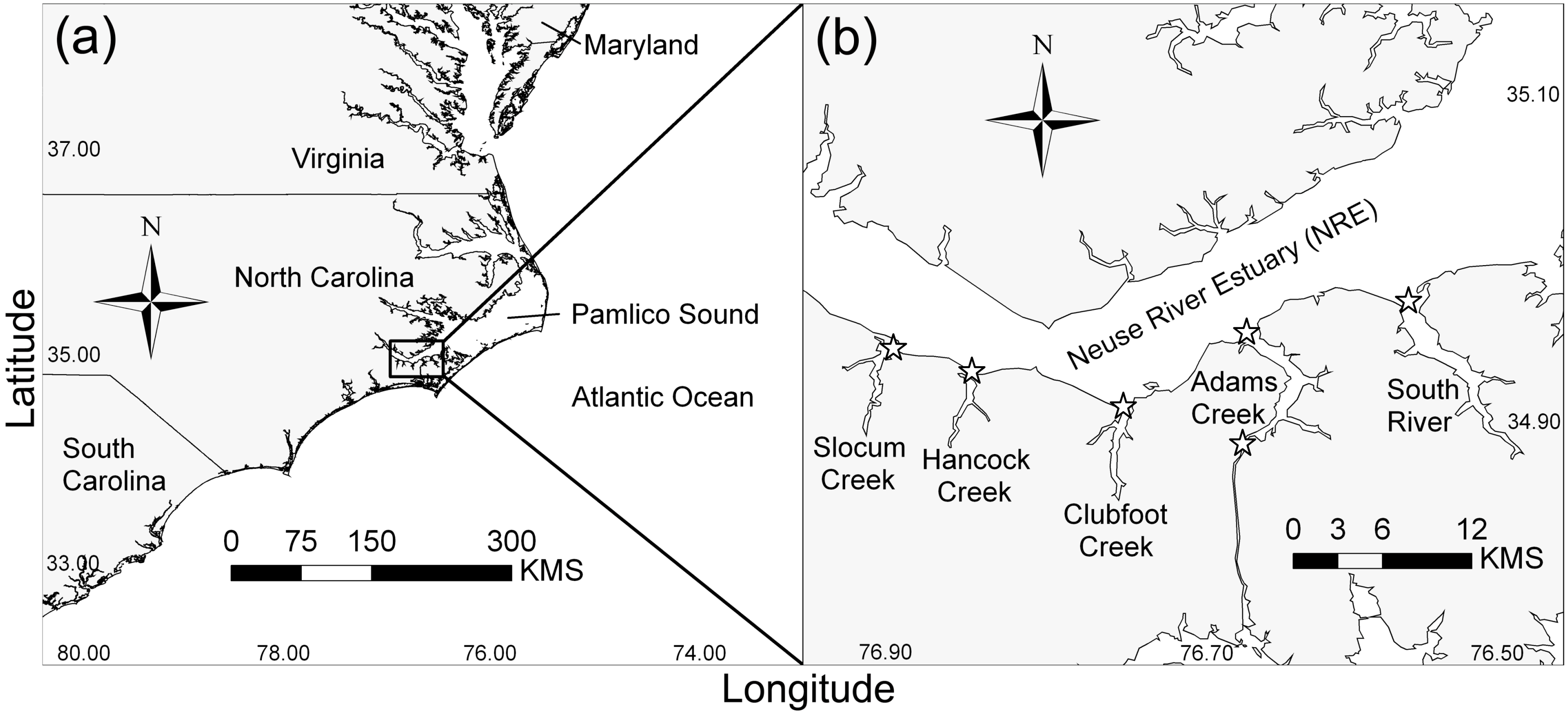
(a)
Maryland
Virginia
North Carolina
Pamlico Sound
Atlantic Ocean
South Carolina
N
37.00
35.00
33.00
80.00
78.00
76.00
74.00
0 75 150 300 KMS
(b)
N
35.10
34.90
Neuse River Estuary (NRE)
Slocum Creek
Hancock Creek
Clubfoot Creek
Adams Creek
South River
0 3 6 12 KMS
76.90
76.70
76.50
Latitude
Longitude

Fig. 1

.

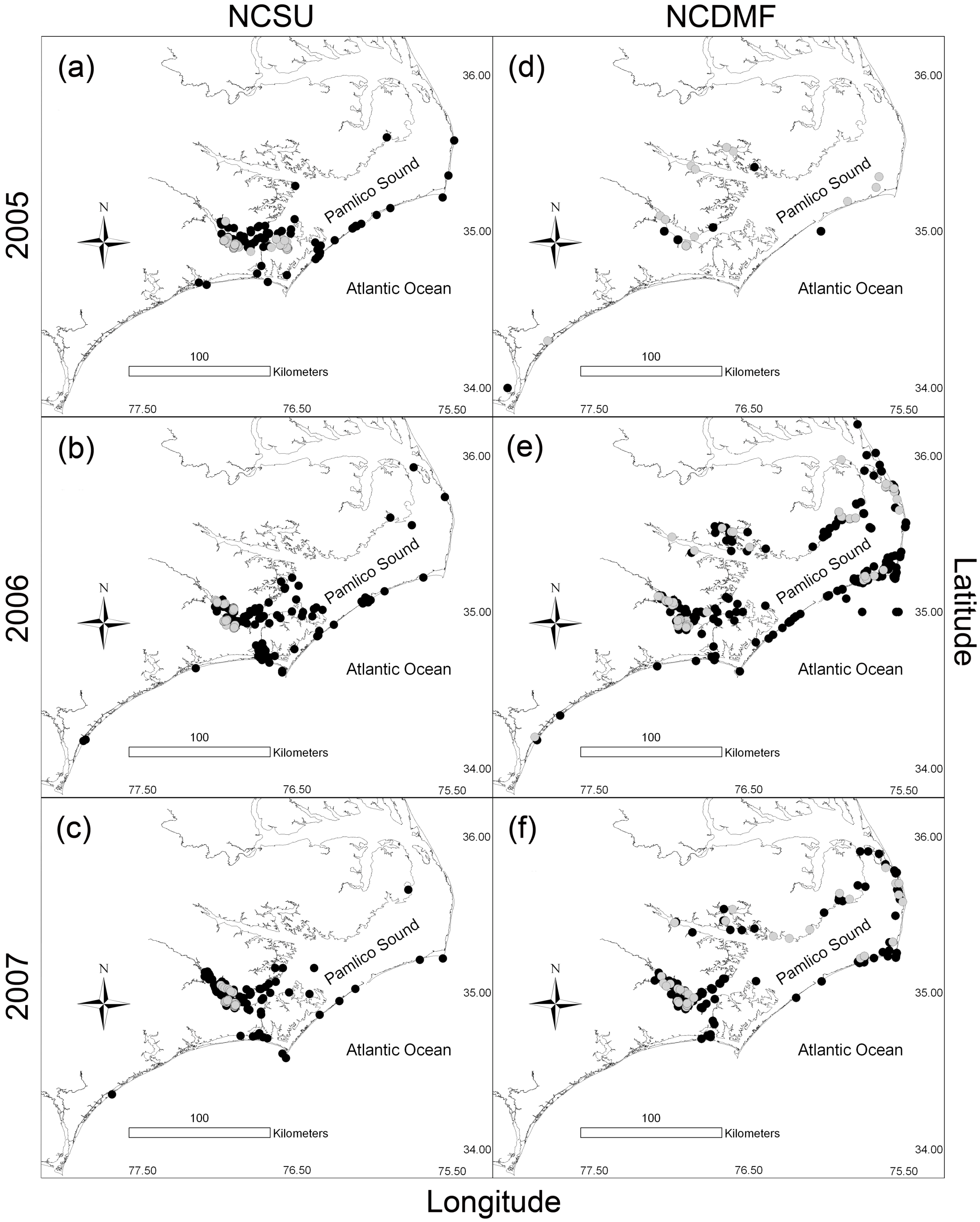
NCSU
NCDMF
2005
2006
2007
(a)
(b)
(c)
(d)
(e)
(f)
Pamlico Sound
Atlantic Ocean
N
100
Kilometers
36.00
35.00
34.00
77.50
76.50
75.50
Latitude
Longitude

Fig. 2

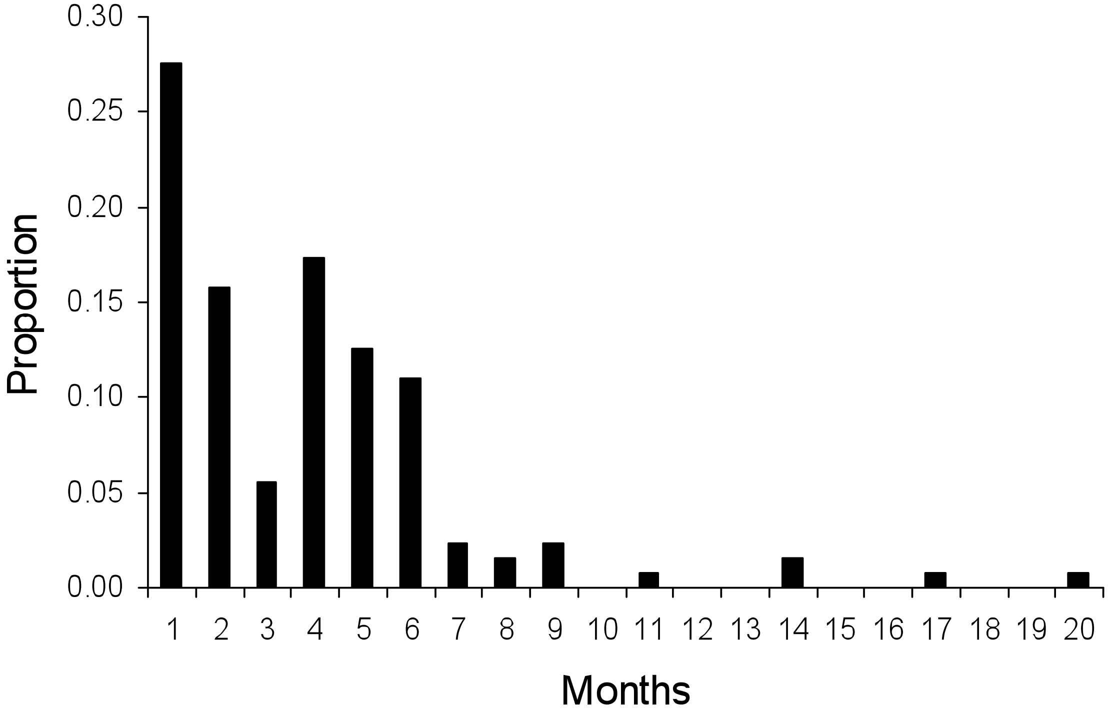
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Proportion
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
Months

Fig. 3

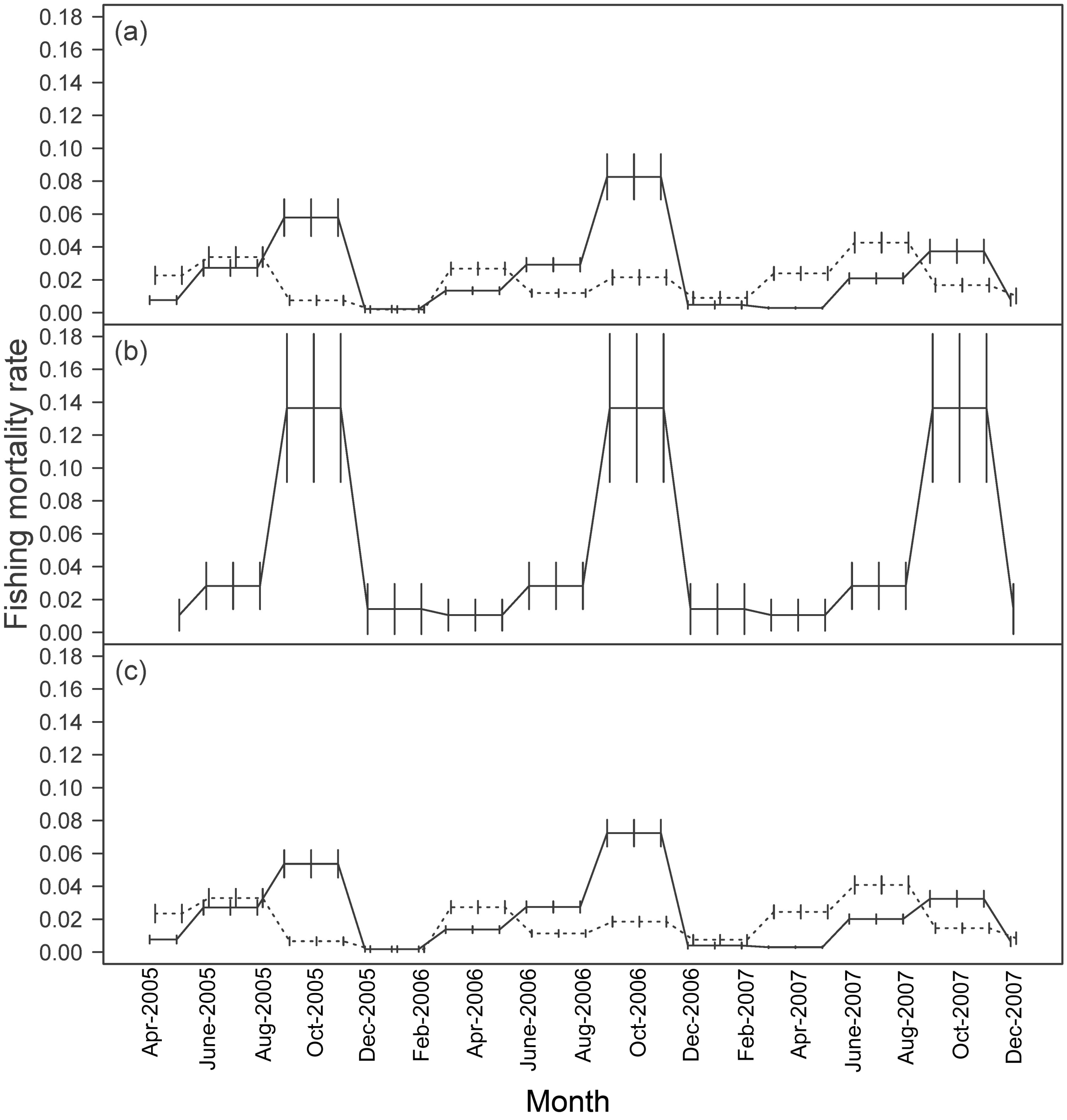
(a)
(b)
(c)
Fishing mortality rate
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Apr-2005
June-2005
Aug-2005
Oct-2005
Dec-2005
Feb-2006
Apr-2006
June-2006
Aug-2006
Oct-2006
Dec-2006
Feb-2007
Apr-2007
June-2007
Aug-2007
Oct-2007
Dec-2007
Month

Fig. 4

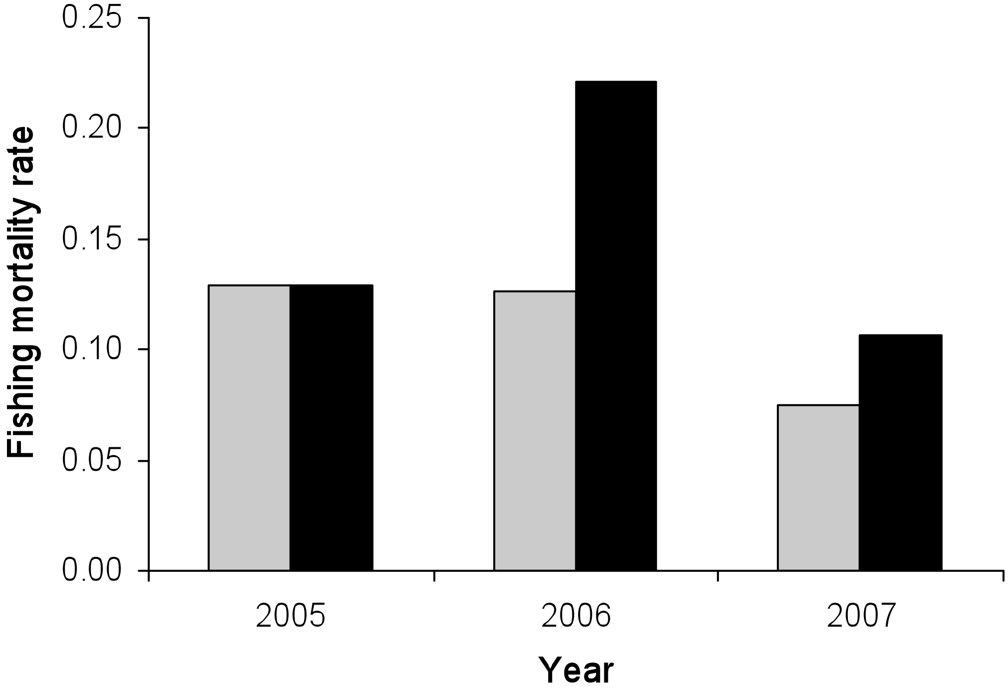
0.25
0.20
0.15
0.10
0.05
0.00
Fishing mortality rate
2005
2006
2007
Year

Fig. 5

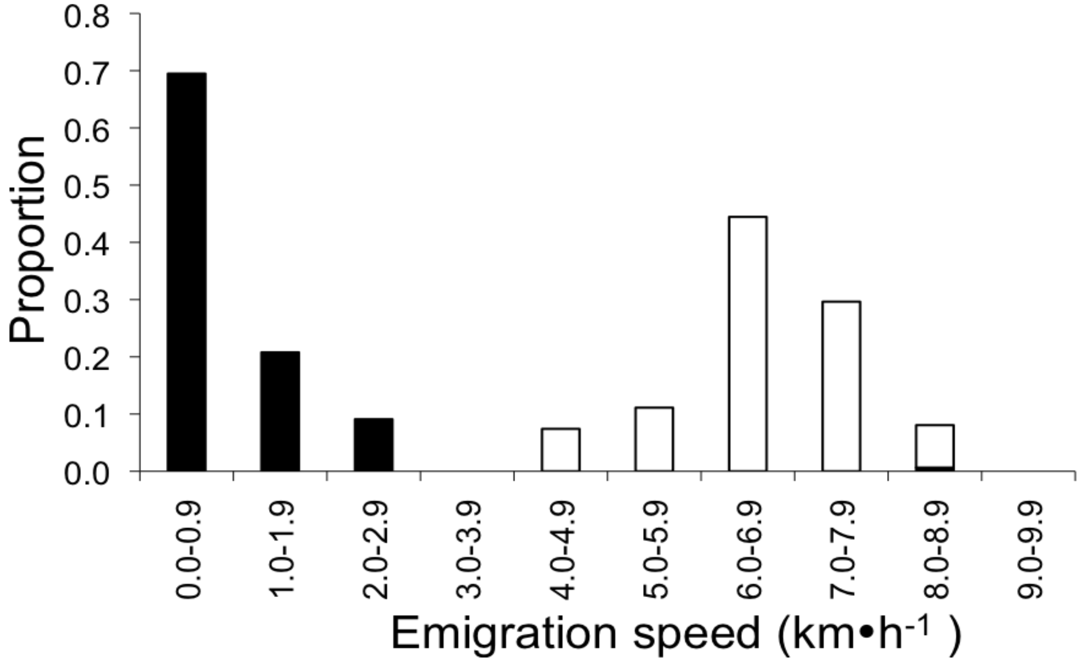
Proportion
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0-0.9
1.0-1.9
2.0-2.9
3.0-3.9
4.0-4.9
5.0-5.9
6.0-6.9
7.0-7.9
8.0-8.9
9.0-9.9
Emigration speed (km•h-1)

Fig. 6