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Using generalized linear models to estimate selectivity from short-term recoveries of tagged red drum *Sciaenops ocellatus*: Effects of gear, fate, and regulation period

Nathan M. Bacheler^{a,*}, Joseph E. Hightower^b, Summer M. Burdick^{a,1}, Lee M. Paramore^c, Jeffrey A. Buckel^a, Kenneth H. Pollock^d

^a Center for Marine Sciences and Technology, Department of Biology, North Carolina State University, 303 College Circle Drive, Morehead City, NC 28557, USA

^b U.S. Geological Survey, North Carolina Cooperative Fish and Wildlife Research Unit, Department of Biology, North Carolina State University, Raleigh, NC 27695, USA

^c North Carolina Division of Marine Fisheries, Post Office Box 539, 604 Harbor Road, Wanchese, NC 27981, USA

^d Department of Biology, Box 7617, North Carolina State University, Raleigh, NC 27695-7617, USA

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ABSTRACT

Estimating the selectivity patterns of various fishing gears is a critical component of fisheries stock assessment due to the difficulty in obtaining representative samples from most gears. We used short-term recoveries (n = 3587) of tagged red drum Scigenops ocellatus to directly estimate age- and length-based selectivity patterns using generalized linear models. The most parsimonious models were selected using AIC, and standard deviations were estimated using simulations. Selectivity of red drum was dependent upon the regulation period in which the fish was caught, the gear used to catch the fish (i.e., hook-andline, gill nets, pound nets), and the fate of the fish upon recovery (i.e., harvested or released); models including all first-order interactions between main effects outperformed models without interactions. Selectivity of harvested fish was generally dome-shaped and shifted toward larger, older fish in response to regulation changes. Selectivity of caught-and-released red drum was highest on the youngest and smallest fish in the early and middle regulation periods, but increased on larger, legal-sized fish in the late regulation period. These results suggest that catch-and-release mortality has consistently been high for small, young red drum, but has recently become more common in larger, older fish. This method of estimating selectivity from short-term tag recoveries is valuable because it is simpler than full tag-return models, and may be more robust because yearly fishing and natural mortality rates do not need to be modeled and estimated.

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1. Introduction

Almost no fishing gear catches fish equally well with respect to body size or age. For example, nets and pots are selective because small fish can escape through the mesh (Hamon et al., 2000; Rudershausen et al., 2008), while larger fish may out-swim towed trawl nets (Wells et al., 2008; Binion et al., 2009) or may be too big to become entangled in stationary gill nets (Myers and Hoenig, 1997). Hook-and-line gear is also selective and is based on the relationship of hook size to mouth size (Millar and Fryer, 1999; Bacheler and Buckel, 2004; Alos et al., 2008). In addition to gear selectivity effects, fish often segregate geographically by size or age, and fishers target fish in particular areas that maximize their profit (Walters and Martell, 2004). The net result is that selectivity makes obtaining a representative or random sample of the size or age composition nearly impossible.

For these reasons, estimating the selectivity patterns (i.e., gear selectivity and relative vulnerability by length or age) of a fishery is a central component of fisheries stock assessment (Hilborn and Walters, 1992). Typically, one of four methods is used to estimate selectivity of a fishery. First, selectivity can be estimated internally in an age-structured assessment model if catches by age and year are reliably estimated. However, this can be difficult in practice because the models have many parameters that are often correlated. It is common that equally good fits can be obtained from models with drastically different selectivity vectors (Kimura, 1990; Sigler, 1999). Poor estimates or incorrect assumptions about selectivity can result in erroneous estimates of stock abundance

^{*} Corresponding author. Present address: University of Wisconsin – Green Bay, Natural and Applied Sciences ES 317, 2420 Nicolet Drive, Green Bay, WI 54311, USA. Tel.: +1 920 465 2247.

E-mail address: bachelen@uwgb.edu (N.M. Bacheler).

¹ Present address: U.S. Geological Survey, Western Fisheries Research Center, Klamath Falls Field Station, 2795 Anderson Avenue, Suite 106, Klamath Falls, OR 97603, USA.

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Fig. 1. Study site showing coastal North Carolina and locations of tagged (gray circles) and recovered (black circles) red drum used in analyses.

and harvest rate. For instance, Myers et al. (1997) suggested that incorrect selectivity information from Atlantic cod (*Gadus morhua*) assessment models resulted in gross overestimates of spawning biomass, and was one of the reasons for their collapse in Canada.

Another common method to estimate selectivity is to compare the sizes of fish caught from multiple gear types deployed at the same time and place. These estimates of selectivity are considered indirect and relative because the true composition of the fished stock is unknown (Millar, 1992). For this reason, the true selectivity patterns of each gear cannot be determined because a variety of selectivity patterns can be fit equally well to the data (Millar, 1995; Millar and Fryer, 1999).

The most robust method for estimating selectivity is using tagging. Selectivity is estimated using the relative return of tags across a variety of length or age classes (e.g., Schultz, 2004). The major advantage of this approach is that it provides direct information about selectivity because the length or age composition of the tagged group is known (Myers and Hoenig, 1997). A drawback is that it requires large numbers of tagged fish in each length or age category, which is rarely accomplished in a single tagging program. Moreover, multiple tag types cannot be analyzed together because of potential differences in tag retention rates or post-tagging mortality by tag type. To address these drawbacks, Myers and Hoenig (1997) developed an approach to estimate selectivity by combining data from many separate tagging experiments in a generalized linear model framework. They analyzed data from 137 tagging experiments to show that selectivity of large Atlantic cod caught in otter trawls increased from the 1960s to the 1980s.

The last method is to estimate age-dependent selectivity internally in a tag-return model (Jiang et al., 2007a,b; Bacheler et al., 2008). Here, fishing mortality for a particular age class and year is modeled as a yearly fishing mortality parameter multiplied by an age-specific selectivity parameter, and parameters are estimated using maximum likelihood (Jiang et al., 2007a). This method requires that fishing and natural mortality rates be modeled over all years of the study and estimated separately. Bacheler et al. (2008) used this approach to estimate selectivity patterns for red drum (*Sciaenops ocellatus*), an estuarine species found in the southeast United States and Gulf of Mexico. Traditional stock assessment models could not be used to estimate red drum selectivity because harvest occurred within a minimum and maximum size limit (i.e., window limit) centered on age-2 fish (with a smaller proportion of age-1 and age-3 fish; Bacheler et al., 2009a); it was impossible for the assessment model to determine if the lack of age-3 harvest was due to reduced selectivity or high mortality rates on previous age groups (Latour et al., 2001). A benefit of the tag-return approach (Bacheler et al., 2008) to estimate selectivity is being able to use all tag recoveries occurring over time. Alternatively, the Myers and Hoenig (1997) tagging approach only uses short-term tag recoveries, but a key advantage of this approach is that a clearer picture of selectivity may be obtained with fewer assumptions.

Here, we estimate the age- and length-based selectivity patterns of red drum in North Carolina using the tagging method described by Myers and Hoenig (1997). We refer to selectivity as the combination of gear selectivity and other factors such as spatial distribution or size regulations that in combination result in age- or length-specific differences in relative vulnerability to fishing (Hilborn and Walters, 1992). The specific objectives were twofold. First, we quantified age-based selectivity patterns of red drum to assess whether the disappearance of fish growing out of the window limit was due to reduced selectivity or increased mortality. These results provide an alternative analysis of age-based selectivity with which to compare to Bacheler et al. (2008). The second objective was to determine the length-based selectivity patterns of harvested and, more importantly, released fish, the latter of which provides important information about sizes of fish experiencing catch-and-release mortality from various gears. We extend previous work by employing an information-theoretic approach (Burnham and Anderson, 2002) to assess the effect of regulation period, gear type, and fate of the fish on red drum selectivity. Our results highlight the flexibility, simplicity, and underutilization of the Myers and Hoenig (1997) approach to address a variety of potential management objectives for exploited fish populations.

2. Materials and methods

2.1. North Carolina red drum tagging

Two sources of tagged red drum were used. The first was the North Carolina Division of Marine Fisheries (NCDMF) tagging program, which has occurred from 1983 to 2007 throughout North Carolina (Fig. 1). Red drum have been captured and tagged opportunistically by NCDMF using pound nets, hook-and-line, runaround gill net, trammel nets, and electrofishing (see Burdick et al., 2007 for a complete description). Volunteer recreational fishers have been involved in tagging since 1984 and primarily target adult red drum. Commercial fishers assisted in tagging until 1995, primarily tagging subadult red drum caught in pound nets and gill nets in conjunction with NCDMF personnel. The second data source was tagging of mainly subadult (i.e., age-1 to age-3) red drum in 2005–2007 by North Carolina State University (NCSU) personnel within the Neuse River (Fig. 1). In both of these studies, only healthy fish were tagged and released.

Most subadult fish were tagged with Floy[®] internal anchor (FM-84, FM-89SL, and FM-95W)² or spaghetti tags (Floy[®] FT-4), while adults were primarily tagged with nylon dart tags (Floy[®] FT-1 and FT-2), stainless steel dart tags with a monofilament core (Floy[®] FH-69), or, more recently, a stainless steel core (Hallprint[®] FH-69). All tags were labeled with a unique tag number, "REWARD" message, and an address to send the tag and phone number to report the tag. A two-dollar (US) reward was given for returned NCDMF tags until 1989, and the reward amount increased to five dollars or a hat in 1990. All NCSU tags were labeled with the same "REWARD" message, and reward was similar (e.g., US\$5, hat, or tshirt). Fish recovered in states outside of North Carolina (n = 36) were excluded from selectivity analyses given the different regulations that exist in other states.

2.2. Generalized linear model to estimate selectivity

To address our objectives, three separate analyses were conducted. The first two analyses examined the age-based selectivity patterns of red drum. Fish were aged at tagging using a 6-month age-length key developed by NCDMF 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 NC red drum ageing data from otoliths, and annuli have been validated by Ross et al. (1995). A 6-month age-length key (January–June and July–December) was used because of rapid summer growth rates that subadult red drum experience in NC (Ross et al., 1995). The key provided very good separation of length-groups for fish younger than age 4. Sexually mature red drum were grouped into a single age-bin (age 4 and older [4+]; Ross et al., 1995). Thus, we used four age groups (ages 1, 2, 3, and 4+) for all age-based analyses. Previous aging work on adult red drum in NC determined that maximum age was 62 years (Ross et al., 1995), suggesting that age-4+ red drum in our study potentially ranged from age 4 to 62. These age bins also allowed a direct comparison to the age groups of Bacheler et al. (2008).

For the third objective concerning length-based analyses, we analyzed selectivity using 11 total length (TL) bins of 100 mm each. All fish less than 300 mm were grouped into a single length bin,

as were fish larger than or equal to 1200 mm. The combination of 100-mm TL bins and a 120-day period after tagging for allowable recoveries ensured that relatively few fish would grow into the next largest bin, sample sizes in most bins were sufficient, and bins were small enough that the resolution of the selectivity curve was useful. In the cases where tagged red drum were recaptured multiple times within 120 days of tagging, only the first recapture was used.

Appropriate definition of the "experiment" variable is a critical step in a generalized linear model (glm) approach to estimate selectivity, because it is a nuisance variable in the analysis and separates the variation we are not interested in from age- or length-based selectivity variation in which we are interested. Myers and Hoenig (1997) defined an experiment literally as a single release of fish in an area over a short period of time, whereas Clark and Kaimmer (2006) defined an experiment as all the releases of a given tag type within a regulatory area and year. We defined an experiment as all releases of a unique tag type (n=8 tag types). This prevented any relative differences in tag loss, tagging mortality, or tag reporting rate among the various tag types to influence selectivity estimates.

The first analysis examined age-based selectivity of red drum for three gears, three regulation periods, and two fates of recovered red drum (i.e., caught-and-released or harvested). In recent years, approximately two-thirds of harvested red drum in North Carolina has come from the recreational hook-and-line fishery, with commercial gill and pound nets accounting for most of the remaining harvest (Takade and Paramore, 2007; Bacheler et al., 2009a); other gears were excluded from all analyses due to low sample sizes of recovered fish. All hook-and-line rigs were considered together here. Similarly, all mesh sizes and net dimensions were considered jointly for gill and pound nets. The three regulation periods for the red drum fishery were defined as: "early" (1983–1991), "middle" (1992–1998), and "late" (1999–2007; Table 1). We also analyzed selectivity of harvested fish separately from released fish.

Selectivity patterns were estimated using the glm approach described by Myers and Hoenig (1997). This method estimates ageor length-based selectivity of red drum by fitting a model for the expected return rate $E[C_{i,a,g,f,p}]$ of tagged fish:

$$E[C_{i,a,g,f,p}] = N_{i,a}R_{i,g}U_{i,g}S_{a,g,f,p}$$

$$\tag{1}$$

where $N_{i,a}$ is the number of fish tagged in experiment *i* in age (or length) bin *a*, $R_{i,g}$ is the product of the proportion of fish that survive tagging, the proportion of tags that are not lost (shed), and the proportion of recovered tags that is reported for gear type *g* for fish tagged in experiment *i*, $U_{i,g}$ is the exploitation rate of fish tagged in experiment *i* and recovered by gear type *g*, and $S_{a,g,f,p}$ is the selectivity imposed by gear type *g* in regulation period *p* in age (or length) bin *a* for fish of a particular fate *f*. Here, *R* and *U* were modeled as nuisance parameters and not estimated. All predictor variables (age or length, gear, fate, and period) were included in the model as categorical variables. All glm analyses were performed using the

Table 1

Primary size limits (mm total length [TL]), bag limits (number of fish), and annual cap in the North Carolina red drum recreational and commercial fisheries during three regulation periods considered in this paper. Window means only fish within the length range could be harvested.

Regulation period	Recreational regulations	Commercial regulations
Early (1983–1991)	Minimum size = 356 mm Only 2 fish > 812 mm	Minimum size = 356 mm
Middle (1992–1998)	Window = 457-686 mm Bag limit = 5 fish Only 1 fish > 686 mm	Window = 457-686 mm Annual cap = 113,636 kg
Late (1999–2007)	Window = 457-686 mm Bag limit = 1 fish	Window = 457-686 mm Bag limit = 7 fish

² 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.

glm procedure in R (R Development Core Team, 2008), using the log link function and binomial error structure (Myers and Hoenig, 1997). No obvious patterns were observed in the residuals of the models.

The second analysis repeated the first age-based analysis except that the gear variable was removed so that selectivity was estimated across all gears for each age class, fate, and regulation period. There were two reasons for this separate analysis. First, it allowed for a direct comparison to the selectivity estimates of Bacheler et al. (2008), who examined selectivity across all gears. Second, the current configuration of the red drum stock assessment requires a selectivity value of age-3 versus age-2 red drum across all gears, so estimates produced in this analysis can be directly applicable to the red drum stock assessment.

To estimate the lengths of red drum for our third analysis, length-based selectivity was estimated for fish within the same three regulation periods, three gears, and two fates as used in the age-based analysis. Consequently, in this analysis the subscript *a* in Eq. (1) refers to length instead of age bins.

Some data transformation was required after estimating selectivity, due to the log-transformation used in the glm model. The back-transformed (exponentiated) selectivity estimates were divided by the maximum selectivity value within each combination of period, gear, and fate. This approach allowed selectivity to be estimated on a relative scale between 0 and 1.

We used a simulation approach to estimate the precision of our selectivity estimates. For each unique combination of experiment, period, gear, fate, and age or length level, we generated 1000 sets of new tag returns using a random binomial generator ("rbinom" function in R), which only required the observed number of red drum tagged and returned. The glm was then fit to each of the new simulated data sets, and back-transformed and re-scaled selectivity estimates were predicted for each unique combination of independent variables. The standard deviation of the 1000 simulated selectivity estimates was used as a measure of precision for the selectivity estimates based on the observed tag returns.

The minimum allowable number of tag returns from a particular experiment was examined by comparing estimates of selectivity and variances using the following criteria: (1) at least one tag return per experiment, (2) at least ten returns per experiment, (3) at least 100 returns per experiment, and (4) at least one tag return in at least 50% of the length bins per experiment. The four data selection criteria yielded similar results, so we used a minimum of one tag return per experiment for all analyses.

A description of the programming method in R is provided in Appendix A.

2.3. Model selection

We used Akaike's information criterion (AIC; Akaike, 1973; Burnham and Anderson, 2002) to compare the selectivity patterns of full models to a variety of reduced models. Burnham and Anderson (2002) advocate for carefully developing a limited set of reduced models based on a priori hypotheses. In our study, a limited number of reduced models were included in the model set based on our knowledge of the red drum fishery and the results of Bacheler et al. (2008), who showed that selectivity was affected by age of red drum, regulation period, and fate of the fish. The model with the lowest AIC value was considered the most parsimonious, or one that represents the data adequately with the fewest number of parameters (Box and Jenkins, 1970). AIC was calculated as:

$$AIC = -2\log\left[L(\hat{\theta})\right] + 2K,$$
(2)

where $L(\hat{\theta})$ is the likelihood of model θ and K is the number of parameters in the model.

Overdispersion in tag-return data is often observed because the data consist of counts (Anderson et al., 1994). We dealt with the issue of overdispersion by estimating a variance inflation factor \hat{c} (Burnham and Anderson, 2002; Richards, 2008) for the global model, which was then incorporated in a revised information criterion (Lebreton et al., 1992):

$$QAIC = -\left[\frac{2\log(L(\hat{\theta}))}{\hat{c}}\right] + 2K.$$
(3)

The number of parameters for 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} (age models = 1.56; length model = 1.13), as recommended by Burnham and Anderson (2002). Because QAIC values contain several unknown constants, we calculated the simple differences between each model *i* and the model with the lowest QAIC value (*min*):

$$\Delta QAIC = QAIC_i - QAIC_{min}, \tag{5}$$

which allows an easy interpretation of the ranking of each candidate model. Last, Akaike weights (w_i) were calculated to better interpret the relative likelihood of each model:

$$w_i = \frac{\exp(-(1/2)\Delta_i)}{\sum_{r=1}^{R} \exp(-(1/2)\Delta_r)},$$
(6)

where Δ_i is the Δ QAIC value for the *i*th model and Δ_r is the Δ QAIC value for each value in the set of models. Therefore, the w_i is the weight of evidence for model *i* being the best model in the model set (Burnham and Anderson, 2002).

2.4. Assumptions

(1) Tag loss, post-tagging mortality, natural mortality, and reporting rates are assumed to be independent of fish age or length within each tag type.

Within a particular tag type, there is no reason to believe that tag loss or post-tagging mortality is variable across fish length or age. Natural mortality should be negligible for a 120day period for fish of this size range.

(2) Exploitation and recovery rates did not change within a regulation period for a given tag type.

In previous work, fishing mortality rates of red drum appeared to be quite consistent within each of the three regulation periods examined in this study (Takade and Paramore, 2007; Bacheler et al., 2008).

(3) Fish did not grow out of their length or age bin before they were recovered.

By limiting recoveries to 120 days, we minimized the chance that fish would grow into the next age or length bin. Violations of this assumption would tend to blur the divisions between age or length categories used in the analyses.

(4) Tagged fish are mixed with untagged fish.

Tagging models assume that tagged fish are mixed with untagged fish, so that what happens to tagged fish extrapolates to the larger population. See Section 4 for a full treatment of this assumption for the current analysis.

- (5) Fish are assigned to correct age or length bins.
- The rapid growth and clear separation of length modes through age 3 made it easy to age red drum based on their length at tagging using the 6-month age-length key. Moreover, only length at tagging was used in this analysis, which came from NCDMF employees and a group of trained recreational fishers. We did not use multiple recoveries of tagged fish in our analysis, so the reported lengths of fish from fishers were not required.
- (6) Tag returns are assigned to a correct "fate" category.

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Table	2

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	Number tagged	Harvested			Caught-and-released			Total
		Hook	Gill	Pound	Hook	Gill	Pound	
Early								
Age-1	5605	264	408	116	23	25	275	1111
Age-2	512	31	2	1	10	1	0	45
Age-3	284	6	3	0	0	0	0	9
Age-4+	2868	6	4	0	4	0	0	14
Middle								
Age-1	10,367	104	109	21	359	93	596	1282
Age-2	3396	101	54	9	32	15	18	229
Age-3	605	8	2	1	2	0	0	13
Age-4+	4409	5	0	1	6	0	0	12
Late								
Age-1	3794	20	15	0	104	37	0	176
Age-2	7806	147	72	2	263	77	0	450
Age-3	1874	18	20	0	51	4	0	83
Age-4+	9024	1	0	0	47	0	3	51
Total	50,544	711	689	151	901	252	892	3596

We assume that fishers were truthful about whether they harvested or released tagged red drum in our study.

3. Results

Overall, 50,544 red drum were tagged in total by NCDMF and NCSU in 1983–2007 (Table 2). Red drum ranged from 142 to 1473 mm TL at tagging (Fig. 2). More age-1 red drum (39%) were tagged than age-4+(32%), age-2 (23%), or age-3 fish (6%). Over twice as many fish were tagged in the middle and late regulation periods compared to the early period (Table 2). Tagging of age-2, -3, and -4+ red drum increased over time, while most age-1 red drum were tagged in the middle regulation period, with the fewest in the late regulation period (Table 2). Red drum were tagged throughout all coastal and estuarine habitats of North Carolina (Fig. 1).

Overall, there were 5665 recoveries (11.2% recovery rate); 3596 of these recoveries occurred within 120 days by hook-and-line, gill nets, and pound nets (Table 2) and were used in the selectivity analyses. Fish recovered within 120 days ranged from 172 to 1321 mm TL, with most ranging from 300 to 499 mm TL (Fig. 2). Upon recovery, more fish were released (57%) than harvested (43%), and there was an increasing trend to release more fish in later regulation periods in the hook-and-line and gill net fisheries (Table 2). Tag returns from harvested red drum were primarily from the hook-and-line (46%) and gill net fisheries (44%), with few returns from the pound net fishery (10%); the fewest released red drum came from the gill net fishery (12%). Similar to the distribution of tagging, red drum recoveries occurred broadly throughout coastal North Carolina (Fig. 1).

The most parsimonious age-based model determined by QAIC was our base model that included all main effects (age, regula-



Fig. 2. Number of red drum tagged (light gray) and recovered (dark gray) in North Carolina based on their length (mm total length) or age at tagging. Note the different y-axis values between the two panels.

Table 3

Candidate models fitted to age-based or length-based tag and return data for red drum using generalized linear models; QAIC was used to evaluate model performance. All predictor variables are categorical, and the variable for tag type (i.e., experiment) was included in every model. Variables are as follows: K = number of parameters, w_i = normalized Akaike weights, age = age class, length = length class, period = regulation period, fate = fate of the fish upon recovery, and gear = gear type.

Model	Log likelihood	K	AIC	QAIC	ΔQAIC	Wi
Age model						
Base ^a	-629.0	40	1336.1	597.2	0.0	1.00
Base except age × period	-680.5	34	1427.0	627.5	30.3	0.00
Base except age \times gear	-688.4	34	1442.7	634.0	36.8	0.00
Base except age \times fate	-719.2	37	1510.4	665.4	68.1	0.00
Base except period × gear	-852.3	36	1774.6	772.8	175.6	0.00
Base except gear × fate	-1030.9	38	2135.8	923.7	326.4	0.00
Base except period × fate	-1081.8	38	2237.6	965.5	368.3	0.00
Base except period	-1404.6	26	2859.1	1206.9	609.7	0.00
Base except fate	-1512.5	32	3087.0	1307.6	710.4	0.00
Base except gear	-1688.7	26	3427.5	1440.6	843.3	0.00
Base except all interactions	-2094.7	17	4221.4	1756.4	1159.1	0.00
Base except interactions and gear	-2198.8	15	4425.7	1838.0	1240.8	0.00
Length model						
Base ^a	-892.0	82	1946.0	1559.6	0.0	1.00
Base except length × period	-967.2	62	2056.3	1637.2	77.6	0.00
Base except length × gear	-998.1	62	2118.2	1685.5	126.0	0.00
Base except length × fate	-1089.1	72	2320.2	1848.0	288.4	0.00
Base except period × gear	-1284.5	78	2723.0	2165.7	606.1	0.00
Base except gear × fate	-1282.9	80	2723.8	2167.1	607.6	0.00
Base except period × fate	-1348.4	80	2854.7	2269.5	710.0	0.00
Base except period	-1822.3	54	3750.5	2959.0	1399.4	0.00
Base except fate	-1883.7	67	3899.4	3081.1	1521.5	0.00
Base except gear	-2000.0	54	4106.0	3237.1	1677.5	0.00
Base except all interactions	-2538.1	24	5122.1	4018.9	2459.3	0.00
Base except interactions and gear	-2639.5	22	5321.0	4173.6	2614.0	0.00

^a All main effects and first-order interactions.

tion period, gear, and fate), as well as all first-order interactions (Table 3). Reduced models received essentially no support from the data based on \triangle QAIC values and normalized Akaike model weights (Table 3).

Selectivity tended to increase on older fish, decrease on younger fish, or both in response to regulation changes (Fig. 3). In the early regulation period, selectivity was highest on age-1 red drum for all gears and fate combinations except harvested fish in the hook-andline fishery, which was highest for age-2 fish. In the late regulation period, however, selectivity on harvested fish in all gears was dome-shaped and centered on ages of red drum within the legal window limit (ages 2 and 3). Selectivity of caught-and-released red drum was highest on age-1 fish in the early and middle regulation periods, but increased for all older age classes, especially age-2 and age-3 fish (Fig. 3).

Age-based selectivity estimates across all gears (Fig. 4) were generally similar to estimates of Bacheler et al. (2008), with two differences. First, Bacheler et al. (2008) estimated a lower selectivity of age-1 fish than the present study (Fig. 4). Second, selectivity of harvested and caught-and-released age-3 red drum in the late regulation period was substantially higher in our study than estimated by Bacheler et al. (2008).

Similar to the age-based model, the most parsimonious lengthbased model determined by Δ QAIC values and normalized Akaike model weights was the base model that included all main effects (length, regulation period, gear, and fate), as well as all first-order interactions (Table 3). No reduced models received any support from the data (Table 3).

Length-based selectivity was dome-shaped for most gear, fate, and regulation period combinations (Fig. 5). Generally, selectivity on harvested red drum was highest for fish in the window limit (i.e., 500–599 mm TL), whereas selectivity on caught-andreleased red drum was highest on sublegal fish (i.e., <399 mm TL). Selectivity on the smallest caught-and-released red drum (i.e., <300 mm TL) decreased over time for all gear and fate combinations, while selectivity increased in later regulation periods on most red drum in the window limit and larger (i.e., >400 mm TL; Fig. 5).

4. Discussion

Estimating selectivity is important because it provides the critical link between the length or age structure of catch data to the length or age structure of the actual population (Taylor et al., 2005; Binion et al., 2009). There are a variety of ways to estimate selectivity, but by far the most powerful and direct method is using tag returns because the size or age availability is known (Myers and Hoenig, 1997; Clark and Kaimmer, 2006). We used 25 years of tagging and recovery data to show that the selectivity of red drum has varied by regulation period, fishing gear, and fate of the fish upon recovery. Our results address several data gaps in the management of red drum in North Carolina, while also providing a simple and practical framework for estimating selectivity by combining the Myers and Hoenig (1997) approach with simulation and information theory to select models that are easy to compute and straightforward to interpret and compare.

A critical assumption of the North Carolina red drum stock assessment is the selectivity of age-3 compared to age-2 fish (Vaughan and Carmichael, 2000; Takade and Paramore, 2007). An external estimate is required because survey data are not available and catches of age-3 and older fish decline because of an unknown combination of lower selectivity (due to offshore migration), fishery regulations (due to growth out of the window limit), and prior fishing mortality. Early assessments used the proportion of age-3 red drum legally available for harvest (i.e., proportion of age-3 fish occurring in the window limit), estimated to be 0.70 (Vaughan and Carmichael, 2000). The most recent assessment (Takade and Paramore, 2007) used a value of 0.48 based on a preliminary model run from a tag-return model (Bacheler et al., 2008). Our results suggest that selectivity on age-3 red drum has increased over time for all recovery gears and both fates. Moreover, selectivity was variable across gears within the late regulation period: 0.51 for pound nets,



Fig. 3. Selectivity (\pm 1 standard deviation) of harvested and caught-and-released red drum recovered by one of three different gear types (hook-and-line, gill nets, and pound nets) in four different age groups at tagging. Selectivity in three regulation periods (early = dotted line, open circle; middle = dashed line, filled diamond; late = solid line, filled circle) is shown for each fate and gear combination. Symbols are offset for display purposes.

1.00 for hook-and-line, and 1.00 for gill nets (overall = 1.00). Our results suggest that selectivity of age-3 red drum may be higher than currently assumed, which implies that mortality of age-3 fish may be underestimated in the stock assessment.

Red drum experience high rates of catch-and-release in North Carolina, so accounting for catch-and-release mortalities from the hook-and-line fishery is imperative (Beckwith and Rand, 2005; Vecchio and Wenner, 2007). Unfortunately, age and length data are often unavailable for released fish, so it has been difficult to estimate the ages or lengths of catch-and-release mortalities. Previous assessments estimated sizes of released fish based on the difference in lengths of harvested fish between the early and middle regulation periods, because more smaller fish were harvested in the early period when the minimum size limit was smaller. This simple calculation suggests a higher frequency of smaller fish would be released in the late regulation period. Alternatively, we used the relative returns of tagged red drum to estimate the age and length distribution of released red drum from hook-and-line, gill nets, and pound nets in North Carolina. Our results suggest that discard mortality is most frequent in small, young red drum, except for hook-and-line releases where it has become more common in larger, older fish.

Selectivity of harvested red drum was strongly influenced by regulations, generally decreasing over time on small, young fish and increasing on larger, older red drum in all gears. The decrease in selectivity for small, young fish that were harvested between the early and middle regulation periods was likely due to an increase in the minimum size limit from 356 to 457 mm TL, which greatly reduced the availability of these small fish to harvest. Similar patterns were observed in Florida after window limit regulations were instated (Murphy, 2005). However, selectivity continued to decrease in the late regulation period in our study, despite there being no change in the minimum size limit. The concomitant decrease in selectivity of small, young caught-and-released fish over the same time period suggests that the behavior of fishers may have changed to avoid catching smaller, young red drum. This may have been accomplished, for instance, by using larger hooks in the hook-and-line fishery (e.g., Bacheler and Buckel, 2004), larger mesh sizes in the gill net fishery (Takade and Paramore, 2007), or by shifting their fishing effort to areas where larger red drum are more likely to reside (Bacheler et al., 2009b).

Our selectivity analyses represent an alternative methodology to the previous work of Bacheler et al. (2008). There are three major methodological differences between the approaches of Bacheler et al. (2008) and the current study. First, Bacheler et al. (2008) estimated mortality, selectivity, and reporting rate in a single age-dependent Brownie model (Brownie et al., 1985; Jiang et al., 2007a,b), whereas the current analysis treated mortality and



Fig. 4. Age-based selectivity (±1 standard deviation) of harvested (a and c) and caught-and-released (b and d) red drum estimated across all gear types in the current study (a and b) compared to estimates from Bacheler et al. (2008; c and d). Symbols are offset for display purposes.

reporting rate as nuisance variables by examining tag returns over a relatively short time frame to isolate the effects of selectivity. Thus, the current study has fewer and more realistic assumptions. Second, Bacheler et al. (2008) could only examine selectivity patterns for all gears combined, and only in an age-based analysis; currently, there is no length-based long-term tag-return approach, while it is straightforward to use the Myers and Hoenig (1997) model to estimate length-based selectivities. By estimating selectivity of red drum for three gears in both age- and length-based analyses, we view our current selectivity modeling as a refinement and extension of Bacheler et al. (2008). Third, the current study used a 120-day window for tag returns, while Bacheler et al. (2008) used all tag returns occurring over time.

To extrapolate to the whole population, tagging models also generally assume that tagged fish are well mixed with untagged fish. A statistical framework has been developed for tag-return models to deal with non-mixing (Hoenig et al., 1998), but to the best of our knowledge this issue has not received any attention regarding the Myers and Hoenig (1997) tagging model. We can imagine two types of non-mixing scenarios for the current analysis. The first is spatial non-mixing, where the spatial distribution of tagged fish may be clustered compared to untagged fish; this is the type of non-mixing addressed by Hoenig et al. (1998). Spatial non-mixing may cause tagged fish to have a higher or lower risk of being caught relative to untagged fish, depending on the spatial heterogeneity of fishing. For red drum, spatial non-mixing is likely not a concern because tagging occurred broadly over space, and generally in locations where particular age classes were more abundant. The second is temporal non-mixing, where tagged fish are not evenly available for harvest throughout the year, perhaps due to tagging that is pulsed in certain months. Temporal nonmixing is only an issue when tag returns are limited within a short time period, as was the case in our study (but not traditional multiyear tag-return studies), and only for species that show ontogenetic changes in habitat use such as red drum (Bacheler et al., 2009b). The extent to which temporal non-mixing influenced our selectivity estimates is not known. More work is required to determine how selectivity patterns are influenced when fish are tagged in temporal concentrations throughout the year. Despite the different assumptions about mixing and others discussed above between the current study and Bacheler et al. (2008), selectivity estimates closely agreed for most age groups.

Our results indicate the presence of dome-shaped selectivity curves for many fate and gear combinations in the red drum fishery. Dome-shaped selectivity has been observed previously for a wide variety of sampling gears (Jackson and Noble, 1995; Erzini and Castro, 1998; Binion et al., 2009). The dome-shaped selectivity curves we observed are likely due to the management and ecology of red drum in North Carolina. Selectivity patterns are influenced to a large extent by the window limit centered on one or two age classes and three length classes. However, the age- and lengthdependent emigration of red drum from upper estuarine to coastal environments likely also plays a role in the low selectivity values estimated for larger, older fish (Ross et al., 1995; Latour et al., 2001; Bacheler et al., 2009c). Cases where selectivity was highest on fish below the minimum size limit likely represent situations where red drum are caught incidentally or as bycatch.

An important assumption of this approach is that factors such as tag reporting and natural mortality are independent of the length of the fish (Myers and Hoenig, 1997). Natural mortality is thought to range between about 0.04 and 0.30 annually for red drum of these age and size categories (Takade and Paramore, 2007; Bacheler et al., 2008, 2009c), so the differences among age or size classes would be negligible over a 120-day interval. We were able to use a relatively brief time after tagging, compared to 1–2 years in previous studies employing this methodology (Myers and Hoenig, 1997; Clark and Kaimmer, 2006), because of the intensive fisheries for red drum and the large number of fish tagged. An added benefit of our short recovery window is that it reduces the likelihood that fish would grow out of their length or age class between tagging and recov-



Fig. 5. Selectivity (±1 standard deviation) of harvested and caught-and-released red drum recovered by one of three different gear types (hook-and-line, gill nets, and pound nets) in eleven different length-groups at tagging. Selectivity in three regulation periods (early = dotted line, open circle; middle = dashed line, filled diamond; late = solid line, filled circle) is shown for each fate and gear combination. Symbols are offset for display purposes.

ery. Future work should attempt to choose a recovery window that balances problems associated with using a short window (i.e., temporal non-mixing, low recovery rates) with those of using a large window (i.e., age-dependent natural mortality rates, growth into next age or length bin).

Estimating selectivity using generalized linear models is suited well to an information-theoretic framework (Burnham and Anderson, 2002). Our use of QAIC allowed us to clearly identify the most parsimonious age- and length-based models, using the data to inform us whether recovery gear, regulation period, or fate of the fish influenced the selectivity patterns of red drum. The use of QAIC also permitted us to deal with overdispersion, which is an issue when analyzing count data (Richards, 2008). Most importantly, results of the QAIC approach are straightforward to compute and easy to interpret.

A major advantage of this approach is its flexibility in addressing any number of objectives or hypotheses concerning the factors influencing selectivity of fish stocks. This method is most useful in situations where large-scale tagging projects on exploited fish populations result in a relatively high proportion of recoveries, selectivity is unknown or poorly estimated in assessments, and an independent validation of selectivity would be valuable. Given the numerous tagging programs on fish stocks around the world that meet these requirements, we believe the Myers and Hoenig (1997) approach deserves wider application.

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Appendix A.

This appendix demonstrates how to code and fit the generalized linear model (glm) to estimate selectivity in R. In the example below, we provide code to estimate age-based selectivity. First, an input file ("selectivity.input") is created with seven columns: experiment (E), age class (A), regulation period (P), recovery gear (G), fate of fish at recovery (F), number of fish tagged (released), and number of fish returned (returned). Each row of the input file provides the number of released and returned red drum for each experiment, age class, and regulation period combination. Second, all predictor variables are converted to factor variables using the "as.factor" statement. The code to estimate selectivity ("selectivity") for the glm in R is:

selectivity $\leq glm(returned/released \sim E + A + P + G + F + A :$

P + A : G + A : F + P : G + P : F + G : F, weights = released,

family = binomial(link = log), data = selectivity.input). (A.1)

First-order interactions are indicated by the colon (":"), and the "weights" statement weights the proportion of tags returned in a given experiment, age class, and regulation period combination to the number of tagged fish released during that same time. The above code describes the full (base) model, to which various reduced models can be compared using QAIC. Selectivity estimates are then back-transformed and re-scaled, and standard deviations are simulated as described in Section 2. Code to estimate selectivity in SAS is provided by Myers and Hoenig (1997).

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