Fisheries Research 189 (2017) 18–34

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Full length article

Effects of environmental covariates and density on the catchability of fish populations and interpretation of catch per unit effort trends

Josh Korman[a,*], Michael D. Yard[b]

[a] Ecometric Research Inc., 3560 W 22nd Ave., Vancouver, BC V6S 1J3, Canada
[b] U.S. Geological Survey, Southwest Biological Science Center, Grand Canyon Monitoring and Research Center, 2255 N. Gemini Dr., Flagstaff, AZ 86001, USA

ARTICLE INFO

Article history:
Received 17 November 2016
Received in revised form 6 January 2017
Accepted 7 January 2017
Handled by A.E. Punt

Keywords:
Capture probability
Catchability
Stock assessment
Mark-recapture
Fishery-independent surveys

ABSTRACT

Quantifying temporal and spatial trends in abundance or relative abundance is required to evaluate effects of harvest and changes in habitat for exploited and endangered fish populations. In many cases, the proportion of the population or stock that is captured (catchability or capture probability) is unknown but is often assumed to be constant over space and time. We used data from a large-scale mark-recapture study to evaluate the extent of spatial and temporal variation, and the effects of fish density, fish size, and environmental covariates, on the capture probability of rainbow trout (*Oncorhynchus mykiss*) in the Colorado River, AZ. Estimates of capture probability for boat electrofishing varied 5-fold across five reaches, 2.8-fold across the range of fish densities that were encountered, 2.1-fold over 19 trips, and 1.6-fold over five fish size classes. Shoreline angle and turbidity were the best covariates explaining variation in capture probability across reaches and trips. Patterns in capture probability were driven by changes in gear efficiency and spatial aggregation, but the latter was more important. Failure to account for effects of fish density on capture probability when translating a historical catch per unit effort time series into a time series of abundance, led to 2.5-fold underestimation of the maximum extent of variation in abundance over the period of record, and resulted in unreliable estimates of relative change in critical years. Catch per unit effort surveys have utility for monitoring long-term trends in relative abundance, but are too imprecise and potentially biased to evaluate population response to habitat changes or to modest changes in fishing effort.

1. Introduction

Quantifying temporal and spatial trends in abundance is fundamental for evaluating effects of harvest and changes in habitat on exploited and endangered fish populations. Direct estimation of abundance based on tagging studies can be expensive or difficult to accomplish at management-relevant scales. As a result, many stock assessments depend on indices of abundance that are assumed to change proportionally with the actual abundance (Hilborn and Walters, 1992), i.e.:

$$C_t = q \cdot N_t \cdot E_t \tag{1}$$

where C_t is catch in year t, q is the time-invariant proportion of the population in year t (N_t) that is captured given effort in year t (E_t). q is referred to as catchability or the catchability coefficient in the stock assessment literature, and capture probability in the mark-recapture literature. The validity of the assumption that the catchability is constant has been questioned for decades (e.g., Paloheimo and Dickie, 1964; Ricker, 1975; Wilberg et al., 2010; Gwinn et al., 2016), and violations of this assumption have led to faulty stock assessments that contributed to the collapse of important fisheries (Hilborn and Walters, 1992). Most of the concern about catchability has focused on large commercially-exploited populations (Arreguin-Sanchez, 1996; Rose and Kulka, 1999; Thorson et al., 2016) where stock assessment models depend on fishery-dependent (data collected from commercial or recreational harvest) and sometimes fishery-independent (scientific surveys) surveys to index abundance. However, this issue also applies to smaller recreational fisheries that use information on temporal or spatial patterns in catch rates to evaluate effects of harvest management (Post and Parkinson, 2012), to assessments of endangered species that rely solely on catch per unit effort data (Kimmerer, 2008; Maunder and Deriso, 2011), and to evaluating the effects of flow on fish populations in regulated rivers (Gwinn et al., 2016).

---

[*] Corresponding author.
E-mail addresses: jkorman@ecometric.com (J. Korman), myard@usgs.gov (M.D. Yard).

http://dx.doi.org/10.1016/j.fishres.2017.01.005

Variation in catchability depends largely on temporal and spatial variation in the efficiency of the sampling gear to capture individuals, and how that gear is distributed relative to the distribution of individuals. Conceptually, if a population is distributed randomly over space, catchability can be expected to vary according to:

$$q = \frac{v}{V} \tag{2}$$

where v represents the volume sampled by the gear and V is the volume over which the population is distributed (Hilborn and Walters, 1992). If a population is distributed unevenly over different habitats, the conceptual model can be extended to,

$$q = \sum_h p_h \cdot \frac{v_h}{V_h} \tag{3}$$

where p_h represents the proportion of the population in habitat type h. In exploited fish populations, improvements in fishing technology or changes in the spatial distribution of effort can lead to increases in catchability over time (Arreguin-Sanchez, 1996; Wilberg et al., 2010) by increasing v_h in areas where p_h is large. Fishery-independent surveys attempt to avoid such pitfalls, but are still vulnerable to changes in the spatial distribution of fish relative to locations that are effectively sampled. For example, fishery-independent surveys based on bottom trawls that cannot effectively sample rocky substrate will not provide a reliable index of abundance if the proportion of the population using these habitats changes over time (Thorson et al., 2013). Using Eq. (2), v_h would be lower in rocky areas, and q will decline if p_h in rocky areas increases over time. Catchability can decline with increasing fish density in situations where handling time limits catch (i.e., the ratio of v/V declines with density), or when it causes a population to expand into habitats where the sampling gear is not deployed or has low efficiency (i.e., p_h increases in habitats where v_h is zero or low, Harley et al., 2001). This type of density-dependent change in catchability results in a hyperstable pattern between catch and abundance that can mask changes in population size (Hilborn and Walters 1992; Wilberg et al., 2010). Changes in the size structure of the population can also affect catchability due to variation in the efficiency of sampling gear to capture individuals of different sizes, and effects of fish size on selection of different habitat types where gear efficiency or sampling effort may vary (termed age- or size-selectivity in the stock assessment literature).

Tagging studies that use mark recapture models must estimate the capture probability of marked individuals, and therefore provide a means to directly measure catchability (Arreguin-Sanchez, 1996). Capture probabilities are estimated in part based on the number of marked fish recaptured relative to the number originally released (Williams et al., 2001). Abundance of the unmarked population can then be determined by expanding the catch of unmarked individuals by the capture probability. This step depends on the assumption of equal catchability of marked and unmarked individuals, which in turn requires that the two groups of fish are well mixed over areas that are sampled and those that are not. These assumptions can be relaxed to some extent by increasing the complexity of how capture probability is modelled (e.g., temporary emigration, heterogeneity among individuals). Closed population models rely on the assumption that no marks are lost due to movement, mortality, or tag loss between release and recapture events. Open population models avoid this assumption by estimating the apparent survival of marked individuals between sampling events. Closed models are easier to implement, but since the time between release and recapture must be relatively short to meet the closure assumption that marked fish do not die or move, the assumption of complete mixing of marked and unmarked groups if often more tenuous. Most mark-recapture studies treat capture probability as a nuisance parameter that must be modelled correctly to avoid bias in quantities of interest such as abundance and survival. In addition, most mark-recapture efforts are usually conducted in discrete areas or times relative to the scales used in the management of fish populations. Consequently, patterns in capture probability from mark-recapture studies are rarely viewed more broadly in relation to catchability assumptions used in stock assessments.

Here, data from a large-scale mark-recapture study of rainbow trout (*Oncorhynchus mykiss*) in Glen and Grand Canyons are used to examine variation in capture probability and how this affects inferences about population trends over two decades as inferred from a separate long-term catch per unit effort survey. Rainbow trout were introduced below Glen Canyon Dam beginning in 1964 shortly after dam closure. Changes in the flow regime from the dam beginning in the early 1990s, intended to improve the status of endangered native humpback chub (*Gila cypha*) and restore sand bars (Bureau of Reclamation, 1995) downstream of Glen Canyon, inadvertently led to an increase in natural reproduction of rainbow trout (McKinney et al., 2001; Korman et al., 2012). Although this increase was initially beneficial to the blue ribbon trout fishery in the 25 km-long Glen Canyon tailwater located immediately below the dam, it was later recognized as potentially being detrimental to humpback chub (Coggins et al., 2011) and the stability of the tailwater fishery (J. Korman and M. Yard. Unpublished data). Understanding status, trends, and responses of rainbow trout to previous and ongoing management actions is thus critical to both meeting rainbow trout fishery objectives as well as promoting recovery of humpback chub. These actions have included changes to flow from Glen Canyon Dam to reduce recruitment of rainbow trout in Glen Canyon (Korman et al., 2011) and increase survival rates of juvenile humpback chub in a critical rearing area near the confluence of the Little Colorado River (LCR, Finch et al., 2015). A major mechanical removal of rainbow trout near the LCR has also been conducted (Coggins et al., 2011), and can be triggered in the future depending on abundance of rainbow trout near the LCR and trends in the chub population.

Trends in the abundance of rainbow trout in Glen and Grand Canyons have been assessed since the early 1990s based on catch rates from boat electrofishing. A statistical catch-at-length model was applied to these data to determine effects of dam releases on annual recruitment and the extent of emigration of trout from the tailwater reach to the LCR confluence (Korman et al., 2012). Results from this model, as well as from simpler assessments based on the catch per unit effort time series (McKinney et al., 2001), all rely on the assumptions that capture probability is constant over both space and time and does not depend on trout abundance. In 2011, a large-scale mark-recapture study was initiated to better quantify trends in rainbow trout abundance and movement in Glen and Grand Canyons (Korman et al., 2016). This extensive dataset provides the rare opportunity to reliably estimate demographic and capture probability parameters over the relatively large spatial scale in which the population is managed.

In this paper, we use data from this large scale mark-recapture study in a spatially- and size-stratified open population model to estimate abundance, survival, growth, and capture probability, with an emphasis on the latter parameter. We compare the extent of temporal and spatial variation in capture probability and evaluate how it is affected by population density, fish size, and environmental covariates such as reach morphometry, discharge, and turbidity. Results are used to reconstruct the abundance trend in the Glen Canyon tailwater over the last 25 years from the historical fishery-independent catch per unit effort time series. We discuss how common assumptions about catchability affect inferences on temporal and spatial trends of rainbow trout in Glen and Grand Canyons. Our findings are also relevant to the many tailwater fisheries surveyed solely by catch per unit effort from boat electrofishing (Dibble and Yackulic, 2015), and contribute to a broader