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Kyle W. SHertzer, Nathan M. Bacheler, Lewis G. Coggins Jr, John Fieberg 2016

SEDAR56-RD16

12 January 2018



ICES Journal of Marine Science

ICES Journal of Marine Science (2016), 73(2), 512-519. doi:10.1093/icesjms/fsv197

Original Article

Relating trap capture to abundance: a hierarchical state-space model applied to black sea bass (*Centropristis striata*)

Kyle W. Shertzer^{1*}, Nathan M. Bacheler¹, Lewis G. Coggins Jr², and John Fieberg³

¹National Marine Fisheries Service, Southeast Fisheries Science Center, Beaufort, NC, USA
²United States Fish and Wildlife Service, Yukon Delta National Wildlife Refuge, Bethel, AK, USA
³Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St Paul, MN, USA

*Corresponding author: e-mail: kyle.shertzer@noaa.gov

Shertzer, K. W., Bacheler, N. M., Coggins, L. G. Jr, and Fieberg, J. Relating trap capture to abundance: a hierarchical state-space model applied to black sea bass (*Centropristis striata*). – ICES Journal of Marine Science, 73: 512–519.

Received 2 July 2015; revised 25 September 2015; accepted 6 October 2015; advance access publication 3 November 2015.

Traps are among the most common gears used to capture fish and crustaceans. When traps are deployed in surveys, the data gathered are often used to develop an index of abundance. However, trap catches are known to saturate over time for various reasons, such as space limitation of the gear or intraspecific interactions, and these features can dissociate the catch from local abundance. In this study, we develop a hierarchical state-space model of trap dynamics that is fit to data in a Bayesian framework. The model links trap catch to estimated local abundance, and additionally provides direct estimates of capture probability. For demonstration, we apply the model to data on black sea bass (*Centropristis striata*), which were collected using chevron traps combined with video cameras to give continuous-time observations of trap entries and exits. Results are consistent with the hypothesis that trap catch is generally proportional to local abundance. The model has potential application to surveys where animals not only enter a trap, but also may exit, such that the apparent trap saturation occurs because the system approaches equilibrium.

Keywords: abundance estimation, Bayesian analysis, black sea bass, fish traps.

Introduction

A basic challenge in marine fishery science and management is to quantify fluctuations in animal abundance. This is typically accomplished using stock assessment models, which are ideally fitted (or tuned) to at least one index of abundance. Such an index can be developed from fishery-dependent data on catch per unit effort (Maunder and Punt, 2004; Campbell, 2015) or from fishery-independent data collected through a sampling programme (Pennington and Stromme, 1998; Kimura and Somerton, 2006). Either way, a key assumption is that the index is proportional to actual abundance.

Fish traps are used widely around the world to index the abundance of various types of fish and invertebrates (Evans and Evans, 1996; Wells *et al.*, 2008; Rudershausen *et al.*, 2010). They are common in both commercial fisheries (Miller, 1990) and in scientific surveys (Bacheler *et al.*, 2013a). For many species, trap gear is advantageous for its ability to capture animals effectively, with relatively minimal impact on local habitat. However, the number of animals inside of a trap is known to saturate with soak time for a host of reasons, including space limitation of the gear, interspecies or intraspecies interactions, or the loss and degradation of bait (Miller, 1979; Jury *et al.*, 2001). This feature can result in a catch that relates non-linearly to local abundance and, consequently, can lead to bias of unknown and varying degrees in any index of abundance derived from trap data (Robertson, 1989; Addison and Bell, 1997; Fogarty and Addison, 1997).

Several studies have modelled trap saturation (e.g. Munro, 1974; Addison and Bell, 1997; Fogarty and Addison, 1997). A common recommendation is that traps should be hauled after a short soak time, before the gear becoming saturated. That recommendation attempts to address the non-linearity between local abundance and the saturated catch of longer soak times, which is critical if the resulting data are to be used to index abundance.

Here, we build on those previous studies, developing a hierarchical state-space model (Royle and Dorazio, 2008) of trap dynamics that relates local abundance to catch without the need for an

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International Council for the Exploration of the Sec abbreviated soak time. In this model, animals not only enter the trap, but may also exit. This two-way flow results in a trap catch that saturates, not because of any gear effect, but because the system approaches a steady-state equilibrium (Bacheler *et al.*, 2013b). In addition, the model yields estimates of capture probability, a quantity that has received widespread attention in the sampling of animal populations (Williams *et al.*, 2002).

As an example system, we apply the model to black sea bass (*Centropristis striata*) in Atlantic waters off the southeastern United States. Black sea bass and other reef-associated species are monitored through fishery-independent sampling conducted by the SouthEast Reef Fish Survey (SERFS; see Bacheler *et al.*, 2014), which uses a combination of chevron traps and underwater video gear. Traps are well suited for sampling reef fish because they can fish unattended, can be deployed in many different habitat types, are relatively inexpensive and robust, and catch fish alive so that bycatch individuals can be released (Miller, 1990). Black sea bass are an ideal species for this study because they readily enter and exit the traps (Bacheler *et al.*, 2013b). Furthermore, this application has practical implications because SERFS trap data are used to develop indices of abundance for stock assessments of black sea bass (SEDAR, 2011).

The primary motivation behind our study was to investigate the utility of trap data for monitoring abundance. Our model of trap dynamics has potential application to systems with two-way flow of individuals between areas outside and inside the gear. Using black sea bass as a case study, we focus on the question of whether the equilibrium catch in traps relates linearly to the unobserved local abundance.

Methods

Trap and video sampling

Samples for this study were collected by SERFS off Georgia and Florida on the southeastern United States continental shelf. All sampling occurred during daylight hours between April and September 2012 and 2013, aboard the RV *Savannah*. The SERFS targets reef-fish species that tend to associate with scattered patches of hard substrates in the region. These hard substrates are diverse and can be characterized by flat limestone pavement, ledges, rocky outcroppings, or reefs, often colonized by various types of attached biota (Schobernd and Sedberry, 2009; Fautin *et al.*, 2010). The SERFS deploys chevron traps with attached, outward-looking video cameras using a simple random sampling design, whereby sampling locations are randomly selected each year from a sampling frame of ~3000 hard-bottom stations.

Chevron traps used in this study were shaped like an arrowhead that measured 1.7 m \times 1.5 m \times 0.6 m, and were made from plasticcoated galvanized 12.5 G wire with a mesh size of 3.4 cm \times 3.4 cm (Figure 1a in Bacheler *et al.*, 2013b). The funnel of each trap was constructed from hexagonal wire mesh \sim 3.4 cm in diameter, and the mouth opening was shaped like a teardrop measuring 18 cm wide and 45 cm long. Each trap was baited with 24 menhaden (*Brevoortia* spp.), 16 of which were attached to four freely accessible stringers and the other 8 placed loosely inside the trap. The traps were deployed individually in groups of six with \sim 400 m (minimum, 200 m) between traps. This distance was far enough apart that effective fishing areas did not overlap, thus avoiding the potential for surplus gear deployment to affect catch per unit effort (Groeneveld *et al.*, 2003). Soak times were \sim 90 min. For this study, a video camera on each trap was turned inward to monitor the trap itself, positioned so that reef fish entries and exits through the mouth opening could be quantified (Figure 1b in Bacheler *et al.*, 2013b; see Supplementary material for an example video segment). To do so, each trap was deployed with a highdefinition GoPro Hero[®] video camera attached to the side of the trap. Cameras were turned on before traps were deployed and turned off after the traps were retrieved, so that video captured the entirety of each gear deployment.

Data collection and treatment

We recorded the time of day when the trap reached the bottom and the time when the trap retrieval process began. For all analyses, soak time was defined as the time that elapsed between when the trap reached the bottom (began fishing) and when its retrieval commenced (stopped fishing). In general, a soak time of 90 min was sufficient for the catch of black sea bass to saturate (Bacheler *et al.*, 2013b). The times of each individual entry and exit for black sea bass were recorded for the entire soak time. To qualify as an entry or exit, an individual fish must have completely crossed the plane of the trap mouth. We could not distinguish unique individuals within a species, so the same individual may have entered and exited the trap multiple times. The number of individuals in the trap for each minute of soak time was calculated as the cumulative number of entries minus the cumulative number of exits, and we define the catch to be the terminal abundance inside the trap.

In all, 36 videos of chevron traps were collected in 2012/2013 documenting entries and exits of black sea bass; however, a subset of those videos was appropriate for our analysis. Five videos were excluded because few (<15) black sea bass were caught. Five were excluded because black sea bass comprised <80% of the total catch; this criterion was applied because we did not attempt to model interspecies interactions. Four were excluded because the catch had not yet saturated during the soak time, and therefore, these videos provided no information on local abundance. These filters left 22 time-series of black sea bass trap dynamics, with observed catches ranging from 18 to 188 fish. For fitting the model to these data, we began each time-series in the first minute when black sea bass entered the trap. Thus, our model does not attempt to quantify search behaviour, but rather the process of entries and exits once the trap has been discovered by fish on the sampling site.

Model of trap dynamics

Our underlying model is a two-state, first-order Markov chain that tracks the flow of animals between the local area outside of the trap and inside the trap (Figure 1):

$$X_{t+1} = -aX_t + bY_t,\tag{1}$$

$$Y_{t+1} = aX_t - bY_t. (2)$$

Here, X is the unobserved local abundance outside of the trap, Y the abundance inside the trap, t represents time, parameter a represents the rate of entry into the trap, and parameter b represents the rate of exit. We define X as the local abundance within the effective fishing area of the trap, which could depend on a range of factors such as bait efficiency, environmental conditions (e.g. temperature, current), and ecological influences (e.g. prey and predator abundances). Throughout, we refer to the "effective fishing area" as a "site." Given that animals on the site are either outside or inside the trap,



Figure 1. Conceptual model of trap dynamics at a sampling location. Individuals enter the trap at per capita rate a, and exit the trap at per capita rate b. Assuming a closed system, the total abundance equals abundance outside (X) and inside (Y) the trap.

the total abundance is N = X + Y. Furthermore, we know the initial conditions of the state variables, X(0) = N and Y(0) = 0. Thus, this system is fully defined by three parameters: *a*, *b*, and *N*.

Equations (1) and (2) predict that abundance within the trap will saturate over time. This occurs not because of any gear effect, but simply because the system reaches equilibrium. As *t* increases, *Y* approaches aN/(a + b). This asymptotic relationship reveals two notable features of the model. First, if *a* and *b* are constant, and given a long enough soak time, the catch relates linearly to total abundance at the site. Second, the asymptotic relationship provides an estimate of capture probability, a/(a + b), defined as the proportion of total (local) abundance that is contained within the trap, once the trap dynamics reach an equilibrium state.

We constructed a generalized version of the model in which local abundance and entry and exit rates were all site-specific:

$$X_{i,t+1} = -a_i X_{i,t} + b_i Y_{i,t},$$
(3)

$$Y_{i,t+1} = a_i X_{i,t} - b_i Y_{i,t},$$
(4)

with $N_i = X_{i,t} + Y_{i,t} = X_{i,0}$ at site *i*. We used a compound gamma-Poison mixture to model the unobserved total abundance at each sampling location (N_i):

$$N_i \sim \text{Poisson}(\lambda_i), \text{ with } \lambda_i \sim \text{Gamma}(\alpha_N, \beta_N).$$
 (5)

We specified uniform hyperpriors for α_N and β_N :

$$\alpha_N \sim U(0, 20); \quad \beta_N \sim U(0, 2).$$
 (6)

We modelled expected entry (a_i) and exit rates (b_i) as normally distributed random effects on the logit scale:

$$logit(a_i) \sim N(\mu_a, \sigma_a^2),$$
 (7)

$$\operatorname{logit}(b_i) \sim N(\mu_b, \sigma_b^2). \tag{8}$$

We used normal and uniform hyperprior distributions for the mean and standard deviations of the random effect distributions, respectively:

$$\mu_a \sim N\left(0, \frac{1}{3}\right); \quad \mu_b \sim N\left(0, \frac{1}{3}\right).$$
 (9)

$$\sigma_a \sim U(0, 6); \quad \sigma_b \sim U(0, 6).$$
 (10)

Last, we modelled the number of entries $(A_{i,t})$ and exits $(B_{i,t})$ at each time-step using binomial distributions:

$$A_{i,t} \sim \operatorname{Bin}(X_{i,t}, a_i). \tag{11}$$

$$B_{i,t} \sim \operatorname{Bin}(Y_{i,t}, b_i). \tag{12}$$

Our model did not attempt to quantify observation error, which is negligible because the observed entries, exits, and trap abundance could be monitored accurately and with high precision. However, Equations (11) and (12) account for process error, and since the numbers of entries and exits depend on the current state of the system, the approach naturally includes autocorrelation in the trapping process.

Fitting the model to data

We fit the model to data in a Bayesian framework using JAGS version 3.4.0 (Plummer, 2003) and R version 3.1.1 (R Development Core Team, 2014) with the package R2jags (Su and Yajima, 2015) to communicate between the two platforms. We ran three independent chains, each for 50 000 iterations. Posterior distributions were computed after discarding the first 10 000 iterations (burn-in). We assessed convergence qualitatively by inspecting posterior density plots and trace plots, and quantitatively using the Brooks–Gelman–Rubin statistic (Brooks and Gelman, 1998). For all parameters, Brooks–Gelman–Rubin statistics were <1.03, indicating successful convergence.

Point estimates of parameters were taken as the median from the posterior distributions, and credible intervals were represented by the 2.5 and 97.5 percentiles. In addition, predicted time-series of the catches were computed by simulation. For each set of parameter values from the Markov chain Monte Carlo (MCMC) procedure, stochastic trap dynamics were simulated using Equations (11) and (12) to provide 120 000 predictions of each sampling event (i.e. trap). From these predictions, we computed central tendencies (medians) and credible intervals (2.5, 97.5 percentiles) of the trap abundance over time.

Before fitting the model to actual data, we considered whether all parameters were estimable. To test this, we fit the model to simulated data that were similar in structure to our real dataset. We found that the known, data-generating parameters could be estimated accurately.

Results

In general, the model matched well to the observed data (Figure 2). For most traps, both predicted and observed trap abundance saturated by the time the gear was extracted. Several instances of mismatch were apparent early in the time-series, where observations fell outside the credible intervals. This may have occurred because of factors unaccounted for by the model, for example, spatial variability in search or schooling behaviour.

Point estimates of entry rates across sampling sites ranged from 0.003 to 0.138, with a mean value near 0.024 (Figure 3a). The corresponding estimates of exit rates ranged from 0.005 to 0.047, with a mean near 0.019 (Figure 3b). Point estimates of site abundance ranged from 50 to 751 individuals, with large differences among trapping sites in the level of precision, as indicated by 95% credible intervals (Figure 3c).

Expected capture probabilities (Figure 3d) were not estimated by the model directly, but instead were computed as a function of the estimated parameters, $a_i/(a_i + b_i)$. The mean capture probability was 0.43, but there was much variability across sites. The coefficient



Figure 2. Observed (open circles) and predicted (solid lines: 2.5, 50, and 97.5 percentiles) abundances of fish within traps over time. Trap identification number is shown in the upper left corner of each panel. Note differences of scale in the *y*-axes.

of variation (*CV*) of capture probabilities was CV = 0.63. Values were negatively correlated with estimated abundance (Pearson correlation = -0.69; p < 0.01).

Estimated total abundance generally increased with trap catch (Figure 4). A simple linear regression of observed trap catch on point estimates of site abundance had a positive slope of 0.09



Figure 3. (a) Model estimates of entry rates by trapping site. (b) Model estimates of exit rates by trapping site. (c) Model estimates of total abundance at each site. (d) Expected capture probabilities at each site, computed from the point estimates of exit rates and the entry rate, as described in the text. In (a) – (c), point estimates are represented by medians from posterior distributions, and credible intervals by 2.5 and 97.5 percentiles.

(s.e. = 0.04; Student's *t*-test: t = 2.05, p = 0.05). Although this linear relationship was a feature of the underlying deterministic model, it need not have resulted from the fitted stochastic model

where entry and exit rates were treated as random effects. For example, if the model predicted a pattern of smaller (or larger) entry rates when observed catch was larger, we would expect a



Figure 4. Relationship between the point estimates of abundance on the site and the trap catch (abundance in trap at time of haul). Solid line shows a linear regression to the values (filled circles).

non-linear relationship between trap catch and estimated site abundance. To test for this type of potential non-linearity, we applied a likelihood ratio test, comparing the simple linear regression with a regression that had additional square, cubic, and quartic terms (i.e. $Y = \beta_0 + \beta_1 N + \beta_2 N^2 + \beta_3 N^3 + \beta_4 N^4$). In this test, the null model of simple linear regression was favoured ($\chi^2 = 2.35$, p = 0.50). Similar results were found when comparing the simple linear regression with extended models that dropped the quartic term ($\chi^2 = 1.96$, p = 0.38) or dropped the cubic and quartic terms ($\chi^2 = 0.02$, p = 0.89). Although these results are not conclusive evidence that trap catch relates linearly to abundance, they are consistent with that hypothesis.

Discussion

A key feature of the model developed in this paper is that it relates trap catch to local abundance. Without an approximately linear relationship between catch and abundance, any index of abundance derived from the data is likely to be variably biased. We say "approximately linear" because ecological systems are inherently stochastic. However, we note that deviation surrounding an expected relationship can often be modelled through index standardization techniques that account for influential factors such as bottom temperature, depth, or latitude (Maunder and Punt, 2004).

Another feature of the model is that it provides direct estimates of capture probabilities when soak time is sufficient for the system to equilibrate. In fisheries applications, reliable estimates of capture probability are frequently only possible with substantial investments in capture–recapture studies. Here, we demonstrate the utility of camera-based observations to obtain estimates of capture probability for each trap deployment. Such fine-scale information makes possible the analysis of the variability in capture probability, which is rarely feasible in capture–recapture studies because of small sample sizes. Future efforts could evaluate the effects of various environmental, ecological, and physiological conditions on capture probability by incorporating candidate covariate effects into the modelling framework. For example, entry rates could be made a function of water temperature.

Estimates of capture probability generated through fine-scale camera observation studies could be useful in other applications, such as defining prior distributions of capture probability for use in N-mixture (Royle, 2004) or occupancy models (MacKenzie *et al.*, 2002; Coggins *et al.*, 2014). Additionally, if coupled with sufficient information on spatial distribution of the population, estimates of capture probability could be paired with spatially representative samples of trap catches to estimate abundance. Such information could be used both as an abundance index and as an alternative assessment method. Clearly, estimating capture probability when conducting fisheries independent sampling increases the utility and applicability of the information substantially.

Our dataset on black sea bass, through the use of inward-looking video, provided a rare opportunity to fit models of trap dynamics. For proof of concept, we chose to filter the dataset to include only those traps that contained mostly our focal species (black sea bass) and were without known predators. Future work might relax these filters and attempt to elucidate potential species interactions. However, for most surveys that catch multiple species, we would not have the benefit of inward-looking cameras to quantify real-time species interactions. When developing indices of abundance from multispecies surveys, it might be worth considering filtered data that are relatively clean for the species in question, unless the effects of interactions are well understood.

In our model, we treated the entry rates and exit rates across traps as random effects. Of course, other configurations of this model are possible, such as treating one of the rates as a random effect and the other as a fixed effect, or both rates as fixed effects. Indeed, we considered all four configurations during earlier stages of model development, and we chose to focus on the model with both rates as random effects because it provided the best (lowest) deviance information criterion. In addition, our simulation study supported that all parameters were estimable, so it seemed sensible *a priori* to fit the full random effects model, allowing the variance component of either transition rate to be estimated near zero if it displayed little variation among trapping locations. We also considered different configurations of prior and hyperprior distributions, and found results to be insensitive to these model changes.

Catch of black sea bass reached steady-state equilibria at a wide range of values (18-188 fish), suggesting that gear effects were not the primary limiting influence. Furthermore, our model demonstrates that the steady states are reached once entries and exits balance (Bacheler et al., 2013b). This explanation is contrary to the common assumption that trap catch asymptotes as a result of diminishing entry rates, highlighting the importance of understanding the mechanism underlying the apparent saturation of catches. The choice of modelling approach may differ if saturation is known to result from a gear effect, such as space limitation or bait degradation, or from interactions among different species or individuals of the same species. For example, crabs and lobsters are less likely to enter traps already containing conspecifics (Miller, 1990; Addison and Bell, 1997; Jury et al., 2001). In those cases, our model could be modified to account for entry (or exit) rates that depend on abundance in the traps.

In addition, our model results are consistent with the hypothesis that trap catch of black sea bass is generally proportional to local abundance, as indicated by the model's close fit to data. Even so, we acknowledge that a good fit does not exclude the possibility of other potential model structures performing well. In a recent assessment of this stock, an index of abundance developed from chevron traps was compared with multiple indices developed from baited hooks (SEDAR, 2011). We would not expect these indices to track each other if chevron traps provided a biased index because of non-linearity between the catch and abundance. However, they were strongly correlated, suggesting that the various indices were all driven by the same causal signal (e.g. abundance).

Many different gears are used around the world to monitor marine fish abundance and biodiversity, each with advantages and shortcomings. In the southeast United States and elsewhere, video surveys have become prevalent, primarily because they can be effective without causing appreciable harm to fish or habitat (Harvey et al., 2012; Mallet and Pelletier, 2014; Schobernd et al., 2014). Nonetheless, understanding trap dynamics remains important for several reasons. First, traps are still a widely used survey gear, even while other sampling methods are gaining popularity. Second, even if all trapping were to cease today, historical trap data can provide time-series of abundance signals for use in stock assessments. For example in the southeast United States, trap monitoring of Atlantic reef fish such as black sea bass started in 1990, whereas videos were not used broadly until 2011. Third, traps are commonly used by commercial fisheries, and if catch saturation is not due to a gear effect, those data may be useful to infer relative abundance. Fourth, traps are one of the few sampling gears that can be effective in untrawlable habitats or where visibility for video or dive surveys may be poor. Fifth, traps can provide biological samples (otoliths for ageing, reproductive tissue, diet information, mercury content, DNA) that can be invaluable for assessment and management. Furthermore, approaches that combine multiple gears, such as traps and videos, may prove to be the most effective means for monitoring marine fish (Coggins et al., 2014).

Whether the catch from traps relates linearly to abundance depends on the mechanism(s) underlying catch saturation. One possible mechanism, explored here, is the balancing of entries and exits. In the black sea bass example, the hypothesis that trap catch was proportional to local abundance was consistent with our model results, and it seemed well supported by additional lines of evidence. For this and other species with similar trapping behaviour, such a result supports the critical assumption in play when using trap data to develop indices of abundance.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

We thank SERFS staff, volunteers, and the captain and crew of the RV *Savannah* for making the fieldwork possible. The paper benefited greatly from comments by Todd Kellison, Katie Siegfried, Shijie Zhou, and anonymous reviewers.

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Handling editor: Shijie Zhou