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ARTICLE

Estimating population abundance at a site in the open ocean: combining information from conventional and telemetry tags with application to gray triggerfish (*Balistes capriscus*)

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Abstract: Estimates of animal abundance are widely used to support conservation and resource management. For populations in open systems, abundance estimates from tagging data can be highly uncertain or biased. Here, we develop a novel approach to estimate abundance of an open population by pairing two models, each utilizing distinct tagging data. Using data from telemetry tags, we infer movement rates to and from the study site with a Markovian model allowing for an environmental effect. Then, using data from conventional passive tags, we apply a Lincoln–Petersen abundance estimator modified to account for mortality and movement. After developing the model within a Bayesian framework, we demonstrate its application to data on gray triggerfish (*Balistes capriscus*) tagged in the Atlantic Ocean off North Carolina, USA. For this open population, we estimate site abundance to be ~1000 fish (~2000 fish·km^{-2}) and additionally find evidence for an effect of hurricanes on movement. The general approach may be useful for fisheries, wildlife, and other ecological studies utilizing multiple tag types, particularly for estimating abundance of an open population.

Résumé : Les estimations de l'abondance d'animaux sont largement utilisées pour appuyer la conservation et la gestion des ressources. Pour les populations au sein de systèmes ouverts, les estimations de l'abondance obtenues de données de marquage peuvent s'avérer très incertaines ou biaisées. Nous présentons une nouvelle approche pour estimer l'abondance d'une population ouverte qui jumèle deux modèles utilisant des données de marquage différentes. En utilisant des données d'étiquettes télémétriques, nous inférons les taux de déplacement en direction et en provenance du site d'étude à l'aide d'un modèle markovien qui permet l'intégration d'un effet environnemental. Puis, en utilisant des données d'étiquettes passives classiques, nous appliquons un estimateur d'abondance de type Lincoln–Petersen modifié pour tenir compte de la mortalité et des déplacements. Après avoir présenté le modèle dans un cadre bayésien, nous démontrons son application à des données sur des balistes capris (*Balistes capriscus*) étiquetés dans l'océan Atlantique au large de la Caroline du Nord (États-Unis). Pour cette population ouverte, nous estimons l'abondance au site d'étude ~1000 poissons (~2000 poissons·km^{-2}) et observons en outre des signes d'un effet des ouragans sur les déplacements. L'approche générale pourrait être utile pour les études sur les pêches, les espèces sauvages et d'autres études écologiques reposant sur plusieurs types d'étiquettes, notamment pour estimer l'abondance de populations ouvertes. [Traduit par la Rédaction]

Introduction

Estimating abundance is one of the most basic challenges in population ecology. As such, ecologists have devoted much attention toward understanding how abundance changes over space and time or in response to some type of disturbance or management action. For marine fish populations, including those that are harvested or of conservation concern, stock assessment models are a common tool for estimating abundance. These models generally estimate abundance indirectly using information on population, fishing, and sampling processes (each with their own assumptions and uncertainties) to provide resource managers with advice on catch levels or exploitation rates (Maunder and Piner 2015; Dichmont et al. 2016). In contrast, capture–recapture approaches can provide more direct estimates of abundance (Williams et al. 2002; Kéry and Schaub 2012), but generally without the analogous management advice. Contemporary stock as-

sessments can integrate multiple sources of data into a single modeling framework, including data obtained by tagging individual fish (Goethel et al. 2011; Maunder and Punt 2013; Sippel et al. 2015).

In addition to information on abundance, analysis of tagging data can provide insight into key population dynamic processes such as natural mortality, fishing mortality, capture vulnerability, movement, and habitat use (reviews by Crossin et al. 2017; Pine et al. 2003; Runde et al. 2018; Thorstad et al. 2013). To draw inference on these parameters, numerous types of passive and active tags have been used throughout the long history of marking animals. Passive tags, which we refer to in this paper as conventional, require recapture if the tag is to be observed subsequent to the original marking. Active tags (e.g., radio, satellite, acoustic) are electronic, allowing for real-time tracking and virtual recapture.

Conventional tags have been most useful for estimating abundance, mortality, and capture probability (Pine et al. 2003). Their application requires animals to be collected, marked, then re-

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leased; the population is subsequently resampled to examine the proportion of animals captured in future events relative to those from previous efforts.

The simplest statistical estimators of abundance assume that the population is closed (Petersen 1896; Lincoln 1930; Otis et al. 1978), both demographically (no births, deaths, emigration, or immigration) and geographically (no movement on or off the study site during sampling). Open-population models relax that assumption, but generally require higher capture probabilities to allow for separation between an animal that was present but not captured and one that was not captured because of mortality or emigration (Pollock et al. 1990).

Active tags have been utilized in marine systems for many fish, mammal, and bird species, primarily to quantify movement, habitat use, and mortality (Arnold and Dewar 2001; Thorstad et al. 2013; Hays et al. 2016). The use of telemetry tags in particular has increased due to technological advances including autonomous receivers, tag miniaturization, and improvements in battery life (Hussey et al. 2015). Telemetry provides high probability of detection when animals are moving within an array of autonomous receivers and eliminates the need for physical recapture to draw inference on location or survival. However, it generally does not allow for estimation of abundance, because it provides information on only the proportion of the population that is tracked.

Although the majority of analytical methods rely on a single active or conventional tag type, the use of multiple types simultaneously can improve estimation (Johnson et al. 2010). Most studies that utilize multiple tag types do so to allow for the separation of component processes that would otherwise not be uniquely identifiable, such as natural and fishing mortality (e.g., Pollock et al. 2004; Bacheler et al. 2009) or mortality components and migration (e.g., Kurota et al. 2009; Ellis et al. 2017). Fewer studies have used multiple tag types to estimate absolute abundance or density (e.g., Johnson et al. 2010; Gopalaswamy et al. 2012; Ivan et al. 2013; Ketz et al. 2018).

Here we present an analytical method to improve abundance estimates by simultaneously integrating information from telemetry and conventional tags. The approach combines a movement model with the Lincoln–Petersen abundance estimator (Petersen 1896; Lincoln 1930) modified to allow for a demographically and geographically open population. The movement model relies on data from telemetered fish to estimate temporally varying movement rates into and out of the site, while simultaneously accounting for tag loss or mortality. The abundance estimator applies those movement rates to fish marked with conventional tags to infer abundance. Thus, the approach not only avoids the assumption of a closed population, but also models movement explicitly. Although we focus on estimates of absolute abundance, the methods are interchangeable with estimating population density, given that the sampling area is known. This novel approach has potential to be useful in a variety of fisheries, wildlife, and other ecological studies (for example, estimating or monitoring abundance at a marine protected area). We demonstrate its utility with an application to gray triggerfish (*Balistes capriscus*) at an open-ocean site in the western North Atlantic.

Materials and methods

Modeling approach

Movement submodel

A two-state Markov model tracks the location of telemetry-tagged individuals, with X_t denoting the abundance of tagged fish inside the acoustic array on day t, and Y_t denoting the abundance of tagged fish outside. A third absorbing state L_t accounts for the cumulative number of tagged fish that are lost to the system, because they either lose their transmitter or die (Fig. 1). These fish must be accounted for; otherwise, estimates of movement rates would be biased low. Tag loss and mortality are not of primary

Fig. 1. Model diagram, where X_t represents the number of fish telemetry-tagged and present within the acoustic array on day t, Y_t represents the number of fish tagged but outside the array, and L_t represents the cumulative number of fish lost to the system (tag loss or mortality). Dashed arrows indicate stochastic processes that occur at the daily rate shown (exit rate a_t, entry rate b_t, or loss rate ψ), and the solid arrow indicates a deterministic loss process quantified by observations (L_t^X).
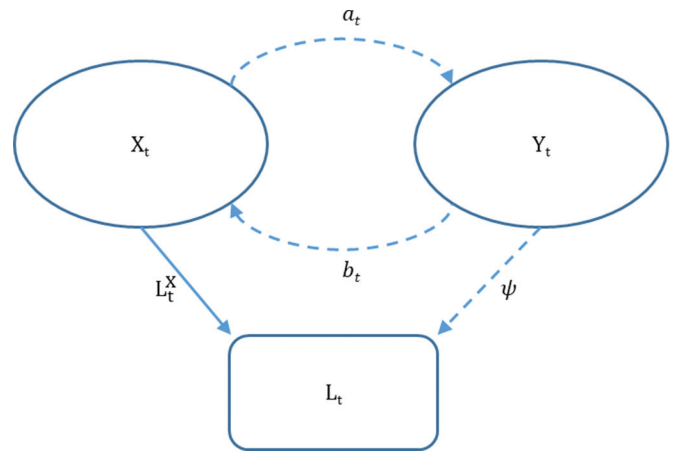
interest here, so we model these losses as a single process; however, it is possible and may be desirable to distinguish them in studies where both are considered important. Telemetry-tagged fish are assumed to be detected when located within the array, similar to a recapture probability of 1.

The number of fish inside the array that lose their tag or die on day t (L_t^X) is known, because those animals (actually, tags) stop moving for the remainder of the study or else exhibit identifiably different swimming behavior in the case of predation. Thus, the known tag loss or mortality inside the array is simply applied in the model as a deterministic process. Tag loss or mortality outside the array is unobserved, but is accounted for as a stochastic process using a binomial distribution, $L_t^Y \sim \text{Bin}(Y_t, \hat{\psi})$. Assuming that losses occur at the same rate (ψ) inside and outside the array, ψ can be estimated from the observed data, $L_t^X \sim \text{Bin}(X_t, \hat{\psi})$.

The state variables of the model are governed by

$$(1) \qquad X_{t+1} = X_t - A_t + B_t - L_t^X$$

$$(2) \qquad Y_{t+1} = Y_t + A_t - B_t - L_t^Y$$

$$(3) \qquad L_{t+1} = \sum_{\tau=1}^{t} \left(L_\tau^X + L_\tau^Y \right)$$

where A_t is the number of telemetered fish that exit the site on day t, and B_t is the number that enter the site. We modeled the observed number of exits and entries of telemetered fish on each day using binomial distributions:

$$(4) \qquad A_t \sim \text{Bin}\left[\left(X_t - L_t^X \right), a_t \right]$$

$$(5) \qquad B_t \sim \text{Bin}\left[\left(Y_t - L_t^Y \right), b_t \right]$$

The daily exit rate (a_t) and entry rate (b_t) are parameters to be estimated from the observed telemetry data on A_t and B_t. Depending on the study, these rates may be modeled as constant through time or variable, treated as a random effect or as a function of covariates. In our example application, we demonstrate an environmental effect on movement (see section below, Environmental effect on movement).

Fig. 2. Location of tagging study indicated by the black circle along the North Carolina coast (left panel) and a close-up view of the study site (right panel) showing locations of the receivers, reference transmitter, tagging, and recaptures. Bathymetry data provided by the National Centers for Coastal Ocean Science.
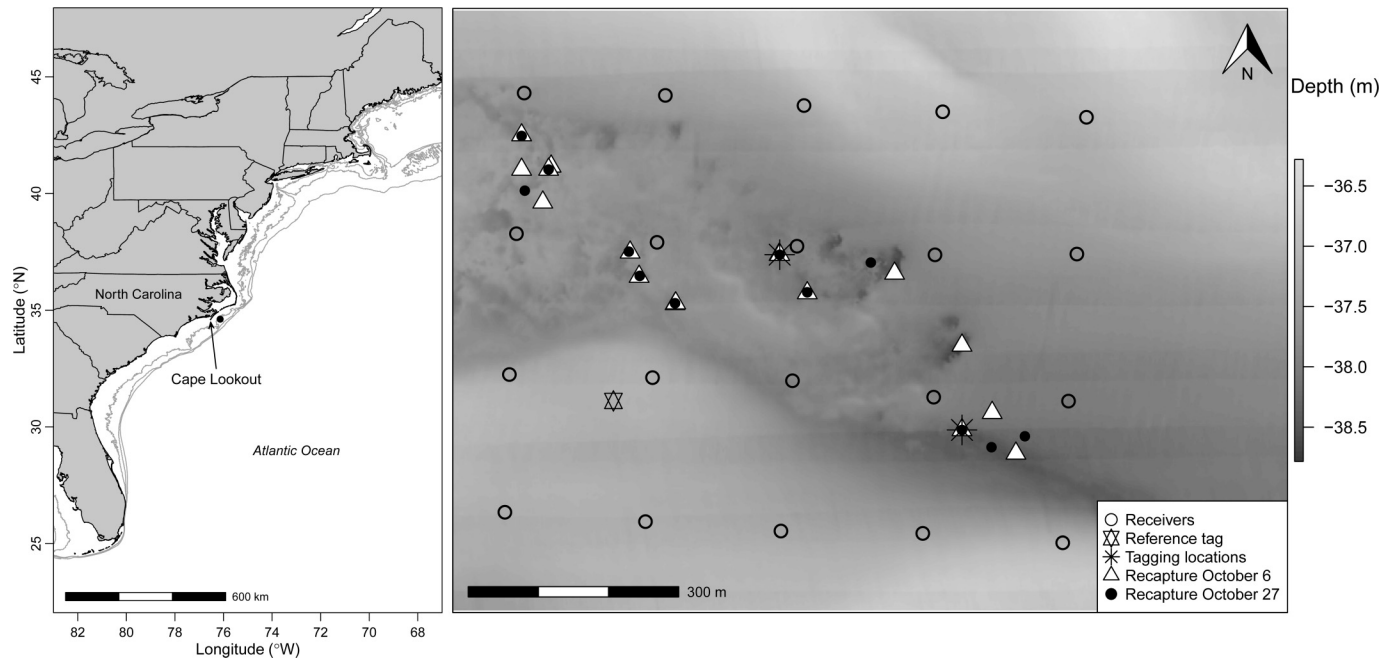
Abundance estimator

Using conventionally tagged fish, we estimate total abundance (N) with a modified Lincoln–Petersen estimator. The standard estimator is

$$(6) \qquad N = nK/k$$

where n is the number of fish initially tagged, K is the number of fish captured at a subsequent sampling event, and k is the number of recaptures that were tagged. However, this estimator assumes stationarity of the population (i.e., that the population is closed demographically and geographically). Here, we relax those assumptions.

To account for release mortality of conventionally tagged fish, we apply the survival rate λ assuming a binomial distribution, $n' \sim \text{Bin}(n, \lambda)$, where n' is the number of fish initially tagged that survive release. A similar approach could be applied on a daily basis to model natural or fishing mortality, although we do not do that here because neither source of mortality is expected to occur in our short-term gray triggerfish application.

To account for movement, we apply the movement model estimated from telemetered fish, but without the absorbing state. That state is excluded because mortality is already accounted for as described above, and tag loss is believed to be negligible for the conventional tag type used in our study of triggerfish (Gil et al. 2017; Ellis et al. 2018). For the other two states, X'_t represents the number of conventionally tagged fish inside the array at time t, and Y'_t represents the number outside:

$$(7) \qquad X'_{t+1} = X'_t - A'_t + B'_t$$

$$(8) \qquad Y'_{t+1} = Y'_t + A'_t - B'_t$$

with the initial condition, $X'_{t=1} = n'$. The primary assumption is that movement rates of fish with telemetry tags is the same as

those of fish with conventional tags, such that $A'_t \sim \text{Bin}(X'_t, a_t)$ and $B'_t \sim \text{Bin}(Y'_t, a_t)$. Then, for a recapture event on any given day $t = \tau$, the Lincoln–Petersen abundance estimator is modified by substituting X'_τ for n:

$$(9) \qquad N_\tau = X'_\tau K/k$$

to account both for survival of tagged fish and for their movement to and from the study site. This estimator is robust to the type of movement behavior (e.g., diffusive, directional, or a combination), even if the overall system dynamics are not. This is because the estimator applies at the time of recapture, not the time of tagging, such that X'_τ and the ratio K/k account for the cumulative effect of movement, independent of its type (see online Supplementary material 1[1]).

Application to gray triggerfish

Gray triggerfish are a marine species distributed widely throughout the Gulf of Mexico and Atlantic Ocean. Off the southeastern United States, from North Carolina to the Florida Keys, the stock is managed by the South Atlantic Fishery Management Council as part of their Snapper–Grouper Fishery Management Plan. They are captured primarily by hook-and-line gear, with annual landings in recent decades averaging near 266 metric tons, split approximately evenly between recreational and commercial fleets (Burton et al. 2015).

Gray triggerfish associate with hard-bottom reef habitat. They mature quickly, with about 90% of fish mature by age-1 (Kelly-Stormer et al. 2017), and have moderate growth, obtaining a mean size of ~350 mm fork length (FL) by age-3 (Burton et al. 2015). Mean maximum size is 457 mm FL, and maximum observed age is 15 years.

Tagging and sampling methods

We conducted this study at a natural hard-bottom reef site 35 km east of Cape Lookout, North Carolina (Fig. 2). The specific

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site was composed of a mix of low-relief hard-bottom and soft-bottom habitats as determined by a multibeam sonar map (Fig. 2). This site was chosen based on high catches of gray triggerfish in previous studies (Bacheler and Smart 2016; Runde 2017). Tagging methods are detailed in Bacheler et al. (2018) and summarized below.

We used a VEMCO positioning system (VPS) to quantify the fine-scale movements of telemetered gray triggerfish at our study site (Espinoza et al. 2011; Herbig and Szedlmayer 2016). The VPS uses an array of underwater receivers to determine the location of fish with transmitters by knowing how long the acoustic signal from transmitters takes to reach each receiver. We deployed a 4 × 5 grid of VR2AR receivers on 31 August 2017 that were separated 200 m from each other; thus, the receiver array spanned 0.48 km² (Fig. 2). A reference transmitter was also deployed in the receiver array to estimate the positional error of fish with transmitters. Fish inside the grid were considered present at the site, as were fish outside the grid if detected by at least three receivers. The telemetry observations fitted by the movement model (eqs. 4 and 5) comprised the daily number of fish that left the site without returning that same day (exits) and the daily number that entered the site and remained through that day (entries).

The positional error of transmitters was determined from the reference tag deployed at a known location within the receiver array. Median positional error rates ranged ~1 m early in the study to just over 2 m by the end of the study, and spatial precision appeared to be unaffected by environmental conditions (Bacheler et al. 2018). This reference suggests high spatial precision of telemetered gray triggerfish and supports the assumption of high detectability.

Fish were caught on 15 September 2017 in traps (N = 16 traps; 0.6 m × 0.6 m × 0.5 m) that were baited with approximately 2 kg of *Brevoortia* spp. and were soaked for 50–80 min at the study site. Once traps were retrieved, gray triggerfish were placed in a 300 L holding tank containing ambient seawater on board the research vessel. Some fish (N = 30; size range 250–335 mm FL; mean 291 mm FL) were telemetry-tagged with VEMCO V13–1x transmitters that weighed 11 g in air, had a 110–250 s time offset, and had a battery life of 904 days. Transmitters were attached externally to gray triggerfish because signals can be detected from farther away than with surgically implanted transmitters (Dance et al. 2016) and external attachment is much faster (Jepsen et al. 2015), reducing the surface interval and minimizing barotrauma effects (Burns et al. 2002). Transmitters were attached to the dorsal musculature of gray triggerfish using polydioxanone absorbable suture, and this procedure took ~90 s in air. Most fish (73%) were vented before release with a hollow 16-gauge needle to reduce the amount of air in their abdomen, allowing them to swim back towards the bottom after release. Other gray triggerfish (N = 112; size range 232–335 mm FL; mean 282 mm FL) were captured, conventionally tagged with yellow Floy FM-95W internal anchor tags in their abdomen (which vented most fish), and released at the study site.

Conventionally tagged fish were estimated in a previous study to have a release survival probability of $\hat{\lambda} = 0.60$ given that they were caught in traps and accounting for condition upon release (Runde 2017). Thus, the number of fish initially tagged (n) that survived release was assumed to be $n' \sim \text{Bin}(n, 0.60)$. Other sources of mortality (natural, fishing), as well as loss of conventional tags, were considered negligible for this application (Runde 2017), especially given the short duration of our study.

Recapture events occurred on 6 October (N = 24 traps) and 27 October (N = 12 traps), corresponding to days 22 and 43 of the study, respectively (Fig. 2). Traps used for recapture had the same design as those used for initial capture and were soaked for ~90 min. Recapture traps also included an outward-looking GoPro Hero 4 camera. Thus, in addition to data on physical recap-

Fig. 3. (A) Observed numbers of telemetered gray triggerfish entering and exiting the study site. On day 1, N = 30 telemetered fish. (B) Mean wave orbital velocity (WOV) at the study site. In both panels, horizontal lines indicate days when Hurricanes Jose and Maria passed nearby. [Colour online.]
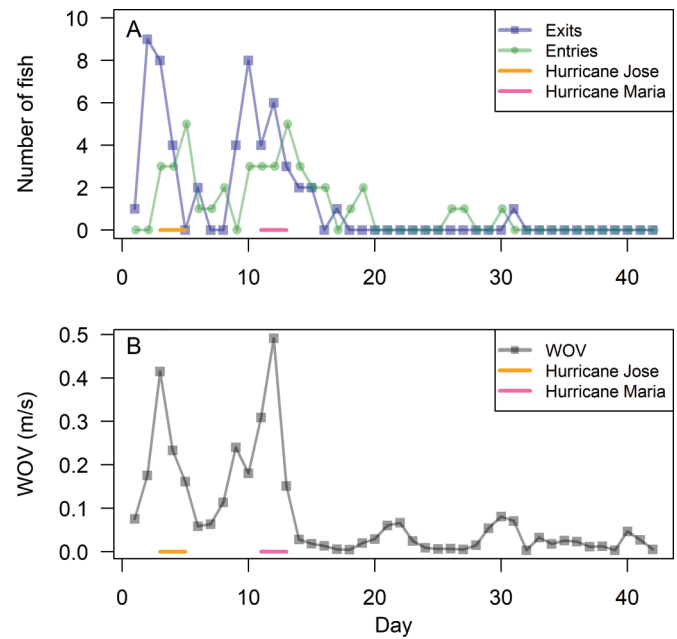
tures from traps, we also analyzed resighting information from videos. Video files were read over a series of 30 s snapshots from the moment the trap landed on the bottom until the video ended (sensu Schobernd et al. 2014). Although tag numbers could not be read on video, counts were provided separately for fish with conventional (internal anchor) tags and fish without conventional tags. Individuals could not be identified on video and therefore may have been counted more than once; we assumed that the degree to which this occurred was equal for tagged and untagged fish, such that the ratio between K and k was informative. For each recapture event, counts of triggerfish with and without conventional tags were summed across video frames (snapshots) and traps (cameras) to provide values of K and k. Fish were excluded from the video analysis if their tag status could not be determined because of orientation or range from the camera.

Environmental effect on movement

Movement rates appeared to be higher during the first portion (approximately half) of the sampling period than during the second (Fig. 3A). That time of increased movement corresponds to when two hurricanes passed across the study site, first Hurricane Jose on 17–19 September 2017 and then Hurricane Maria on 25–27 September 2017. We thus posit an environmental effect on movement rates. To account for this, we modeled movement rates (a_t, b_t) as logistic functions of an environmental covariate Z:

$$(10) \qquad a_t = \exp(\alpha_1 + \alpha_2 Z_t)/\{1 + [\exp(\alpha_1 + \alpha_2 Z_t)]\}$$

$$(11) \qquad b_t = \exp(\beta_1 + \beta_2 Z_t)/\{1 + [\exp(\beta_1 + \beta_2 Z_t)]\}$$

Thus, the model has four estimated parameters, $\boldsymbol{\theta} = (\alpha_1, \alpha_2, \beta_1, \beta_2)$, where α_2 and β_2 quantify a potential environmental effect on movement rates out of and into the study site. We examined the credible intervals of those two parameters and concluded that an environmental effect was present if the 95% credible intervals excluded zero. A strictly positive interval would indicate a significantly positive correlation between the environmental covariate

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Fig. 4. Rates of exit (A) and entry (B) as a function of the environmental covariate (wave orbital velocity), estimated using telemetered gray triggerfish in the movement model. Thick lines indicate median posterior estimates, surrounded by 95% credible intervals.

Fig. 5. Rates of exit (A) and entry (B) by day, as estimated from telemetered gray triggerfish. Thick lines indicate median posterior estimates, surrounded by 95% credible intervals. [Colour online.]
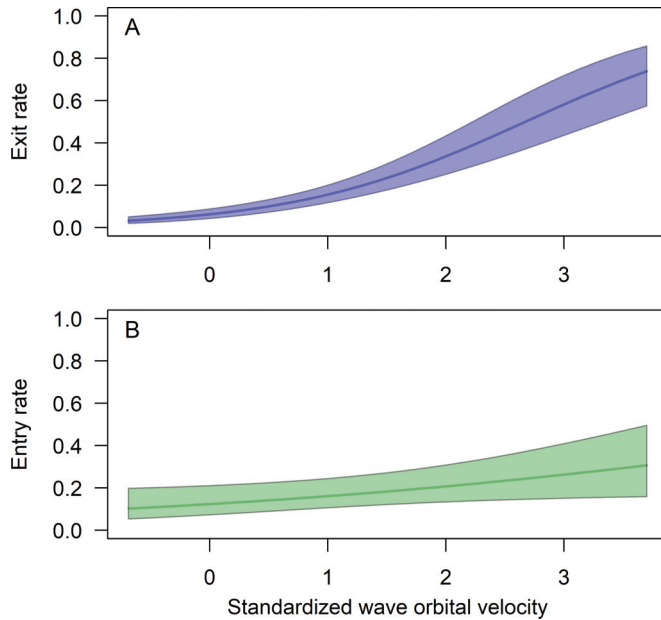
and movement, and a strictly negative interval would indicate a significantly negative correlation.

For the environmental covariate, we used wave orbital velocity as a measure of storm activity (Fig. 3B). Wave orbital velocity quantifies wave-generated oscillatory flow at the seabed, computed from surface properties of wave height and period (see Bacheler et al. (2019) for further details). Surface measurements were taken in hourly intervals at a nearby (~70 km) buoy, NOAA Station 41025 (http://www.ndbc.noaa.gov/), and wave orbital velocities computed from those measurements were scaled to the depth of our study site (37 m). For use in the model, we averaged the hourly values to represent daily velocities and then standardized velocities such that Z had a mean of 0 and standard deviation of 1.

Model implementation

We combined the movement submodel and abundance estimator in a Bayesian hierarchical framework, in which movement rates were estimated from observations of telemetry-tagged fish and applied to conventionally tagged fish. The four movement parameters ($\theta = (\alpha_1, \alpha_2, \beta_1, \beta_2)$) were modeled using normal prior distributions:

$$(12) \qquad \theta_i \sim N(\mu_i, \tau_i)$$

where μ_i is the mean of the ith parameter, and τ_i is the precision (i.e., inverse variance, $\tau = 1/\sigma^2$). We used normal and half-Cauchy hyperprior distributions for the means and standard deviations:

$$(13) \qquad \mu_i \sim N(0, 1/3)$$

$$(14) \qquad \gamma_i \sim Cauchy(0, 1/3); \qquad \tau_i = |\gamma_i|$$

Using the Cauchy distribution for variance parameters (Gelman 2006; Gelman et al. 2008), here with the location parameter equal to 0 and the scale parameter equal to ⅓, is equivalent to using a Student's t distribution with degrees of freedom equal to 1.

Markov chain Monte Carlo (MCMC) was performed using JAGS version 4.3.0 (Plummer 2017), run in R version 3.4 (R Core Team 2017) with the R package R2jags (Su and Yajima 2015). We ran
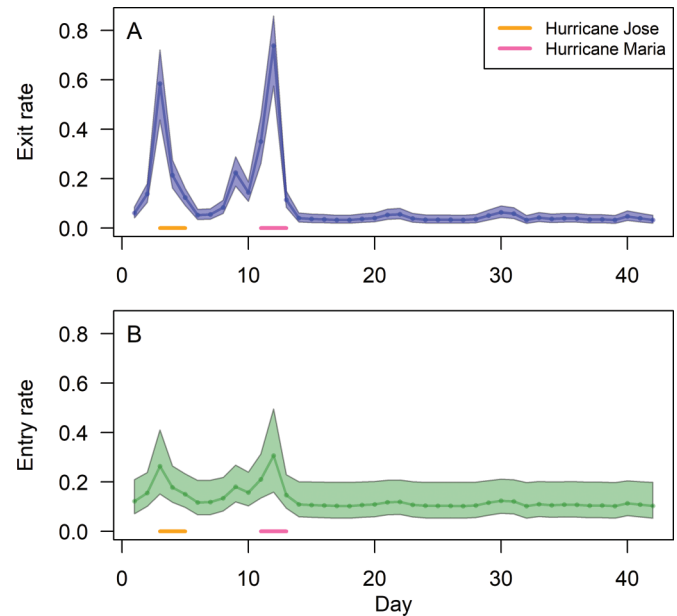
three independent Markov chains, each for 60 000 iterations. Posterior distributions were computed after a burn-in period of 20 000 iterations. Convergence was assessed through visual inspection of trace, density, and autocorrelation plots and by examining the Brooks–Gelman–Rubin statistic for values near 1 (Brooks and Gelman 1998). JAGS code to estimate movement rates is provided (Supplementary material 2[1]).

Based on estimates of movement from the telemetry data, the MCMC procedure provided posterior distributions of the number of conventionally tagged fish at the study site on each day (X'_t). These distributions, along with recapture data from traps or videos, were used in eq. 9 to compute posterior distributions of site abundance on sampling days. To evaluate the importance of the movement submodel for estimating abundance, we repeated the computations assuming no emigration, by replacing X'_t in eq. 9 with n', the time-invariant number of initially tagged fish that survived release.

Results

Movement of gray triggerfish

During the course of the study, six fish lost their transmitter (or died) within the acoustic array. These losses occurred on days 8, 9, 15, 17, 18, and 26. Using these data, we fitted $L^X_t \sim Bin(X_t, \psi)$ to estimate a daily loss probability of $\hat{\psi} = 0.0125$. In the movement model, this rate was applied to telemetered fish outside the array as a stochastic, unobserved process: $L^Y_t \sim Bin(Y_t, \hat{\psi})$.

The movement model estimated that exit and entry rates both increased with the environmental covariate, wave orbital velocity (Fig. 4). Posterior median parameter values (95% credible intervals) from eqs. 10 and 11 were $\alpha_1 = -2.70$ (−3.10, −2.33), $\alpha_2 = 1.01$ (0.77, 1.26), $\beta_1 = -1.96$ (−2.54, −1.32), and $\beta_2 = 0.31$ (0.02, 0.57). All diagnostics indicated that the MCMC algorithm had converged. The result that credible intervals of α_2 and β_2 were strictly positive provides evidence that exit rates and entry rates, respectively, were positively and significantly correlated with the environmental covariate. However, the environmental effect appeared to be stronger on exit rates than on entry rates (Fig. 4).

As functions of the environmental covariate, exit and entry rates varied daily (Fig. 5). Movement rates were most variable in

Fig. 6. (A) Estimated daily number of conventionally tagged gray triggerfish alive at the study site (X'_t). Thick line indicates median posterior estimates, surrounded by 95% credible intervals. Filled circles indicate days 22 and 43 when recapture events occurred. (B) Posterior distributions of total abundance at the study site estimated from trap and video gear on day 22, with solid vertical lines indicating median estimates. (C) Posterior distribution of total abundance at the study site estimated from video gear on day 43, with the solid vertical line indicating the median estimate. In panels B and C, dashed lines indicate median estimates that would occur if movement were not accounted for. [Colour online.]
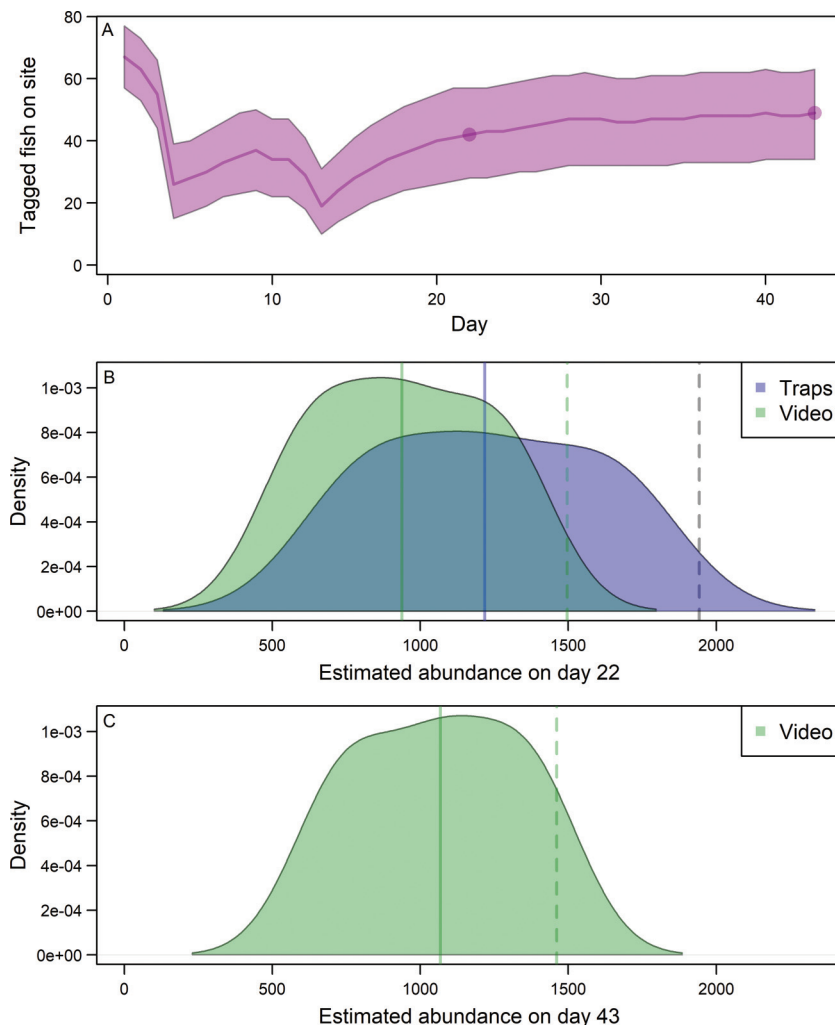
the early part of study, until about day 15, after which movement stabilized. In turn, the proportion of tagged fish inside the study site reached an approximate equilibrium.

Abundance estimates

Applying the movement model to conventionally tagged fish that survived release showed an initial decline inside the study site until about day 13 (Fig. 6A). On days 22 and 43 when recapture events occurred, the posterior median (95% credible interval) estimates of conventionally tagged fish alive at the study site were $X'_{22} = 42$ (28, 57) and $X'_{43} = 49$ (34, 63).

On day 22, $K = 203$ gray triggerfish were recaptured in traps, $k = 7$ (3.4%) of which had conventional tags, and $K = 2725$ were seen on videos (not necessarily unique individuals), of which $k = 122$ (4.5%) had conventional tags. Using those values in eq. 9, along with the posterior distribution of X'_{22}, provided posterior median (95% credible interval) estimates of abundance at the study site (Table 1; Fig. 6B): $N_{22} = 1218$ (812, 1653) from traps and $N_{22} = 938$ (625, 1273) from videos.

On day 43, no conventionally tagged fish were recaptured in traps, and thus those data were not used for estimating abundance. However, $K = 1112$ gray triggerfish were seen on videos, of

Table 1. The estimated numbers of conventionally tagged triggerfish alive and inside the array on day t (X'_t) and the corresponding abundances estimated on the site (N_t).

Day of sampling	X'_t	Gear	K	k	N_t
$t = 22$	42 (28, 57)	Traps	203	7	1218 (812, 1653)
		Video	2725	122	938 (625, 1273)
$t = 43$	49 (34, 63)	Traps	173	0	—
		Video	1112	51	1068 (741, 1374)

Note: Video counts are summed across cameras and sampling frames and do not necessarily represent unique individuals. Also shown are the numbers of triggerfish captured in traps or sighted on video (K) and the associated numbers that had conventional tags (k). Estimates of X'_t and N_t are posterior median values (95% credible intervals).

which $k = 51$ (4.6%) had conventional tags. These values along with the posterior distribution of X'_{43} resulted in the estimated abundance of $N_{43} = 1068$ (741, 1374) at the study site (Table 1; Fig. 6C).

For comparison, in the model that did not account for movement, abundance estimates were $N_{22} = 1943$ (1653, 2233) from traps and $N_{22} = 1497$ (1273, 1720) and $N_{43} = 1461$ (1243, 1679) from

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videos (Figs. 6B and 6C). In each case, the median estimate was substantially larger (~40%–60%) than the analogous (i.e., same day, same gear) estimate obtained when movement was modeled, with no or little overlap in the credible intervals. These differences indicate the magnitude of bias that would have occurred if movement were ignored.

Discussion

The analytical approach developed here applies the Lincoln–Petersen estimator of abundance, modified through use of a Markovian movement model to relax the assumption of a closed population. The approach integrates data streams that have traditionally been viewed separately into a single framework. Recapture of conventionally tagged animals provides information on abundance, and monitoring telemetry-tagged animals provides information on movement. Accounting for movement reduces bias in the abundance estimator that would otherwise result from violation of the closed-population assumption. Furthermore, with entry and exit rates quantified, the abundance estimator is robust to the type of movement, whether diffusive or directional (Supplementary material 1[1]). The type of movement, however, would affect overall dynamics of the system, with diffusive movement leading toward equilibrium numbers (except for noise) of tagged and untagged fish inside the array and directional movement leading toward depletion of tagged fish inside the array. In general, knowledge about movement is critical to a robust understanding of population dynamics (Morales et al. 2010) and in developing effective management policies such as reserve design (Egli and Babcock 2004; Lea et al. 2016).

Different approaches have been adopted to account for animal movement when estimating abundance with tagging data. A multisite study design can provide information on movement and home ranges using conventional tags, and spatial capture–recapture models have been developed for analysis of such data (e.g., Efford 2004; Conroy et al. 2008; Royle et al. 2009). Capello et al. (2016) proposed a method to utilize satellite, archival, or acoustic tagging techniques to estimate abundance of migratory animals (in their case, tropical tunas that associate with fish aggregation devices). Barker (1997) proposed a model that utilizes resightings of conventional tags between capture periods, allowing for the animals' geographic range to be broader than the study site. Similar to our approach, Ivan et al. (2013) used telemetry data to characterize animal movement for the purpose of adjusting an otherwise closed-population estimator of density (that due to Huggins 1989). Their adjustment quantifies the proportion of time that each tagged animal spent on the study site and was vulnerable to recapture (Ivan et al. 2013). Our approach, although conceptually similar, differs by modeling temporal variation in movement explicitly, which can readily accommodate the use of covariate information. Furthermore, unlike the Jolly–Seber model (Pollock 1991; Pine et al. 2003; Kéry and Schaub 2012), the approach here does not require unique identification of individuals, which allows for relatively noninvasive sampling gears such as video cameras.

Although our approach accounts for movement without assuming a closed population, it does require several other assumptions. Chief among them are that (i) movement of telemetry-tagged fish is representative of movement of conventionally tagged fish, (ii) detection probability of telemetry-tagged fish is 100% when inside the acoustic array, and (iii) all fish have equal capture or sighting probability at each sampling event (although these rates need not be equal across events). To investigate validity of the assumption that movement is representative, future studies could utilize double tagging, where a subset of animals are tagged with both telemetry and conventional tags. In our study of gray triggerfish, the assumption of 100% detection inside the array was supported by high spatial precision of the reference tag (Fig. 2;

Bacheler et al. 2018). Receivers were placed every 200 m, and detection distances even during storms ranged 300–400 m. In other studies where this assumption is questionable, it may be possible to model imperfect detection (e.g., Kéry et al. 2009). The assumption of equal catchability across individuals is difficult to evaluate in our study. The small number of trap recaptures (Table 1) may indicate trap shyness; however, we would expect the assumption of equal sighting probability to hold for camera counts, which is a potential advantage of using video gear.

We further assumed in the movement model that stochastic losses of fish outside the array could be described by a single binomial process (Fig. 1). If these losses comprise both tag loss and mortality, and if these sources can be separated in the data, it may be desirable to model them as distinct processes. We could not reliably distinguish the two sources in our data, but believe the six cases where transmitters stopped moving inside the array to be primarily or entirely tag loss. This was supported by a tank-holding study in which no telemetry-tagged individuals died and by video observations in which fish were seen with two holes in their upper back, indicative of tag loss (Bacheler et al. 2018). In addition, no telemetry tags inside the array displayed erratic swimming behavior that might be consistent with predation. Similarly, for conventionally tagged fish, we assumed that release mortality was the only source of mortality and that fishing (F) and natural (M) mortality did not occur during the course of our study. Again, we think this is a reasonable assumption for our case study, but note that it is not a requirement of the method. Either F or M or both could be included in a similar fashion as release mortality, by decrementing the number of conventionally tagged fish, assuming exponential decay. For gray triggerfish in the southeastern United States, Burton et al. (2015) used catch curve analysis to estimate average annual total mortality of $Z = F + M = 0.95$. That rate would indicate survival of $\exp[-0.95(22/365)] = 0.94$ up to our first sampling event on day 22 and survival of $\exp[-0.95(43/365)] = 0.89$ up to our second sampling event on day 43. Thus, if we were to apply that rate, our abundance estimates would be 94% (day 22) or 89% (day 43) of the current values (Fig. 6). Nonetheless, we believe $Z = 0$ to be approximately true, because we did not detect any natural or fishing mortality of telemetry-tagged fish, the morphology of gray triggerfish is such that mortality due to predation should be minimal, and we did not directly observe fishing on or near the study site during the study. We cannot rule out the possibility of some fishing mortality on conventionally tagged fish, but note that tropical storms during the first half the study would have made boating activity highly unlikely.

In our study of gray triggerfish, movement at a depth of 37 m was associated with storm activity (Bacheler et al. 2019). During the course of sampling, two hurricanes passed over the study site and were correlated with elevated movement rates. Effects of storms on movement have been documented for other marine animals, such as American lobsters (Homarus americanus; Jury et al. 1995), black sea bass (Centropristis striata; Secor et al. 2019), red snapper (Lutjanus campechanus; Patterson et al. 2001), summer flounder (Paralichthys dentatus; Sackett et al. 2007), and several species of coastal sharks (Heupel et al. 2003; Udyawer et al. 2013). However, few previous studies have reported a hurricane effect on movement of demersal fishes in the open ocean (e.g., Patterson et al. 2001; Secor et al. 2019).

Bacheler et al. (2019) compared several environmental variables and found wave-generated disturbance at the seabed to be the most likely proximate cue for storm-related movement of gray triggerfish. Here, that disturbance was quantified using wave orbital velocity, although we note that wave-generated dynamic pressure would be a viable alternative covariate, as it correlates perfectly with wave orbital velocity. Over the course of our study, daily wave orbital velocity averaged 0.08 m·s⁻¹, but during hurricanes exceeded 0.30 m·s⁻¹ (Fig. 3B), which is a rule-of-thumb threshold velocity for moving sediment of diameter 0.1 mm (Dean

and Dalrymple 1984). Including the environmental covariate in the model has practical implications for estimating abundance. For example, rerunning our model with constant movement rates (i.e., no covariate, achieved by fixing $\alpha_2 = \beta_2 = 0$) resulted in daily abundance estimates that were –16% to 121% larger than they were when the environmental effect was included. The wider discrepancies (50%–121%) occurred during the first half of the time series on days when movement rates were most variable (Fig. 5). Thus, not only does the movement model itself reduce bias in the abundance estimates, but including the environmental covariate additionally accounts for temporal patterns in movement rates.

Without information on an environmental effect, a similar movement model approach could still be applied. The simplest alternative would be to model entries and exits with time-invariant, fixed rates. A more flexible alternative would be to model entries and exits as time-varying random effects. Intermediate levels of complexity might include combinations of those two alternatives (e.g., modeling entry rates as fixed and exit rates as random effects) or allowing fixed rates to vary across time blocks. Additionally, our approach to include an environmental effect is of intermediate complexity, as it provides model structure while allowing rates to change through time along with the covariate.

The movement model applied here predicted that the abundance of conventionally tagged fish at the study site declined until about day 13 (Fig. 6A). This occurred for two reasons. First, all tagged fish started on day 1 inside the study site, and thus near the beginning of the study, more tagged fish were eligible to exit than enter. This effect would be apparent even if exit and entry rates were time-invariant, as the system would approach an equilibrium number of fish inside and outside the study site. Second, the effect of the environmental covariate was stronger on exit rates than on entry rates (Figs. 4, 5). This seemingly disproportionate effect on exit rates is consistent with an overall increase in movement, as tagged fish that exit the study site are counted if they go anywhere else, but fish that enter are counted only if they go to one particular place (the study site). Adjusted for movement, the abundance model estimated that ~1000 gray triggerfish (~2000 fish·km⁻²) were present on the study site (Fig. 6), reflecting the relatively high abundance of gray triggerfish expected from previous sampling at this particular reef location.

In general, the estimates of abundance represent only the portion of the population vulnerable to the sampling gear. For example, if the gear is size-selective, abundance estimates pertain only to fish of vulnerable sizes. In addition, when using multiple gears for resampling as we did, an implicit assumption is that the gears share a common selectivity. In our case study, we think it is a reasonable assumption that all fish on the sampling site were vulnerable to both gears (i.e., selectivity equals 1). Video gear is generally not size-selective. Trap gear can be size-selective, but in our study, two lines of evidence were more consistent with constant selectivity. First, the relative sizes of all fish observed on video appeared similar to those of tagged fish, which were initially captured for tagging in traps. Second, if video gear selected a broader range of sizes than traps did, we would expect K (all fish sighted) from video to represent a larger proportion of the population than k (tagged fish sighted on video, but previously captured in traps for tagging), inflating the ratio of K/k. Following eq. 9, the inflated ratio would result in a larger estimate of abundance from video than from traps. However, our results showed the opposite (Fig. 6B).

The combined telemetry–conventional tag approach is best suited for estimating or monitoring abundance at relatively small sites that can accommodate an array of acoustic receivers, for example, small marine reserves or marine protected areas. However, if the goal is to estimate absolute abundance over a much larger region, for example the range of the stock, the approach is better interpreted as a proof of concept and a stepping stone. To

that ideal, we envision spatial repetition of our study design throughout the range of the stock and across habitat types (e.g., bottom structure, depth, latitude). Estimates of local abundance at multiple locations across space could then be linked to habitat type, and assuming that linkage applies to suitable habitat not sampled, total stock abundance could be derived from a map of all habitat across the stock's range. Further, more widespread repetition of recapture events would allow for estimation of observation error in the conventional tag sampling, separate from the movement process error already included in the model. Modeling observation error could accommodate sampling events where the number of recaptures is very low or even zero (e.g., Friedenberg et al. 2018), as occurred in our study with trap recaptures on day 43.

A time series of absolute abundance alone could serve as the basis for a management control rule, although it is not itself a replacement for stock assessment. Stock assessment models do more than estimate abundance; they provide management guidance on target and limit reference points for biomass levels, catch levels, and exploitation rates, and they provide information on the historical and current status of the stock and fishery relative to those reference points. Nonetheless, values of those reference points depend critically on the scale of abundance, and there exists some skepticism that assessments can estimate absolute abundance reliably (e.g., Hilborn 2002). This may be because most assessments must infer population size from data sources that contain only indirect or partial information on the scale of abundance, such as catches, age or size compositions, indices of relative abundance, and life-history characteristics (Maunder and Piner 2015). A time series of absolute abundance estimates would provide direct information and could be fitted statistically to account for imperfect observations alongside the other data sources in an integrated stock assessment model (Maunder and Punt 2013). Even a single year of such information, perhaps in tandem with a time series of relative abundance, would help anchor the scale of annual abundance — and all of the associated management quantities — estimated by a multiyear assessment.

Analysis of telemetry tag data alone provides information on movement, but not abundance. Analysis of conventional tag data alone can provide estimates of abundance, but these estimates are biased if model assumptions are not met. The use of both tag types simultaneously, analyzed within an integrated framework as described here, offers improved inference of abundance by accounting for release mortality and animal movement. With the continued advancement of aquatic telemetry, in terms of both technology and cost-effectiveness (Hussey et al. 2015), we expect to see increased opportunity for combining telemetry and conventional tags in open, marine systems, as well as corresponding improvements to the information and advice provided to natural resource managers.

Acknowledgements

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References

Arnold, G., and Dewar, H. 2001. Electronic Tags in Marine Fisheries Research: A 30-Year Perspective. *In* Electronic Tagging and Tracking in Marine Fisheries. Reviews: Methods and Technologies in Fish Biology and Fisheries. Vol 1. *Edited by* J.R. Sibert and J.L. Nielsen. Springer, Dordrecht.

Bacheler, N.M., and Smart, T.I. 2016. Multi-decadal decline in reef fish abundance and species richness in the southeast United States assessed by standardized trap catches. Mar. Biol. 163: 26. doi:10.1007/s00227-015-2774-x.

Bacheler, N.M., Buckel, J.A., Hightower, J.E., Paramore, L.M., and Pollock, K.H. 2009. A combined telemetry–tag return approach to estimate fishing and natural mortality rates of an estuarine fish. Can. J. Fish. Aquat. Sci. 66: 1230–1244. doi:10.1139/F09-076.

Bacheler, N.M., Shertzer, K.W., Buckel, J.A., Rudershausen, P.J., and Runde, B.J. 2018. Behavior of gray triggerfish *Balistes capriscus* around baited fish traps determined from fine-scale acoustic tracking. Mar. Ecol. Prog. Ser. 606: 133–150. doi:10.3354/meps12780.

Bacheler, N.M., Shertzer, K.W., Cheshire, R.T., and MacMahan, J.H. 2019. Tropical storms influence the movement behavior of a demersal oceanic fish species. Sci. Rep. 9: 1481. doi:10.1038/s41598-018-37527-1.

Barker, R.J. 1997. Joint modeling of live-recapture, tag–resight, and tag–recovery data. Biometrics, 53: 666–677. doi:10.2307/2533966.

Brooks, S., and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. J. Comp. Graph. Stat. 7(4): 434–455. doi:10.2307/1390675.

Burns, K.M., Koenig, C.C., and Coleman, F.C. 2002. Evaluation of multiple factors involved in release mortality of undersized red grouper, gag, red snapper and vermilion snapper. Mote Marine Laboratory Technical Report No. 790 [online]. Available from https://dspace.mote.org:8443/bitstream/2075/294/3/MTR%20790.pdf [accessed 10 Septmeber 2018].

Burton, M.L., Potts, J.C., Carr, D.R., Cooper, M., and Lewis, J. 2015. Age, growth, and mortality of gray triggerfish (*Balistes capriscus*) from the southeastern United States. Fish. Bull. 113(1): 27–39. doi:10.7755/FB.113.1.3.

Capello, M., Deneubourg, J.L., Robert, M., Holland, K.N., Schaefer, K.M., and Dagorn, L. 2016. Population assessment of tropical tuna based on their associative behavior around floating objects. Sci. Rep. 6: 36415. doi:10.1038/srep36415.

Conroy, M.J., Runge, J.P., Barker, R.J., Schofield, M.R., and Fonnesbeck, C.J. 2008. Efficient estimation of abundance for patchily distributed populations via two-phase, adaptive sampling. Ecology, 89: 3362–3370. doi:10.1890/07-2145.1. PMID:19137943.

Crossin, G.T., Heupel, M.R., Holbrook, C.M., Hussey, N.E., Lowerre-Barbieri, S.K., Nguyen, V.M., et al. 2017. Acoustic telemetry and fisheries management. Ecol. Appl. 27: 1031–1049. doi:10.1002/eap.1533. PMID:28295789.

Dance, M.A., Moulton, D.L., Furey, N.B., and Rooker, J.R. 2016. Does transmitter placement or species affect detection efficiency of tagged animals in biotelemetry research? Fish. Res. 183: 80–85. doi:10.1016/j.fishres.2016.05.009.

Dean, R.G., and Dalrymple, R.A. 1984. Water Wave Mechanics for Engineers and Scientists. Prentice Hall Inc., N.J.

Dichmont, C.M., Deng, R.A., Punt, A.E., Brodziak, J., Chang, Y., Cope, J.M., et al. 2016. A review of stock assessment packages in the United States. Fish. Res. 183: 447–460. doi:10.1016/j.fishres.2016.07.001.

Efford, M. 2004. Density estimation in live-trapping studies. Oikos, 106: 598–610. doi:10.1111/j.0030-1299.2004.13043.x.

Egli, D.P., and Babcock, R.C. 2004. Ultrasonic tracking reveals multiple behavioural modes of snapper (*Pagrus auratus*) in a temperate no-take marine reserve. ICES J. Mar. Sci. 61: 1137–1143. doi:10.1016/j.icesjms.2004.07.004.

Ellis, T.A., Buckel, J.A., and Hightower, J.E. 2017. Winter severity influences spotted seatrout mortality in a southeast US estuarine system. Mar. Ecol. Prog. Ser. 564: 145–161. doi:10.3354/meps11985.

Ellis, T.A., Hightower, J.E., and Buckel, J.A. 2018. Relative importance of fishing and natural mortality for spotted seatrout (*Cynoscion nebulosus*) estimated from a tag-return model and corroborated with survey data. Fish. Res. 199: 81–93. doi:10.1016/j.fishres.2017.11.004.

Espinoza, M., Farrugia, T.J., Webber, D.M., Smith, F., and Lowe, C.G. 2011. Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fish. Res. 108: 364–371. doi:10.1016/j.fishres.2011.01.011.

Friedenberg, N.A., Hoover, J.J., Boysen, K., and Killgore, K.J. 2018. Estimating abundance without recaptures of marked pallid sturgeon in the Mississippi River. Conserv. Biol. 32(2): 457–465. doi:10.1111/cobi.12972.

Gelman, A. 2006. Prior distributions for variance parameters in hierarchical models (comment on article by Browne and Draper). Bayesian Anal. 1(3): 515–534. doi:10.1214/06-BA117A.

Gelman, A., Jakulin, A., Pittau, M.G., and Su, Y. 2008. A weakly informative default prior distribution for logistic and other regression models. Ann. Appl. Stat. 2: 1360–1383. doi:10.1214/08-AOAS191.

Gil, M.d.M., Palmer, M., Grau, A., Massutí, E., and Pastor, E. 2017. Comparing tagging strategies: effects of tags on retention rate, mortality rate and growth in hatchery-reared juvenile meagre, *Argyrosomus regius* (Pisces: Sciaenidae). Sci. Mar. 81: 171–178. doi:10.3989/scimar.04583.26B.

Goethel, D.R., Quinn, T.J., II, and Cadrin, S.X. 2011. Incorporating spatial structure in stock assessment: Movement modeling in marine fish population dynamics. Rev. Fish. Sci. 19: 119–136. doi:10.1080/10641262.2011.557451.

Gopalaswamy, A.M., Royle, J.A., Delampady, M., Nichols, J.D., Karanth, K.U., and Macdonald, D.W. 2012. Density estimation in tiger populations: combining information for strong inference. Ecology, 93: 1741–1751. doi:10.1890/11-2110.1. PMID:22919919.

Hays, G.C., Ferreira, L.C., Sequeira, A.M.M., Meekan, M.G., Duarte, C.M., Bailey, H., et al. 2016. Key questions in marine megafauna movement ecology. Trends Ecol. Evol. 31: 463–475. doi:10.1016/j.tree.2016.02.015. PMID:26979550.

Herbig, J.L., and Szedlmayer, S.T. 2016. Movement patterns of gray triggerfish, *Balistes capriscus*, around artificial reefs in the northern Gulf of Mexico. Fish. Manag. Ecol. 23: 418–427. doi:10.1111/fme.12190.

Heupel, M.R., Simpfendorfer, C.A., and Hueter, R.E. 2003. Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle. J. Fish. Biol. 63: 1357–1363. doi:10.1046/j.1095-8649.2003.00250.x.

Hilborn, R. 2002. The dark side of reference points. Bull. Mar. Sci. 70(2): 403–408. Available from https://www.ingentaconnect.com/content/umrsmas/bullmar/2002/00000070/00000002/art00004?crawler=true.

Huggins, R.M. 1989. On the statistical analysis of capture experiments. Biometrika, 76(1): 133–140. doi:10.1093/biomet/76.1.133.

Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., et al. 2015. Aquatic animal telemetry: a panoramic window into the underwater world. Science, 348(6240): 1255642. doi:10.1126/science.1255642.

Ivan, J.S., White, G.C., and Shenk, T.M. 2013. Using auxiliary telemetry information to estimate animal density from capture-recapture data. Ecology, 94: 809–816. doi:10.1890/12-0101.1.

Jepsen, N., Thorstad, E.B., Havn, T., and Lucas, M.C. 2015. The use of external electronic tags on fish: an evaluation of tag retention and tagging effects. Anim. Biotelem. 3: 49. doi:10.1186/s40317-015-0086-z.

Johnson, H.E., Mills, L.S., Wehausen, J.D., and Stephenson, T.R. 2010. Combining ground count, telemetry, and mark–resight data to infer population dynamics in an endangered species. J. Appl. Ecol. 47: 1083–1093. doi:10.1111/j.1365-2664.2010.01846.x.

Jury, S.H., Howell, W.H., and Watson, W.H., III. 1995. Lobster movements in response to a hurricane. Mar. Ecol. Prog. Ser. 119: 305–310. doi:10.3354/meps119305.

Kelly-Stormer, A., Shervette, V., Kolmos, K., Wyanski, D., Smart, T., McDonough, C., and Reichert, M.J.M. 2017. Gray triggerfish reproductive biology, age, and growth off the Atlantic Coast of the southeastern USA. Trans. Am. Fish. Soc. 146: 523–538. doi:10.1080/00028487.2017.1281165.

Kéry, M., and Schaub, M. 2012. Bayesian Population Analysis Using WinBUGS: A hierarchical perspective. Academic Press, Waltham, Mass.

Kéry, M., Dorazio, R.M., Soldaat, L., Van Strien, A., Zulderwijk, A., and Royle, J.A. 2009. Trend estimation in populations with imperfect detection. J. Appl. Ecol. 46: 1163–1172. doi:10.1111/j.1365-2664.2009.01724.x.

Ketz, A.C., Johnson, T.L., Monello, R.J., Mack, J.A., George, J.L., Kraft, B.R., et al. 2018. Estimating abundance of an open population with an N-mixture model using auxiliary data on animal movements. Ecol. Appl. 28: 816–825. doi:10.1002/eap.1692. PMID:29405475.

Kurota, H., McAllister, M.K., Lawson, G.L., Nogueira, J.I., Teo, S.L.H., and Block, B.A. 2009. A sequential Bayesian methodology to estimate movement and exploitation rates using electronic and conventional tag data: application to Atlantic Bluefin tuna (*Thunnus thynnus*). Can. J. Fish. Aquat. Sci. 66: 321–342. doi:10.1139/F08-197.

Lea, J.S.E., Humphries, N.E., von Brandis, R.G., Clarke, C.R., and Sims, D.W. 2016. Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. Proc. R. Soc. B. 283: 20160717. doi:10.1098/rspb.2016.0717. PMID:27412274.

Lincoln, F.C. 1930. Calculating waterfowl abundance on the basis of banding returns. Circular No. 118. United States Department of Agriculture, Washington, D.C.

Maunder, M.N., and Piner, K.R. 2015. Contemporary fisheries stock assessment: many issues still remain. ICES J. Mar. Sci. 72: 7–18. doi:10.1093/icesjms/fsu015.

Maunder, M.N., and Punt, A.E. 2013. A review of integrated analysis in fisheries stock assessment. Fish. Res. 142: 61–74. doi:10.1016/j.fishres.2012.07.025.

Morales, J.M., Moorcroft, P.R., Matthiopoulos, J., Frair, J.L., Kie, J.G., Powell, R.A., et al. 2010. Building the bridge between animal movement and population dynamics. Phil. Trans. R. Soc. B. 365: 2289–2301. doi:10.1098/rstb.2010.0082. PMID:20566505.

Otis, D.L., Burnham, K.P., White, G.C., and Anderson, D.R. 1978. Statistical inference from capture data on closed animal populations. Wildl. Monogr. 62.

Patterson, W.F., III, Watterson, J.C., Shipp, R.L., and Cowan, J.H., Jr. 2001. Movement of tagged red snapper in the northern Gulf of Mexico. Trans. Am. Fish. Soc. 130: 533–545. doi:10.1577/1548-8659(2001)130<0533:MOTRSI>2.0.CO;2.

Petersen, C.G.J. 1896. The Yearly Immigration of Young Plaice into the Limfjord from the German Sea. Report of the Danish Biological Station to the Home Department (1895). Vol. 6. pp. 5–84.

Pine, W.E., Pollock, K.H., Hightower, J.E., Kwak, T.J., and Rice, J.A. 2003. A review of tagging methods for estimating fish population size and components of mortality. Fisheries, 28: 10–23. doi:10.1577/1548-8446(2003)28[10:AROTMF]2.0.CO;2.

Plummer, M. 2017. JAGS Version 4.3.0 user manual [online]. Available from https://sourceforge.net/projects/mcmc-jags/.

Pollock, K.H. 1991. Review papers: modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present, and future. J. Am. Stat. Assoc. **86**(413): 225–238. doi:10.1080/01621459.1991.10475022.

Pollock, K.H., Nichols, J.D., Brownie, C., and Hines, J.E. 1990. Statistical inference for capture–recapture experiments. Wildl. Monogr. **107**: 3–97. Available from https://www.jstor.org/stable/3830560.

Pollock, K.H., Jiang, H., and Hightower, J.E. 2004. Combining telemetry and fisheries tagging models to estimate fishing and natural mortality rates. Trans. Am. Fish. Soc. **133**: 639–648. doi:10.1577/T03-029.1.

R Core Team. 2017. R: a language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/.

Royle, J.A., Karanth, K.U., Gopalaswamy, A.M., and Kumar, N.S. 2009. Bayesian inference in camera trapping studies for a class of spatial capture–recapture models. Ecology, **90**: 3233–3244. doi:10.1890/08-1481.1. PMID:19967878.

Runde, B.J. 2017. Estimating and mitigating discard mortality of reef fishes. Master's thesis. North Carolina State University, Raleigh.

Runde, B.J., Harris, J.E., and Buckel, J.A. 2018. Symposium review: using electronic tags to estimate vital rates in fishes. Fisheries, **43**: 268–270. doi:10.1002/fsh.10077.

Sackett, D.K., Able, K.W., and Grothues, T.M. 2007. Dynamics of summer floun-der, *Paralichthys dentatus*, seasonal migrations based on ultrasonic telemetry. Estuar. Coast. Shelf Sci. **74**: 119–130. doi:10.1016/j.ecss.2007.03.027.

Schobernd, Z.H., Bacheler, N.M., and Conn, P.B. 2014. Examining the utility of alternative video monitoring metrics for indexing reef fish abundance. Can. J. Fish. Aquat. Sci. **71**: 464–471. doi:10.1139/cjfas-2013-0086.

Secor, D.H., Zhang, F., O'Brien, M.H.P., and Li, M. 2019. Ocean destratification and fish evacuation caused by a Mid-Atlantic tropical storm. ICES J. Mar. Sci. **76**(2): 573–584. doi:10.1093/icesjms/fsx241.

Sippel, T., Eveson, J.P., Galuardi, B., Lam, C., Hoyle, S., Maunder, M., et al. 2015. Using movement data from electronic tags in fisheries stock assessment: A review of models, technology and experimental design. Fish. Res. **163**: 152–160. doi:10.1016/j.fishres.2014.04.006.

Su, Y.S., and Yajima, M. 2015. R2jags: using R to run 'JAGS'. R package version 0.5-7 [online]. Available from https://cran.r-project.org/package=R2jags.

Thorstad, E.B., Rkardsen, A.H., Alp, A., and Okland, F. 2013. The use of electronic tags in fish research — an overview of fish telemetry methods. Turk. J. Fish. Aquat. Sci. **13**: 881–896. doi:10.4194/1303-2712-v13_5_13.

Udyawer, V., Chin, A., Knip, D.M., Simpfendorfer, C.A., and Heupel, M.R. 2013. Variable response of coastal sharks to severe tropical storms: environmental cues and changes in space use. Mar. Ecol. Prog. Ser. **480**: 171–183. doi:10.3354/meps10244.

Williams, B.K., Nichols, J.D., and Conroy, M.J. 2002. Analysis and Management of Animal Populations. Academic Press. San Diego, Calif.