



Annual indices of Atlantic bluefin tuna (*Thunnus thynnus*) larvae in the Gulf of Mexico developed using delta-lognormal and multivariate models★

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Abstract – Fishery independent indices of spawning biomass of Atlantic bluefin tuna in western North Atlantic Ocean are presented which utilize National Marine Fisheries Service ichthyoplankton survey data collected from 1977 through 2007 in the Gulf of Mexico. Indices were developed using similarly standardized data from which previous indices were developed (i.e. abundance of larvae with a first daily otolith increment formed per 100 m² of water sampled with bongo gear). Indices were also developed for the first time from standardized data collected with neuston gear [i.e. abundance of 5-mm larvae (i.e. seven-day-old larvae) per 10 minute tow]. Indices of larval abundance were developed using delta-lognormal models, including following covariates: time of day, time of month, area sampled and year. Due to the large frequency of zero catches during ichthyoplankton surveys, a zero-inflated delta-lognormal approach was also used to develop indices. Finally, a multivariate delta-lognormal approach was employed to develop indices of annual abundance based on both bongo and neuston catches. The results of these approaches were compared with one another and with other indices of larval abundance previously developed for the Gulf of Mexico. Residual analyses indicated that abundance indices of Atlantic bluefin tuna larvae were more appropriately developed from bongo-collected data through the zero-inflated delta-lognormal approach than other data sets and modeling approaches. Also, when modeling bongo-collected data with the zero-inflated delta-lognormal approach, the index values increased, indicating some correction for zero-inflation, and their variability decreased as compared to indices developed with the delta-lognormal approach.

Key words: Mathematical models / Multivariate analysis / Fish larvae / Atlantic Ocean

Résumé – Des indices d'abondance, indépendants de la biomasse « féconde » du thon rouge de l'Atlantique nord-ouest, sont présentés en utilisant les données ichthyoplanctoniques des campagnes océanographiques américaines (NMFS) collectées dans le golfe du Mexique de 1977 à 2007. Des indices sont développés en utilisant des données standardisées à partir des indices antérieurs (abondance des larves dont les otolithes présentent une seule zone d'accroissement journalier, par 100 m² d'eau échantillonnée avec un filet bongo). Des indices sont aussi développés pour la première fois à partir de données collectées avec un filet à neuston et standardisées (abondance de larves de 5-mm, âgées de 7 jours) par trait de 10 minutes. Des indices d'abondance larvaire sont développés en utilisant des distributions delta-log normales, incluant les covariables suivantes : jour, mois, zone échantillonnée, année. Du à la fréquence importante de captures nulles durant ces campagnes d'ichtyoplancton, un ajustement, au moyen d'une distribution delta-log normale pour des données présentant une grande quantité de valeurs nulles, est aussi utilisé pour développer des indices. Finalement, une approche delta-log normale multivariée est employée pour développer des indices d'abondance annuelle, basés sur les captures aux filets bongo et à neuston. Les résultats sont comparés entre eux et avec des indices d'abondance larvaire du golfe du Mexique, développés antérieurement. Des analyses des valeurs résiduelles de l'ajustement indiquent que ces indices d'abondance de larves de thon rouge sont plus appropriés lorsqu'ils sont développés à partir des données larvaires collectées au filet bongo, et suivant une distribution delta-log normale pour des données avec une grande quantité de valeurs nulles (« zero-inflated ») que ceux résultant d'autres séries de données ou d'autres modèles. Les valeurs des indices augmentent lorsque les données sont traitées par ce modèle, indiquant quelque correction pour cette inflation de zéros, et leur variabilité diminue, comparée aux indices développés avec l'ajustement delta-log normal.

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1 Introduction

The objective of fishery-independent surveys is to make inference about the size (in numbers and/or biomass) and age structure of targeted populations. Annual abundance indices based on such surveys are usually derived from catch or catch-per-unit-effort (CPUE) data and are a vital part of current management regimes of many fisheries. Collection, analysis and dissemination of such information are a paramount function of the National Oceanic and Atmospheric Administration (NOAA), National Marine Fisheries Service (NMFS).

Fishery managers became concerned of the status of stocks of Atlantic bluefin tuna, *Thunnus thynnus*, in the late 1960's, and in 1975 the International Commission for the Conservation of Atlantic Tunas (ICCAT) implemented regulations for management of the western Atlantic stock. Since then, annually conducted international assessments of western Atlantic bluefin tuna have indicated a large decline in abundance (Anonymous 2008). Most abundance indices used during assessments of western Atlantic bluefin tuna were of a fishery-dependent nature. Scott et al. (1993) presented a spawning biomass index based upon the abundance of Atlantic bluefin tuna larvae collected during fishery independent surveys conducted by NMFS in the Gulf of Mexico. Since that time, this index, which is a series of Pennington (1983) delta-distribution estimators, has been updated regularly (Scott and Turner 1994).

Fish larvae in many cases are overdispersed as a result of the spawning behavior of adults and/or physical oceanographic processes, resulting in catch data which are not normally distributed. Therefore, samples taken from such overdispersed populations contain many small or zero values and few very large values, and simple estimates of mean abundance from sample data may either be too low if many low values are included or too high if very large values are included. Such zero-inflated CPUE data is prolific in fisheries biology and becoming more important as fish stocks decline and rare species become more difficult to detect. Zero-inflation can occur due to "true zero" observations (e.g. from the study of rare organisms) or "false zero" observations (e.g. from sampling or observer errors) or both. Martin et al. (2005) reviewed many recent approaches to model such data for statistical inference with the use of generalized linear models. Data with zero-inflation due to true zeros can be modeled by two approaches: two-part modeling (e.g. delta-lognormal method; Lo et al. 1992) and mixture modeling (e.g. zero-inflated Poisson [ZIP] or zero-inflated negative binomial [ZINB] [Martin et al. 2005; Minami et al. 2007]); while zero-inflation due to false zeros can be mitigated by the use of zero-inflated binomial (ZIB) mixture models (Tyre et al. 2003; Martin et al. 2005; Steventon et al. 2005). For data with zero-inflation due to both true and false zeros, Martin et al. (2005) reports that there are currently no reported models in the literature.

Model-based estimators have been popularized since they may reduce the likelihood of false conclusions about trends in abundance (McConnaughey and Conquest 1993). They may also produce estimators with better precision (Pennington 1983, 1996; Lo et al. 1992). One model-based alternative to the arithmetic mean of the sample is the delta-lognormal method (Lo et al. 1992). The index computed by this method is a

mathematical combination of yearly abundance estimates from two distinct generalized linear models: a binomial (logistic) model which describes proportion of positive abundance values (i.e. presence/absence) and a lognormal model which describes variability in only the nonzero abundance data (Lo et al. 1992).

However, for many fishery-independent CPUE data sets, large frequencies of zeros are observed relative to what is predicted by models based on standard distributional assumptions. Recently, in many fields, it has become popular to model such data using regression models based on an assumption that the response is generated by a mixture of a standard count distribution (e.g. binomial, Poisson, or negative binomial) with a degenerate distribution with point mass of one at zero, creating a zero-inflated distribution (Hall 2000; Vieira et al. 2000). As mentioned earlier, Martin et al. (2005) reports that there are currently no reported models in the literature for data with zero-inflation due to both true and false zeros, and the use of mixture models based ZIP or ZINB distributional assumptions may not account for "false zeros" when modeling the data. Therefore, a more appropriate way to model these types of data would be to replace the binomial model portion of a delta-lognormal approach with a zero-inflated binomial (ZIB) model. This would allow one to take into account both "true zeros" by using a two-part modeling approach (i.e. the delta-lognormal method), while adjusting for any "false zeros" with the ZIB modeling approach.

In many surveys, multiple gear-types are used in gathering data. In most cases, CPUE values resulting from differing gears are neither directly additive nor easily standardized between gears, making it difficult to model with a traditional delta-lognormal approach. Therefore, a more appropriate way to model these types of data would be to replace the binomial and lognormal submodels of a delta-lognormal approach with multivariate binomial and multivariate lognormal submodels.

The objective of this paper is to present abundance indices of bongo- and neuston-collected Atlantic bluefin tuna larvae based on delta-lognormal (DL), zero-inflated delta-lognormal (ZIDL), and multivariate delta-lognormal (MDL) models. The indices resulting from these methods will be compared to an index developed using the Pennington delta-distribution (PDD) method as employed in the development of previous larval bluefin tuna indices (Scott et al. 1993; Scott and Turner 1994).

2 Methodology

Methodologies concerning general ichthyoplankton surveys conducted by NMFS in the Gulf of Mexico have been extensively reviewed (Richards and Potthoff 1980; McGowan and Richards 1986). Likewise, methodologies concerning the use of this survey data to assess bluefin tuna larvae were reviewed (Richards 1990; Murphy 1990). Ichthyoplankton surveys were conducted from numerous NOAA vessels during mid to late April through May from 1977 through 2007 in the offshore waters of the US Gulf of Mexico. Sampling station locations were usually located on a 30-nautical-mile grid. A double oblique plankton tow was conducted at every station through 1983 and at every other station from 1984 through

2007. Each tow was conducted to 200 m or to within 1–5 m of the bottom if the water depth is less than 200 m and was made using a paired 61-cm bongo net plankton sampler with a 0.333 mm mesh. Ship speed during the tow was maintained at approximately 1.5 knots to maintain a 45° wire angle on the deployment cable. A flow meter inside the mouth of each bongo net was used to determine the volume of water sampled. In addition to the bongo tow, a neuston net tow was made at each station. This was a surface tow taken at a speed of 1.5 knots for 10 minutes duration. The net was fished from the side of the vessel, outside of the vessel’s wake, and the cable paid out was adjusted to insure the net fished the top 0.5 m of the water. The frame of the net was a 1 by 2 m m rectangle, and the mesh was 0.947 mm.

Identifications and measurements (to the nearest 0.1 mm body length) of bongo-collected larvae by the Polish Plankton Sorting and Identification Center in Szczecin, Poland were verified for all survey years except 2007. Data from 2007 were included in the analyses, but were considered provisional. The methodologies of Scott et al. (1993) and Scott and Turner (1994) were used to standardize larval data. The mean number of larvae per 100 m² at first daily otolith increment formation for each station sampled between April 20 and May 31 each year of the time series (1977–2007) were estimated and used to index abundance. The calculation of the number of larvae per 100 m² resulted from the need to incorporate the depth over which each volumetrically-sampled bongo tow was integrated [i.e. the number of larvae per volume (m³) multiplied by sampled the depth (m)]. The indices were estimated as

$$I_{s,y} = \frac{\sum_{i=1}^k R_D e^{-Z(D_{s,y,i-1})}}{A_{s,y}} \quad (1)$$

where y indexes year, s indexes sampling station, $i(= 1, \dots, n)$ indexes individual larvae, A the surface area sampled, Z the larval daily loss rate, D the larval daily ring count, and R the gear efficiency estimate applied. Estimates were constructed using the preferred method as described in Scott et al. (1993) and Scott and Turner (1994), which adjusts the density estimates of each of the sampling stations for estimated larval loss rates and gear efficiency. With these station- and year-specific estimates of larval catch, Scott et al. (1993) and Scott and Turner (1994) then used the delta–distribution method of Pennington (1983) to develop unbiased estimates of average annual larval density (and variability), taken to be the annual index value (and variability).

Identifications and measurements (to the nearest 0.1 mm body length) of neuston-collected larvae by the Polish Plankton Sorting and Identification Center in Szczecin, Poland were also verified for all survey years except 1987, 1988, 2006 and 2007. Specimens from 1987 and 1988 were not measured and currently the location of these specimens is unknown due to damage incurred during Hurricane Katrina. If those samples cannot be recovered in the future this will permanently represent a data hole in the time series. Data from 2006 and 2007 were included in the analyses, but were considered provisional. Both length–frequency and age–frequency histograms were evaluated to determine an appropriate standardization approach for neuston-collected data. The standardized number

per 10-minute neuston tow for each station sampled between April 20 and May 31 each year of the time series (1982–2007) was estimated and used to index abundance.

Unbiased estimators of the mean and variance of the PDD method (Pennington 1983) are presented as

$$I_{\Delta,y} = \begin{cases} \frac{m_y}{n_y} e^{T_y} G_{m_y} \frac{s_y^2}{2}, & m_y > 1, \\ \frac{x_1}{n_y}, & m_y = 1, \\ 0, & m_y = 0 \end{cases} \quad (2)$$

and

$$V(I_{\Delta,y}) = \begin{cases} \frac{m_y}{n_y} e^{2T_y} \left[G_{m_y} (2s_y^2) - \left(\frac{m_y-1}{n_y-1} \right) G_{m_y} \left(\frac{m_y-2}{n_y-1} s_y^2 \right) \right], & m_y > 1, \\ \frac{x_1^2}{n_y}, & m_y = 1, \\ 0, & m_y = 0 \end{cases} \quad (3)$$

respectively, where n_y is the number of observations, m_y is the number of nonzero values, T_y and s_y^2 are the sample mean and sample variance, respectively, of the log of the nonzero values, x_1 denotes the single untransformed value when m_y equals one, and

$$G_{m_y} \left(\frac{s_y^2}{2} \right) = 1 + \frac{m-1}{m} \left(\frac{s_y^2}{2} \right) + \sum_{j=2}^{\infty} \frac{(m-1)^{2j-1}}{m^j (m+1)(m+3) \dots (m+2j-3)} \times \left(\frac{s_y^2}{2} \right)^j \quad (4)$$

This PDD method (Pennington 1983) was used to further update the bongo index for continuity and to develop a new neuston index. This was done to make comparisons between the indices developed from the PDD method and those developed from DL models.

The DL index of relative abundance (I_y) as described by Lo et al. (1992) was estimated as

$$I_y = c_y p_y, \quad (5)$$

where c_y is the estimate of mean CPUE for positive catches only for year y ; p_y is the estimate of mean probability of occurrence during year y . Both c_y and p_y were estimated using generalized linear models. Data used to estimate abundance for positive catches (c) and probability of occurrence (p) were assumed to have a lognormal distribution and a binomial distribution, respectively, and modeled using the following equations:

$$\ln(\mathbf{c}) = \mathbf{X}\boldsymbol{\beta} + \boldsymbol{\varepsilon} \quad (6)$$

and

$$\mathbf{p} = \frac{e^{\mathbf{X}\boldsymbol{\beta} + \boldsymbol{\varepsilon}}}{1 + e^{\mathbf{X}\boldsymbol{\beta} + \boldsymbol{\varepsilon}}}, \text{ respectively,} \quad (7)$$

where \mathbf{c} is a vector of the positive catch data, \mathbf{p} is a vector of the presence/absence data, \mathbf{X} is the design matrix for main effects, $\boldsymbol{\beta}$ is the parameter vector for main effects, and $\boldsymbol{\varepsilon}$ is a vector of independent normally distributed errors with expectation zero and variance σ^2 .

We used the GLIMMIX and MIXED procedures in SAS (v. 9.1, 2004) to develop the binomial and lognormal submodels, respectively, to develop annual DL indices for both bongo- and neuston-collected larvae. Similar covariates were included in both submodels: time of day (two categories: night, 6:00 PM to 6:00 AM, local time; day, 6:00 AM to 6:00 PM, local time), survey date category (four categories: late April, April 20 to April 30; early May, May 1 to May 10; middle May, May 11 to May 20; late May, May 21 to May 31), survey area [original survey area as defined by Scott et al. (1993) divided into three categories: eastern survey area (survey area between 84° and 86° longitude); central survey area (survey area between 86° and 91° longitude); western survey area (survey area between 91° and 94° longitude)] and year. If any variables were not found to be at least marginally significant (i.e. at $\alpha = 0.10$) based on type 3 analysis, then those variables were removed. Type 3 tests are hypothesis tests for the significance of each of the fixed effects to be considered for inclusion in the model (null hypothesis: the change in model likelihood resulting from the inclusion of the effect is zero). The significance of including each effect is evaluated given that all the other effects to be considered are already in the model. The fit of each of the submodels was evaluated using residual analyses, which were accomplished by plotting the residuals by year and by developing a QQ plot of the residuals assuming a normal distribution. Also, a Wilcoxon signed rank test was conducted to test the null hypothesis that the mean of the residuals is zero, assuming that the distribution is symmetric (Lehmann 1998). The performance of the binomial submodel was evaluated with the AUC [i.e. the Area Under the receiver operating characteristic (ROC) Curve] methodology presented by Steventon et al. (2005). The ROC curve is used to assess the fit or predictive accuracy of dichotomous models (McPherson et al. 2004; Boyce et al. 2002). The AUC statistic is developed from the ROC curve, and is both a robust measure of model performance and relatively insensitive to prevalence (proportion of 0 or 1). The AUC statistic does not require the choice of an arbitrary prediction probability threshold defining “presence” vs. “absence,” but rather it summarizes model performance across the range of possible thresholds (Cumming 2000).

Then, $\ln(c_y)$ and p_y were estimated as least-squares means for each year along with their corresponding standard errors, $SE(c_y)$ and $SE(p_y)$, respectively. Before, calculation of I_y , the estimates of $\ln(c_y)$, on the natural log-scale are back-transformed to those on the original (normal) data scale, c_y , using a bias correction as detailed by Lo et al. (1992). From these estimates, I_y was calculated, as in Equation (5), and its variance calculated as

$$V(I_y) \approx V(c_y)p_y^2 + c_y^2V(p_y) + 2c_y p_y \text{Cov}(c, p), \quad (8)$$

where

$$\text{Cov}(c, p) \approx \rho_{c,p} \left[SE(c_y) SE(p_y) \right], \quad (9)$$

and $\rho_{c,p}$ denotes correlation of c and p among years.

In order to develop the ZIDL model to estimate annual indices of abundance for both bongo- and neuston-collected larvae, we replaced the regular binomial portion of the DL model with a ZIB model that takes into account the high proportion of zeros in the abundance data. The ZIB model treats the probability of observing a bluefin tuna larva as a product of the true

probability of the site being occupied (o), and the probability of detection (d) when in fact the site is occupied at the time the sample is taken (Tyre et al. 2003; Steventon et al. 2005). Multiple samples must be taken at each site in order to estimate d , but the number of samples per site (m) does not have to be equal (Tyre et al. 2003). The number of occurrences of an animal for each site over m samples is denoted as x , and the number of sites sampled as n (Steventon et al. 2005).

In the case of this study, a year was treated as a site, since the goal was to develop annual indices of abundance. Therefore, when we considered one year after m samples have been taken (i.e., m bongo stations completed), the probability of observing zero bluefin tuna larvae was

$$P(x = 0) = o(1 - d)^m + (1 - o)(1) \quad (10)$$

and the probability of observing exactly x bluefin tuna larvae, where x is greater than zero was

$$P(x > 0) = o \binom{m}{x} d^x (1 - d)^{m-x} + (1 - o)(0) \quad (11)$$

after Tyre et al. (2003) and Steventon et al. (2005). We then combined these two probabilities to form the likelihood function for a single year y :

$$L(o, d | x, m) = \begin{cases} o(1 - d)^m + (1 - o), & x = 0 \\ o \binom{m}{x} d^x (1 - d)^{m-x}, & x > 0 \end{cases} \quad (12)$$

following the methods of Tyre et al. (2003).

Steventon et al. (2005) expressed the above probability in Equation (12) as a generalized Bernoulli distribution, allowing the combination of multiple years into a full likelihood:

$$L(o, d | \{x_y, m_y, u_y\}) = \prod_{y=1}^n [o(1 - d)^{m_y} + (1 - o)]^{u_y} \times \left[o \binom{m_y}{x_y} d^{x_y} (1 - d)^{m_y - x_y} \right]^{1 - u_y} \quad (13)$$

where u_y is an indicator variable: $u_y = 1$ when $x_y = 0$ and $u_y = 0$ when $x_y > 0$. The values of o and d are not required to be constant, and are usually not over time. These values can be influenced by covariates as follows:

$$o = \frac{e^{X\beta + \varepsilon}}{1 + e^{X\beta + \varepsilon}} \quad (14)$$

and

$$d = \frac{e^{X\beta + \varepsilon}}{1 + e^{X\beta + \varepsilon}}, \quad (15)$$

where o and d are vectors of probability of occupancy and probability of detection, respectively, X is the design matrix for main effects, β is the parameter vector for main effects, and ε is a vector of independent normally distributed errors with expectation zero and variance σ^2 . Certain covariates may be common between both the above models, while others may be completely different (Steventon et al. 2005).

Therefore, in the case of this study, the estimated probability of collecting a bluefin tuna larva during a single ichthyoplankton station is

$$p_{Z1,y} = o \times d \quad (16)$$

and the probability of collecting at least one bluefin tuna larva after m ichthyoplankton stations is

$$p_{Z,y} = o [1 - (1 - d)^m], \quad (17)$$

following the methods of Steventon et al. (2005). We then replace p_y in Equations (5), (8) and (9) with $p_{Z,y}$ from Equation (17) to estimate annual indices of abundance and their corresponding variance using this new zero-inflated approach [$I_{Z,y}$ and $V(I_{Z,y})$, respectively].

The NLMIXED procedure in SAS (v. 9.1, 2004) was employed to model the ZIB model. Initial SAS code for this procedure was provided by Steventon et al. (2005). We modified this code in order to use dummy variables, which were needed to include categorical variables in the model. The variables used in the model were the same as those used in the binomial submodel of the DL model. However, the time of day variable was placed in the detection submodel, while the other variables were placed in the occurrence submodel (see Equations (14) and (15)) contained in the ZIB submodel. Submodel performance was evaluated using AUC (Area Under Curve) methodology (Steventon et al. 2005) and residual analyses, as described above.

In order to develop MDL indices of abundance CPUE data collected with differing gears, we replaced each submodel with its multivariate counterpart. The binomial submodel was replaced with a multivariate binomial logit-normal model as described by Coull and Agresti (2000). This approach models vectors $Y = (Y_1, Y_2, \dots, Y_R)$ of binomial-type responses, by incorporating a separate random effect for each of the R binomial responses, such that $\text{logit}(\pi_s)$ is a multivariate normal random variable. Specifically,

$$\text{logit}(\pi_s) = \alpha_s + \mathbf{X}_s \beta, \quad (18)$$

where π_s is a vector of multivariate probabilities of occurrence, $s = 1, \dots, N$ represents subject (for this study we treated time of day as the subject), \mathbf{X}_s is the $R \times p$ covariate matrix whose r th row is x_{sr} and $\alpha_s \sim N(0, \Sigma)$ (where x_{sr} is a fixed covariate row vector and α_s are i.i.d. random variables). The parameters β describe the effects of the explanatory variables, while Σ contains parameters that reflect the heterogeneity among subjects as well as within-subject dependencies among the R variables. In order to estimate the index values based on the underlying common effect between both gears the following equation was used:

$$p_{MV,y} = \frac{e^{\mathbf{X}_s \beta_y}}{1 + e^{\mathbf{X}_s \beta_y}}, \quad (19)$$

where $p_{MV,y}$ is the probability of occurrence based on the underlying common effects between both gears (β_y) evaluated for year y . Likewise, the lognormal submodel was replaced with a multivariate lognormal model with similar parameter structure as previously described for the multivariate binomial model in Equation (18):

$$\log(c_s) = \alpha_s + \mathbf{X} \beta_s, \quad (20)$$

where c_s is a vector of multivariate non-zero catch rates. Similarly, to estimate the index values based on the underlying common effect between both gears the following equation was used:

$$c_{MV,y} = e^{\mathbf{X}_s \beta_y}, \quad (21)$$

where $c_{MV,y}$ is the estimate of mean CPUE for positive catches only based on the underlying common effects between both gears (β_y) evaluated for year y . Finally, the $I_{MV,y}$ is estimated as in Equation (5):

$$I_{MV,y} = c_{MV,y} p_{MV,y} \quad (22)$$

and its variance calculated as in Equations (8) and (9). The NLMIXED procedure in SAS (v. 9.1, 2004) was employed to model the multivariate submodels of this approach. The variables included in the model were the same as above for the DL model with the addition of three covariance parameters to describe any covariance between the neuston and bongo catch at each station. Submodel performance was evaluated using AUC (area under curve) methodology (Steventon et al. 2005) and residual analyses, as described above.

In order to calculate upper and lower 95% confidence limits (UCL and LCL) for I_y , $I_{Z,y}$, and $I_{MV,y}$, the following equations were used:

$$UCL = (I \times C) \text{ and } LCL = (I/C), \quad (23)$$

where I is the index value,

$$C = e^{(2 \sqrt{\ln(1+CV^2)})}, \quad (24)$$

and CV is the coefficient of variation of the mean index value. Typically, a CV is calculated as standard deviation/mean, and not standard error/mean. This is because CV is usually a measure of the variability of the data. However, here CV was used as a measure of the precision of the mean (i.e. $CV = \text{standard error of the index value}/\text{index value}$). Index values and corresponding CV s and confidence limits were compared on a year by year basis to determine if there were any changes in annual index values developed with the DL and ZIDL approaches for both bongo- and neuston-collected data. Also, the average percent change in both the index values and the CV s over the time series developed with the DL and ZIDL approaches were calculated for both bongo- and neuston-collected data.

3 Results

A preliminary analysis of the data collected in bongo and neuston tows indicated that for most survey years, data can be used from late April through the entire month of May. However, there were several years where surveys were started late or ended early due to mechanical, meteorological and/or other logistical factors. For bongos, the number of stations sampled during the April 20 through May 31 time period ranged from 20 to 97 (Table 1), while the number of neuston tows ranged from 66 to 175 (Table 1). The number of specimens collected in bongo tows per year ranged from 7 to 221, and ranged in length from 1.3 to 10.7 mm (Appendix online-only, Table A1);

Table 1. The total number of samples included in analyses per year, the number of samples containing larvae per year, and the nominal frequency of occurrence per year are represented by n , m , and f , respectively, for both bongo- and neuston-collected larvae.

Survey Year	Bongo			Neuston		
	n	m	f	n	m	f
1977	20	8	0.40	0	.	.
1978	69	33	0.48	0	.	.
1979	0	.	.	0	.	.
1980	0	.	.	0	.	.
1981	35	6	0.17	0	.	.
1982	97	20	0.21	98	32	0.33
1983	93	16	0.17	92	12	0.12
1984	71	6	0.09	70	1	0.01
1985	0	.	.	0	.	.
1986	72	7	0.10	72	9	0.13
1987	78	5	0.06	0	.	.
1988	77	15	0.20	0	.	.
1989	85	14	0.17	143	29	0.2
1990	86	10	0.12	147	11	0.08
1991	69	5	0.07	145	12	0.08
1992	83	14	0.17	145	9	0.06
1993	83	6	0.07	144	11	0.08
1994	84	12	0.14	132	9	0.07
1995	97	8	0.08	175	13	0.07
1996	79	10	0.13	142	9	0.06
1997	74	11	0.15	131	5	0.04
1998	59	5	0.09	117	15	0.13
1999	71	8	0.11	136	9	0.07
2000	74	7	0.10	144	13	0.09
2001	71	11	0.16	133	18	0.14
2002	71	4	0.06	123	6	0.05
2003	38	10	0.26	72	8	0.11
2004	32	6	0.19	66	6	0.09
2005	74	13	0.17	143	8	0.06
2006	75	16	0.21	126	18	0.14
2007	48	10	0.21	79	9	0.11

and the number collected in neuston tows per year ranged from 2 to 174, and ranged in length from 2.5 to 10.5 mm (Appendix online, Table A2).

Both age- and length-frequency histograms of neuston-collected larvae were analyzed to determine the appropriate standardization approach (Fig. 1). Figure 1a depicts the age-frequency histogram of neuston-collected larvae. The daily age of each larva was derived from body length (BL) using the age-length key provided by Scott et al. (1993). This histogram indicated that a larval daily loss rate (Z) could not be developed from the age-frequency data. However, the length-frequency histogram of larval body lengths (Fig. 1b) indicated the larvae were fully recruited by 5 mm, approximately at 7 days old (i.e. 7.69 days old). Therefore, a per-millimeter loss rate of 0.8285 was derived through a nonlinear regression of the descending upper limb of the length-frequency histogram (Fig. 1b),

$$N_{BL} = 40015.3e^{(-0.8285 \cdot BL)}, \quad (25)$$

where N_{BL} is the number of larvae per 0.5 mm size (i.e. BL) bin. This regression was used to standardize the larval data to number of 5 mm larvae per 10-minute neuston tow. With

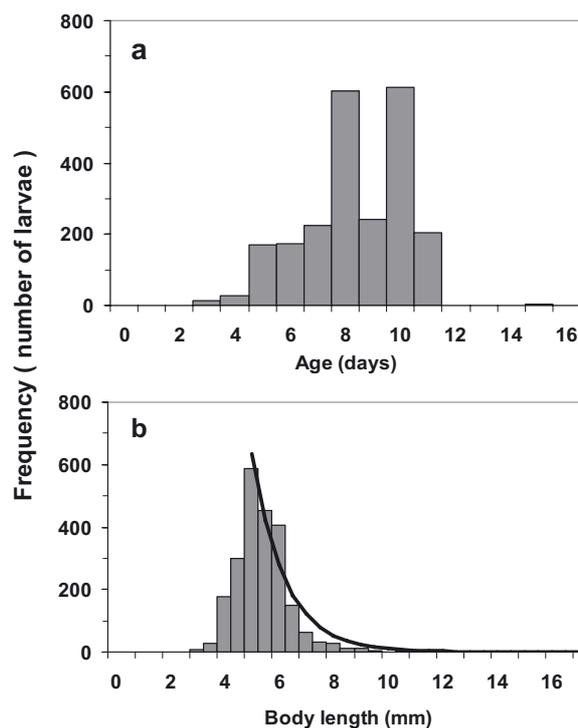


Fig. 1. Age frequency (a) and length frequency (b) distributions of Atlantic bluefin tuna larvae collected in neuston tows ($N = 2270$ larval lengths transformed to age). Age data was summarized in 1-day age classes (bins). Length data was summarized in 1-mm size classes. Figure (b) illustrates the nonlinear regression by which the standardization factor was calculated.

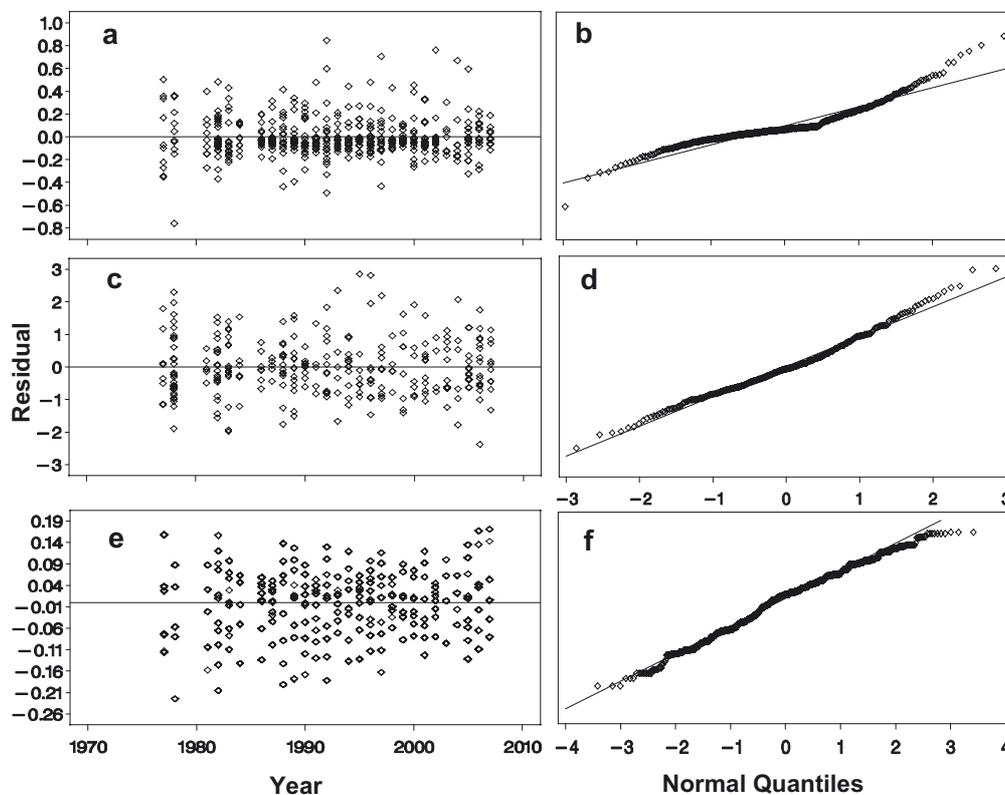
this approach, the inclusion of larvae over 9 mm body length, which was a rare event, resulted in extremely large catches, and were deemed unrealistic. Therefore, larvae over 9 mm and under 5 mm were excluded from further analyses.

The results of type 3 analyses for both submodels used to develop the DL model for bongo-collected larvae are summarized in Table 2. For the binomial submodel all variables were significant (i.e. at $\alpha = 0.05$). For the lognormal submodel, all variables were significant (i.e. at $\alpha = 0.05$) except survey area, which was marginally significant (i.e. at $\alpha = 0.10$). The binomial submodel had an AUC = 0.736. This means that in 74 out of 100 instances, a station selected at random from those with larvae had a higher predicted probability of larvae being present than a station randomly selected from those that had no larvae. Residual analyses indicated the mean of the residuals from the binomial submodel differed significantly from zero (Wilcoxon signed rank test: $S = -6740$, p -value = 0.0072). Residual analyses indicated that the residuals from the binomial submodel differ slightly from a normal distribution, with herding of negative residuals near zero (Fig. 2a) and the slight departure of the residuals from the theoretical normal reference line in Fig. 2b. Residual analyses indicated the mean of the residuals of the lognormal submodel did not differ significantly from zero (Wilcoxon signed rank test: $S = -1181$, p -value = 0.4239), and that the residuals were approximately normally distributed (Fig. 2c,d).

Table 2. Type 3 tests of delta-lognormal model parameters for data collected in bongo tows. Num DF: numerator degrees of freedom; Den DF: denominator degrees of freedom.

Type 3 Tests of Fixed Effects for the Binomial Submodel						
Effect	Num DF	Den DF	χ^2	F Value	Pr > χ^2	Pr > F
Year	27	585	82.18	2.96	<0.0001	<0.0001
Survey date	3	1423	52.75	17.58	<0.0001	<0.0001
Survey area	2	1514	35.29	17.64	<0.0001	<0.0001
Time of day	1	1596	13.38	13.38	0.0003	0.0003

Type 3 Tests of Fixed Effects for the Lognormal Submodel				
Effect	Num DF	Den DF	F Value	Pr > F
Year	27	262	3.90	< 0.0001
Survey date	3	262	3.82	0.0105
Survey area	2	262	2.35	0.0972
Time of day	1	262	5.69	0.0178

**Fig. 2.** Residual plots of the submodels developed from data collected during bongo tows using both the delta-lognormal (DL) approach and the zero-inflated delta-lognormal (ZIDL) approach; (a and b) represent plots of residuals by year and a QQ plot of residuals, respectively, for the binomial submodel for the DL approach; (c and d) represent plots of residuals by year and a QQ plot of residuals, respectively, for the lognormal submodel for both the DL and ZIDL approaches; (e and f) represent plots of residuals by year and a QQ plot of residuals, respectively, for the zero-inflated binomial submodel for the ZIDL approach.

The same variables that were retained in the model-building process of the binomial submodel for the development of I_y for bongo-collected larvae were used in the ZIB model: time of day, survey date category, survey area, and year (Appendix online, Table A3). All the variables except time of day were used in the occupancy submodel while only the time of day was used in the detection submodel for the ZIB model. The time of day variable was used in the detection submodel

as we reasoned that time of day (i.e. day or night) has an effect on the probability of detecting larvae (net avoidance). The ZIB submodel had an AUC = 0.727. This means that in 73 out of 100 instances, a station selected at random from those with larvae had a higher predicted probability of larvae being present than a station randomly selected from those that had no larvae. Residual analyses indicated the mean of the residuals of the ZIB submodel did not differ significantly from zero

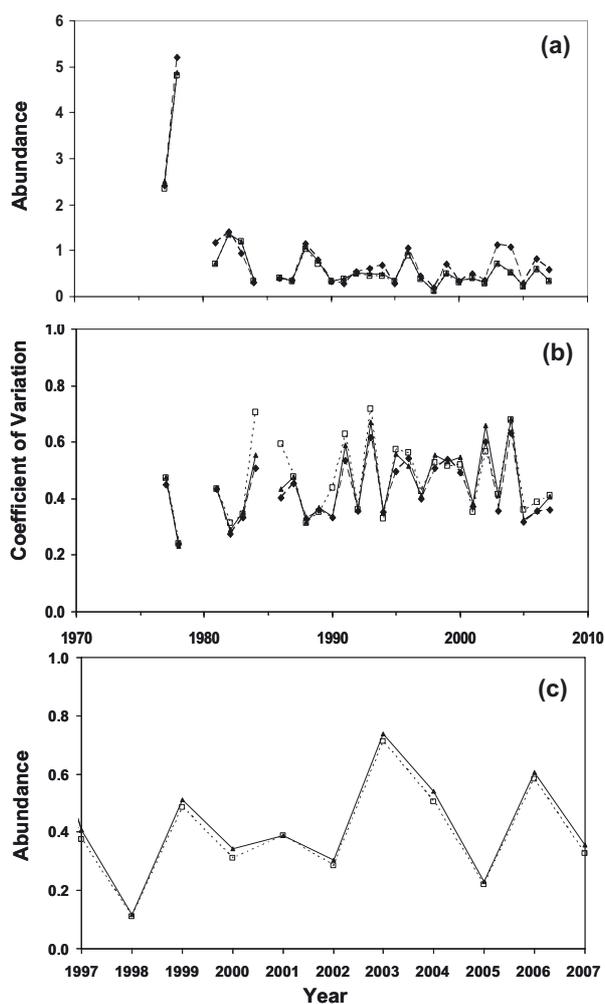


Fig. 3. Abundance indices of larval bluefin tuna (number under 100 m² of sea surface) collected in bongo tows developed from the Pennington delta-distribution method (PDD; \blacklozenge), the delta-lognormal model (DL; \square) and zero-inflated delta-lognormal model (ZIDL; \blacktriangle); (a): annual abundance indices derived from each approach; (b): coefficients of variation of the index values in graph (a); (c) represents a detailed look at the DL and ZIDL index values from 1997 to 2007.

(Wilcoxon signed rank test: $S = -34374.5$, p -value = 0.1695), and that the residuals were approximately normally distributed (Fig. 2e,f). Figure 3 summarizes the indices of larval bluefin tuna (number under 100 m² of sea surface) collected in bongo tows developed from the PDD method, the DL model and ZIDL model. Figure 3a shows a large decrease in the index values derived from all methods from the late 1970s to the mid 1980s.

The results of type 3 analyses for both submodels used to develop the DL model for neuston-collected larvae are summarized in Table 3. For the binomial submodel all variables were highly significant (i.e. at $\alpha = 0.0001$). For the lognormal submodel, the survey date category and survey area variables were not significant (i.e. at $\alpha = 0.05$), and were dropped from the model. The binomial submodel had an AUC = 0.744. Therefore, in 74 out of 100 instances, a station selected at random from those with larvae had a higher predicted

probability of larvae being present than a station randomly selected from those that had no larvae. Residual analyses indicated the mean of the residuals from the binomial submodel differed significantly from zero (Wilcoxon signed rank test: $S = -5635$, p -value = 0.0071). Residual analyses indicated that the residuals from the binomial submodel differ slightly from a normal distribution, with herding of negative residuals near zero (Fig. 4a) and the slight departure of the residuals from the theoretical normal reference line in Fig. 4b. Residual analyses indicated the mean of the residuals of the lognormal submodel did not differ significantly from zero (Wilcoxon signed rank test: $S = -1062$, p -value = 0.4119), and that the residuals were approximately normally distributed (Fig. 4c,d).

Likewise, the same variables that were retained in the model-building process of the binomial submodel for the development of I_y for neuston-collected larvae were used in the ZIB model: time of day, survey date category, survey area, and year (Appendix online, Table A4). Again, all the variables except time of day were used in the occupancy submodel while only the time of day was used in the detection submodel for the ZIB model. The time of day variable was used in the detection submodel as we reasoned that time of day (i.e. day or night) has an effect on the probability of detecting larvae with the neuston gear (net avoidance and diel vertical migration). The ZIB submodel had an AUC = 0.750. Residual analyses indicated the mean of the residuals of the ZIB submodel differed significantly from zero (Wilcoxon signed rank test: $S = -112135.5$, p -value = 0.0170), and that the residuals tended to herd around certain values (Fig. 4e,f). Likewise, Figure 5 summarizes indices of larval bluefin tuna (number per 10-minute tow) collected in neuston tows developed from the PDD method, the DL model and ZIDL model. Figure 5a indicates high interannual variability in the index values regardless of developmental method.

Annual indices of abundance developed from the ZIDL approach were higher than those developed from the DL approach. For indices based on bongo-collected data, there was an average increase of 6% in the index values and a 3% decrease in corresponding CVs (Fig. 3b). For indices based on neuston-collected data, there was an average increase of 8% in the index values and 0.2% decrease in corresponding CV (Fig. 5c). However, for both bongo- and neuston-collected data, index values were not significantly different between the ZIDL approach and the DL approach, based on the overlap of corresponding confidence intervals (Appendix online, Tables A5 and A6).

The parameters developed for the MDL approach were similar to those of the DL approach and included parameters for time of day, survey date category, survey area, and year. Also, three covariance parameters were developed to take into account the covariance between bongo and neuston catch rates (Appendix online, Table A7). Residual analyses indicated the mean of the residuals from the binomial submodel differed significantly from zero (Wilcoxon signed rank test: $S = -30097.5$, p -value < 0.0001). Residual analyses indicated that the residuals from the multivariate binomial submodel differ slightly from a normal distribution, with herding of negative residuals near zero (Fig. 6a) and the slight departure of the residuals from the theoretical normal reference line in Fig. 6b.

Table 3. Type-3 tests of delta-lognormal model parameters for data collected in neuston tows. Num DF: numerator degrees of freedom; Den DF: denominator degrees of freedom.

Type 3 Tests of Fixed Effects for the Binomial Submodel						
Effect	Num DF	Den DF	χ^2	F Value	Pr > χ^2	Pr > F
Year	22	909	97.79	4.38	< .0001	< 0.0001
Survey date	3	1923	61.78	20.59	< .0001	< 0.0001
Survey area	2	2230	39.10	19.55	< .0001	< 0.0001
Time of day	1	2326	19.31	19.31	< .0001	< 0.0001

Type 3 Tests of Fixed Effects for the Lognormal Submodel: <i>Run 1</i>				
Effect	Num DF	Den DF	F Value	Pr > F
Year	22	242	2.43	0.0005
Survey date	3	242	0.88	0.4507
Survey area	2	242	0.47	0.6263
Time of day	1	242	2.96	0.0868

Type 3 Tests of Fixed Effects for the Lognormal Submodel: <i>Run 2</i>				
Effect	Num DF	Den DF	F Value	Pr > F
Year	22	247	2.54	0.0003
Time of day	1	247	3.81	0.0522

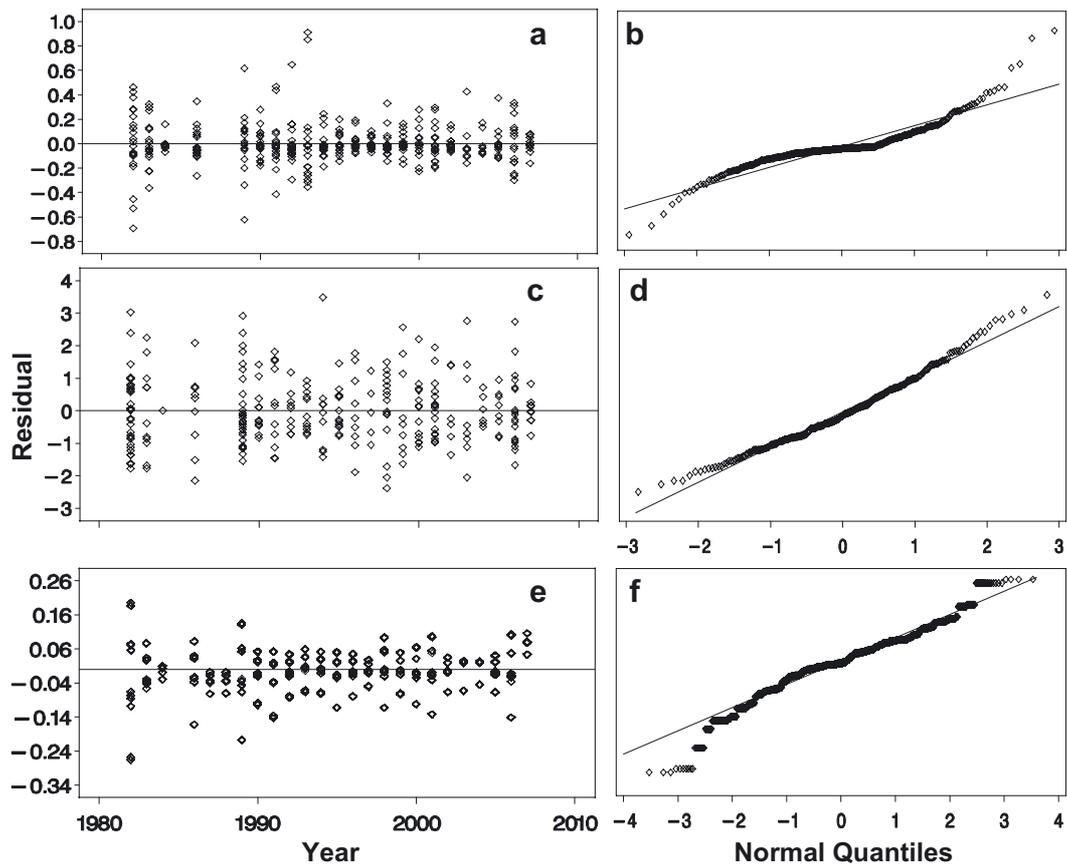


Fig. 4. Residual plots of the submodels developed from data collected during neuston tows using both the delta-lognormal (DL) approach and the zero-inflated delta-lognormal (ZIDL) approach; (a and b) represent plots of residuals by year and a QQ plot of residuals, respectively, for the binomial submodel for the DL approach; (c and d) represent plots of residuals by year and a QQ plot of residuals, respectively, for the lognormal submodel for both the DL and ZIDL approaches; (e and f) represent plots of residuals by year and a QQ plot of residuals, respectively, for the zero-inflated binomial submodel for the ZIDL approach.

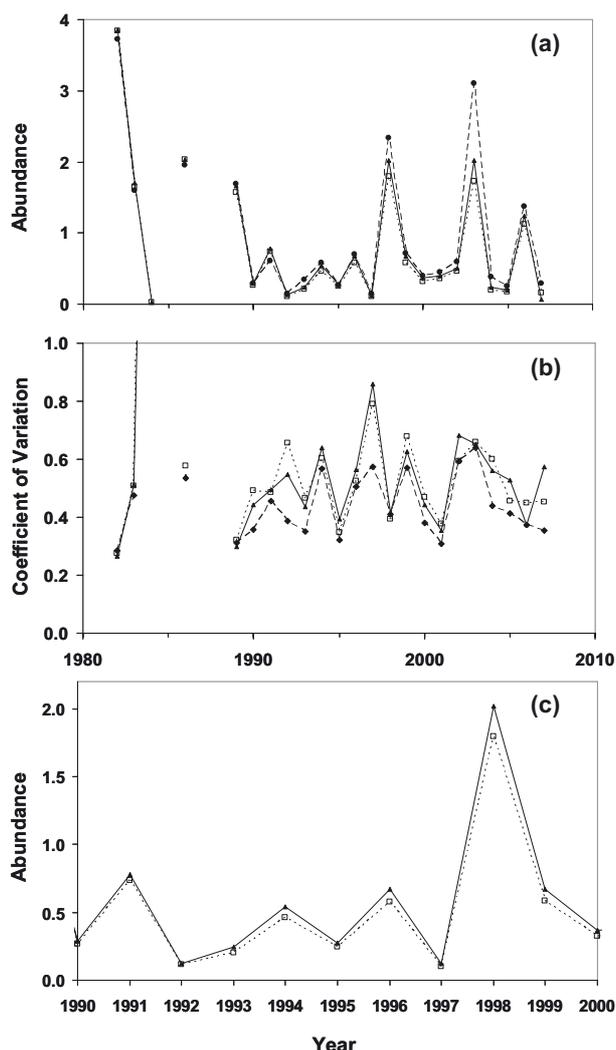


Fig. 5. Abundance indices of larval bluefin tuna (number per 10-minute tow) collected in neuston tows developed from the Pennington delta-distribution method (PDD; \blacklozenge), the delta-lognormal model (DL; \square) and zero-inflated delta-lognormal model (ZIDL; \blacktriangle); (a): annual abundance indices derived from each approach; (b): coefficients of variation of the index values in graph (a); (c) represents a detailed look at the DL and ZIDL index values from 1990 to 2000.

Residual analyses indicated the mean of the residuals of the multivariate lognormal submodel did not differ significantly from zero (Wilcoxon signed rank test: $S = -429.5$, p -value = 0.4903), and that the residuals were approximately normally distributed (Fig. 6c,d). Figure 7 summarizes indices of larval bluefin tuna collected in bongo and neuston tows developed with the MDL approach (Appendix online, Table A8).

4 Discussion

For larval bluefin tuna collected in bongo tows, all indices and corresponding CVs were similar when comparing years between the PDD, DL and ZIDL approaches (Fig. 3). Index values were highest in the early years of the survey and much lower in recent years, and in the 1998 and 2005 survey years

the index values developed via the DL and ZIDL approaches were the lowest of the entire time series. Residual analyses indicated that, while the residuals of the lognormal submodel, used identically in both the DL and the ZIDL model development, were approximately normally distributed, residuals of the binomial submodel for the DL approach were not, and those of the ZIB submodel for the ZIDL approach were approximately normally distributed (Fig. 2). Also, since the AUC values indicated essentially identical model performance for the binomial and ZIB submodels, we reason that the ZIDL modeling approach is most appropriate for the bongo-collected data.

The per-millimeter loss rate of 0.8285 was developed by assuming that the larvae were completely recruited by 5 mm body length and used to standardize the number of larvae collected in neuston tows. This resulted in more realistic standardized catch values than the extreme values resulting from an assumption of a larger body size at full recruitment. For larval bluefin tuna collected in neuston tows, all indices were fairly similar when comparing years between the DL and ZIDL approaches, with the exception of survey years 1998 and 2003 where the DL and ZIDL modeled indices were lower than those developed using the PDD method. However, all approaches produced very similar patterns of abundance. Residual analyses indicated that, while the residuals of the lognormal submodel, used identically in both the DL and the ZIDL model development, were approximately normally distributed, residuals of the binomial submodel for the DL approach and those of the ZIB submodel for the ZIDL approach were not. Therefore, although the AUC values indicated essentially identical model performance for the binomial and ZIB submodels, residual analysis indicated that neither the DL nor the ZIDL approach was appropriate for the neuston-collected data.

Corresponding CVs of the annual index values were similar between different modeling approaches, while those of the PDD method were smaller. When compared to indices developed for bongo-collected larvae, index values were similarly high in the early years of the survey, except for survey year 1984, and much lower in recent years, except for survey years 1998 and 2003. Also, indices of neuston-collected larvae were much more variable between years than those of bongo-collected larvae.

A modeling approach to develop abundance indices is recommended over the PDD method. Modeling allows for standardization of yearly catch estimates for those years where sampling methodology differed slightly from standard techniques. For example, in survey years 2003 and 2004, the survey did not begin until mid-May, which resulted in a Pennington estimator ($I_{A,y}$) for bongo-collected larvae that was biased high for each of those years, since spawning of bluefin in the Gulf of Mexico usually peaks in mid- to late-May (Rooker 2007). Modeled indices ($I_y, I_{Z,y}$) for these two years were estimated to be lower as a result of the significant effect of the survey date categorical variable.

This is a first step in modeling zero-inflated data, while taking into account both “true zeros” (i.e. with the DL portion of the ZIDL approach) and “false zeros” (i.e. with the replacement of the binomial submodel with a ZIB submodel). For both bongo- and neuston-collected larvae, time of day was

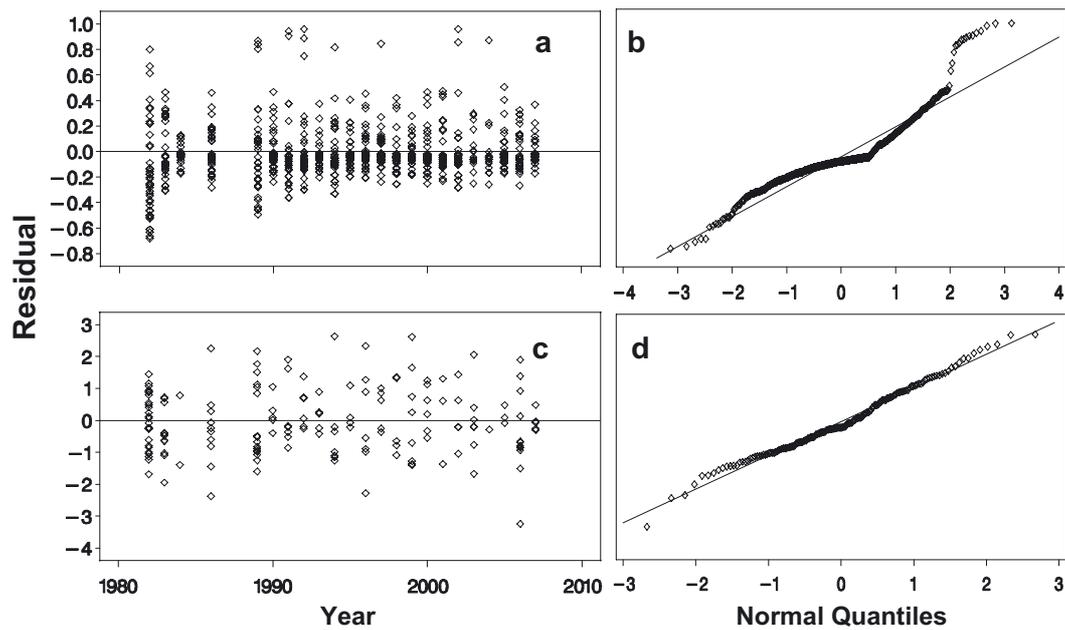


Fig. 6. Residual plots of the submodels developed from data collected during both bongo and neuston tows using multivariate delta-lognormal (MDL) approach. Graphs (a) and (b) represent plots of residuals by year and a QQ plot of residuals, respectively, for the multivariate binomial submodel for the MDL approach. Graphs (c) and (d) represent plots of residuals by year and a QQ plot of residuals, respectively, for the lognormal submodel for the MDL approach.

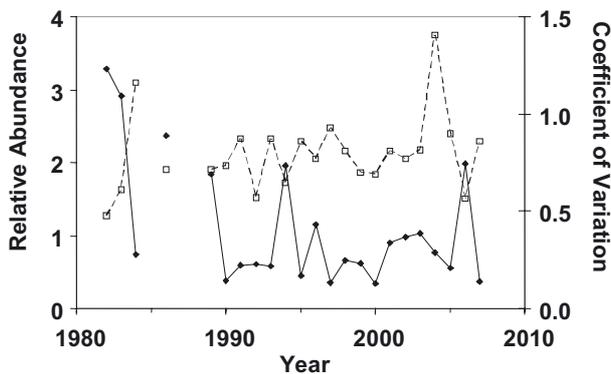


Fig. 7. Relative abundance indices of larval bluefin tuna collected in both bongo and neuston tows developed from the multivariate delta-lognormal model (MDL; ◆) and corresponding coefficients of variation (CV; □).

a significant variable that was included in the various models. When time of day was included in the detection submodel of the ZIB model, some correction for lack of detection was provided. In fact, 96% of ZIDL index values based on bongo catch rates and 96% of ZIDL index values based on neuston catch rates were slightly higher than those derived from the DL approach (i.e. 6% and 8% increase, respectively, but not significantly higher) when compared annually.

Further development is needed in generalizing this approach to take into account complex covariance patterns not presented herein. For example, based on equations 10 to 17, it is assumed that the detection of each larva is independent. We know that larvae, especially bluefin tuna larvae, tend to be

patchy (Richards and Potthoff 1980; McGowan and Richards 1986) in their distribution and hence spatially autocorrelated. Therefore, it would be of benefit for future studies in model development to include generalization of the model presented here by incorporating spatial autocorrelation in the modeling process.

Similar to the univariate indices discussed above, annual index values derived with the MDL approach are higher during the early years of the time series and lower in later years. While the MDL approach is a novel approach by which to gain inference on abundance trends simultaneously from multiple gears, there was a decrease in precision (i.e. increase in CVs) in the resulting index values, which one would expect unless the correlation between the catch rates of the two gears was perfect (i.e. $r = 1$ or -1). Therefore, the MDL approach would be most appropriately employed when the joint index values themselves are deemed more important than their corresponding CVs (e.g. when indices used in stock assessment models are not inversely weighted on CV). Residual analyses indicated that, while the residuals of the multivariate lognormal submodel were approximately normally distributed, residuals of the multivariate binomial submodel for the MDL approach were not, which may indicate that the distributional assumptions of the multivariate binomial submodel were not fully met and further investigation is needed into the MDL approach.

The relatively high variance (i.e. high CV) in index values developed by the various modeling methods described above could be a result of the lack of explanatory variables and not just zero-inflation. However, there was a slight average decrease in CV values for index values of both bongo- and neuston collected data, between the DL approach and the ZIDL approach, which may indicate a slight increase in

precision when applying the ZIDL approach. Environmental information at individual sampling stations, such as water temperature, salinity, dissolved oxygen concentration, etc. could explain much of the variability in catch rates; such information is currently undergoing scrutiny, and will be included in the development of future abundance indices. Also, research is currently being conducted concerning the characterization of larval bluefin tuna habitat based on the analysis of satellite imagery. Findings of this study will be incorporated into the modeling approaches described herein, in order to reduce the variance in annual abundance indices.

Due to the large frequency of zeros in the data, especially in later years, ZIDL index values derived from bongo catch rates were selected as most representative of spawning stock biomass in the U.S. Gulf of Mexico and used in the final stock assessment model during the 2008 Atlantic Bluefin Tuna Stock Assessment Session (Anonymous 2008). This decision also resulted from the fact that the index developed from bongo catch rates was based upon the abundance of one-day-old larvae, assumed to be more indicative of egg abundance and therefore spawning stock biomass, instead of seven-day-old larval abundances, as in the neuston data. Moreover, residual analyses indicated that abundance indices of Atlantic bluefin tuna larvae in the Gulf of Mexico were more appropriately developed from bongo-collected data through the ZIDL approach than other data sets and modeling approaches. Also, when modeling bongo-collected data with the ZIDL approach, the index values increased, indicating some correction for zero-inflation, and their variability decreased as compared to indices developed with the DL approach. Finally, for ZIDL index values derived from bongo catch rates, there is an obvious decrease in catch rates of Atlantic bluefin tuna larvae, which likely indicate a decline in the spawning stock biomass in the US Gulf of Mexico. Such declines have been a concern during several of the Atlantic Bluefin Tuna Stock Assessment conducted by the International Commission for the Conservation of Atlantic Tunas (ICCAT; Anonymous 2008).

Supporting information

Table A1. Summary of bongo data used in these analyses.

Table A2. Summary of neuston data used in these analyses.

Table A3. Parameters of the zero-inflated binomial model for bongo tows. The prefix *o* denotes those parameters in the occupancy submodel, while the prefix *d* denotes those parameters in the detection submodel.

Table A4. Parameters of the zero-inflated binomial model for neuston tows. The prefix *o* denotes those parameters in the occupancy submodel, while the prefix *d* denotes those parameters in the detection submodel.

Table A5. Indices of larval bluefin tuna (number under 100 m² of sea surface) collected in bongo tows developed from the Pennington delta-distribution method, the delta-lognormal model and zero-inflated delta-lognormal model. The total number of samples included in analyses per year, the number

of samples containing larvae per year, and the nominal frequency of occurrence per year are represented by *n*, *m*, and *f*, respectively. Coefficients of variation (CV = standard error of the index value/index value) and lower and upper 95% confidence limits (LCL and UCL, respectively) are provided.

Table A6. Indices of larval bluefin tuna (number per 10-minute tow) collected in neuston tows developed from the Pennington delta-distribution method, the delta-lognormal model and zero-inflated delta-lognormal model. The total number of samples included in analyses per year, the number of samples containing larvae per year, and the nominal frequency of occurrence per year are represented by *n*, *m*, and *f*, respectively. Coefficients of variation (CV = standard error of the index value/index value) and lower and upper 95% confidence limits (LCL and UCL, respectively) are provided.

Table A7. Multivariate delta-lognormal model parameters for data collected in bongo and neuston tows.

Table A8. Indices of larval bluefin tuna collected in bongo and neuston tows developed from the multivariate delta-lognormal model. The number of samples included in analyses per year represented by *n*.

References

- Anonymous, 2008, Report of the 2008 Atlantic Bluefin Tuna Stock Assessment Session, Madrid, June 2008.
- Boyce M.S., Vernier P.R., Nielson S.E., Schmiegelow F.K.A., 2002, Evaluating resource selection functions. *Ecol. Model.* 157, 281–300.
- Coull B.A., Agresti A., 2000, Random effects modeling of multiple binomial responses using the multivariate binomial logit-normal distribution. *Biometrics* 56, 73–80.
- Cumming G.S., 2000, Using between-model comparisons to fine-tune linear models of species ranges. *J. Biogeogr.* 27, 441–55.
- Hall D.B., 2000, Zero-inflated Poisson and binomial regression with random effects: a case study. *Biometrics* 56, 1030–1039.
- Lehmann E.L., 1998, *Nonparametrics: Statistical Methods Based on Ranks*, New Jersey: Prentice Hall.
- Lo N.C.H., Jacobson L.D., Squire J.L., 1992, Indices of relative abundance from fish spotter data based on delta-lognormal models. *Can. J. Fish. Aquat. Sci.* 49, 1515–1526.
- Martin T.G., Wintle B.A., Rhodes J.R., Kuhnert P.M., Field S.A., Low-Choy S.J., Tyre A.J., Possingham H.P., 2005, Zero tolerance ecology: improving ecological inference by modeling the source of zero observations. *Ecol. Lett.* 8, 1235–1246.
- McConnaughey R.A., Conquest L.L., 1993, Trawl survey estimation using a comparative approach based on lognormal theory. *Fish. Bull.* 91, 107–118.
- McGowan M.F., Richards W.J., 1986, Distribution and abundance of bluefin tuna (*Thunnus thynnus*) larvae in the Gulf of Mexico in 1982 and 1983 with estimates of the biomass and population size of the spawning stock for 1977, 1978, and 1981–1983. *ICCAT. Coll. Vol. Sci. Pap.* 24, 182–195.
- McPherson J.A., Jetz W., Rogers D.J., 2004, The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *J. Appl. Ecol.* 41, 811–823.
- Minami M., Lennert-Cody C.E., Gao W., Roman-Verdesoto M.H., 2007, Modeling shark bycatch: The zero-inflated negative binomial regression model with smoothing. *Fish. Res.* 84, 210–221.

- Murphy G.I., 1990, A review of Atlantic bluefin tuna larval surveys. ICCAT. Coll. Vol. Sci. Pap. 32, 262–269.
- Pennington M., 1983, Efficient estimators of abundance, for fish and plankton surveys. *Biometrics* 39, 281–286.
- Pennington M., 1996, Estimating the mean and variance from highly skewed data. *Fish. Bull.* 94, 498–505.
- Richards W.J., 1990, Results of a review of the U.S. bluefin tuna larval assessment with a brief response. ICCAT. Coll. Vol. Sci. Pap. 32, 240–247.
- Richards W.J., Potthoff T., 1980, Distribution and abundance of bluefin tuna larvae in the Gulf of Mexico in 1977 and 1978. ICCAT. Coll. Vol. Sci. Pap. 9, 433–441.
- Rooker J.R., Alvarado Bremer J.R., Block B.A., de Metrio G., Corriero A., Krause R.T., Prince E.D., Rodriguez-Marin E., Secor D.H., 2007, Life history and stock structure of Atlantic bluefin tuna (*Thunnus thynnus*). *Rev. Fish. Sci.* 15, 265–310.
- Scott G.P., Turner S.C., Grimes C.B., Richards W.J., Brothers E.B., 1993, Indices of larval bluefin tuna, *Thunnus thynnus*, abundance in the Gulf of Mexico; modeling variability in growth, mortality, and gear selectivity. *Bull. Mar. Sci.* 53, 912–929.
- Scott G.P., Turner S.C., 1994, An updated index of west Atlantic bluefin spawning biomass based on larval surveys in the Gulf of Mexico. ICCAT Coll. Vol. Sci. Pap. 62, 211–213.
- Steventon J.D., Bergerud W.A., Ott P.K., 2005, Analysis of presence/absence data when absence is uncertain (false zeroes): an example for the northern flying squirrel using SAS[®]. *Res. Br., British Columbia Min. Forests, Victoria BC, Exten. Note* 74.
- Tyre A.J., Tenhumberg B., Field S.A., Niejalke D., Parris K., Possingham H.P., 2003, Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecol. Appl.* 13, 1790–1801.
- Vieira A.M.C., Hinde J.P., Demetrio C.G.B., 2000, Zero-inflated proportion data models applied to a biological control assay. *J. Appl. Stat.* 27, 373–389.