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Scientific publications by ICNAF and NAFO have been in existence since ICNAF began in 1949 with the ICNAF Special Publication series dealing with proceedings of scientific symposia. The *ICNAF Research Bulletin* was started in 1964 to provide a means of publishing results of scientific research relevant to ICNAF. The *ICNAF Research Bulletin* was terminated in September 1979 after the issue of Number 14. The first volume of the NAFO *Journal of Northwest Atlantic Fishery Science* was published in December 1980, after NAFO came into force replacing ICNAF in 1979.

The Northwest Atlantic fisheries have a rich history, and a great deal of research has been sponsored and encouraged by NAFO and its predecessor ICNAF. NAFO has been a leader amongst international organizations in the application of science to fishery management and in the regulation of fisheries in areas beyond national jurisdiction. In accordance with its mandate to disseminate information on fisheries research to the scientific community, the Scientific Council of NAFO publishes the *Journal of Northwest Atlantic Fishery Science*, which contains peer-reviewed primary papers, and *NAFO Scientific Council Studies*, which contains unrefereed papers of topical interest and importance to the Scientific Council. Lists of these and other NAFO publications are given on the back of this issue.

Editorial Policy

The Journal provides an international forum for the primary publication of original research papers, with emphasis on environmental, biological, economic and social science aspects of fisheries and their interactions with marine habitats and ecosystems. While the Journal is intended to be regional in scope, papers of general applicability, and methodological and review papers, irrespective of region, are considered. Space is available for notes and letters to the editor to facilitate scientific discussion of published papers. Both practical and theoretical papers are eligible. All papers are peer-reviewed to determine their suitability for primary publication. Associate Editors arrange for the peer-reviews and ensure that the papers accepted for publication meet the high standards required for the Journal. Manuscripts approved for publication are accepted with the understanding that they are not copyrighted, published or submitted elsewhere except in abstract form. There are no page charges.

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Foreword

The Scientific Council of NAFO publishes the *Journal of Northwest Atlantic Fisheries science*, containing peerreviewed primary literature detailing original research of relevance to fisheries science and management in the northwest Atlantic Ocean. Articles are published electronically under a Creative Commons (Canada) 2.5 license, and are freely available at http://journal.nafo.int. NAFO Scientific Council has resolved to produce annual bound print volumes and these represent a compilation of the web based articles published throughout the year. Additionally, the journal supports the use of digital object identifiers (doi) for electronic media and encourages others to support this initiative.

As always, this volume of the journal covers a range of topics representing ongoing research in the northwest Atlantic, including fisheries Management Strategy Evaluation and fish and cetacean distribution and biology.

In my first comments as General Editor of the journal, I would like to extend my thanks to my predecessor, Neil Campbell, the Associate Editors and reviewers and Alexis Pacey, publications manager at the NAFO Secretariat for their support and assistance. I look forward to continuing our collaboration over the coming years.

December 2016

Tom Blasdale, General Editor Journal of Northwest Atlantic Fisheries Science

Contents

Information, Editorial Policy and Editorial Boardii	ii
NAFO Convention Area Mapi	v
Foreword	v
The impact of different assumptions about reproductive potential and recruitment on a Management Strategy Evaluation for the Greenland halibut stock in NAFO Subarea 2 and Division 3KLMNO	1
Opportunistic Sightings of Cetaceans in Nearshore and Offshore Waters of Southeast Florida	1
Continental shelf residency by adult Atlantic halibut electronic tagged in the Gulf of Maine	3
Perspectives provided by bottom trawl transect surveys conducted in the 1950s and 1960s on the dynamics of commercially exploited groundfish species on southern Grand Bank and St. Pierre Bank	1
Scientific Publications of the Northwest Atlantic Fisheries Organization	1
Information for Preparing Manuscripts for NAFO Scientific Publications	5

The impact of different assumptions about reproductive potential and recruitment on a Management Strategy Evaluation for the Greenland halibut stock in NAFO Subarea 2 and Division 3KLMNO

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Abstract

We tested whether our perception of the performance of the adopted Harvest Control Rule (HCR) for Greenland halibut was robust to using different measures of Reproductive Potential (RP) combined with different assumptions about the stock recruit relationship to drive the stock dynamics in simulations. We tested the HCR using alternative stock recruitment functions (segmented regression, Ricker and modified Ricker) with different RP indices which vary in the level of biological complexity. The RP indices used in increasing order of biological information were: Biomass 10+, SSB with varying maturity at age (SSB), female SSB (FSB), and Total Egg Production (TEP). All Operating Models (OM) were based on the current accepted XSA assessment. Understanding the basis of uncertainty in the S/R relationships is generally the most difficult outstanding problem in fisheries assessment and management and it is a key problem in Management Strategy Evaluation (MSE). A Ricker stock recruitment function fits the Greenland halibut stock recruitment data better than the segmented regression for all the RP indices, except TEP. The results show that the inclusion of more biological information when estimating Reproductive Potential does not improve the stock recruitment fit for either (segmented regression or Ricker). The best fits in both cases were obtained in descending order with: 10+Biomass, SSB, FSB, and TEP. All the OMs based on the segmented regression have very similar results and seem to be robust to assumptions about RP. However, there was variability in the results of the different indices of RP in the Ricker and modified Ricker OMs and some impact on whether performance targets were met. The choice of stock recruit function had a greater impact than the inclusion of more biological information in the index of RP. The inclusion of alternative indices of RP is likely to have more of an impact for stocks with depleted reproductive capacity and/or where alternative indices have a greater effect on the S/R relationships.

1. Introduction

Determination of the reproductive potential (RP) of a population is an important aspect of fish stock assessment. The potential to produce recruits is a major component of population productivity and thus has a large impact on the resilience of a population. Spawning stock biomass (SSB) is often used as the measure of RP as a predictor of recruitment produced. However, SSB may not be the best metric of RP because reproductive potential may not be proportional over time to the spawning stock biomass (Marshall *et al.*, 1998; Scott *et al.*, 2006; Morgan, 2008; Marshall, 2009). Measures of SSB commonly assume biological processes are invariant. However, maturity, sex ratio, fecundity and/or parental condition are known to vary and this may play an important role in variation in egg production. Integrating variation in biological process into our metrics of RP may help to explain variability in recruitment (Marshall *et al.*, 2006; Morgan *et al.*, 2009).

The incorporation of more biological realism into indices of RP affects our perception of the status of populations (Morgan and Brattey, 2005; Marshall *et al.*, 2006; Morgan *et al.*, 2009; Murua *et al.*, 2010). It can also improve estimation of recruitment (Marteinsdottir and Thorarinsson, 1998; Murawski *et al.*, 2001; Kraus *et al.*, 2002). However, this may depend on the stock being examined either because some populations have shown little trend in factors such as maturation and fecundity and/or because the data used to estimate alternative indices of RP are of poor quality or time series are lacking (Tomkiewicz *et al.*, 2003; De Oliveira *et al.*, 2006; Morgan *et al.*, 2011).

Since the perception of stock status and productivity can be affected by the choice of RP index, this could be an important consideration when rules for determining appropriate levels of harvest are developed. Such rules can be tested using management strategy evaluation (MSE, Kell *et al.*, 2007). However, when conducting a Management Strategy Evaluation (MSE), alternative RP indices are often not incorporated (Murua *et al.*, 2010).

An MSE was conducted for the Greenland halibut (Reinhardtius hippoglossoides) stock on the Newfoundland shelf in the Northwest Atlantic (Miller et al., 2008; Shelton and Miller, 2009). Greenland halibut is an important flatfish resource which has had catches in excess of 60 000 t (Healey et al., 2010). The population declined to very low levels in the mid 1990s and a MSE was conducted to evaluate various harvest control rules (HCR) to recover the stock (Shelton and Miller, 2009). The Greenland halibut MSE was extensive with two sets of operating models (OM) conditioned on two different population models. Several different stock recruit (S/R) relationships were considered, as well as different levels of natural mortality and fishery selectivity. Varying growth was considered in the MSE but not possible variation in maturation, sex ratio and fecundity (Miller et al., 2008). Thus it is not known whether the HCR adopted by the NAFO Fisheries Commission (NAFO, 2010a) is robust to the inclusion of information on sex ratio and fecundity into RP.

There have been few tests of whether HCRs are robust to the inclusion of more biological realism into the measures of RP. De Oliveira *et al.* (2010) found that estimates of SSB and fishing mortality were biased when the variation in fecundity was not taken into account in the assessment of western horse mackerel (*Trachurus trachurus*). Although the inclusion of more biological information affected the estimation of the biological reference points (BRPs) and the status of the stock in relation to those biological reference points, Murua *et al.* (2010) found that the HCR for European hake (*Merluccius merluccius*) was robust to the exclusion of more biological information in the indices of RP. Variability in reproductive biology may play an important role in understanding the underlying mechanisms regulating the annual recruitment, but incorporating more biological realism into a forecast model could multiply the uncertainty in forecasts.

Our objective was to test whether the current HCR for the Greenland halibut stock in NAFO Subarea 2 Division 3KLMNO is robust to different measures of RP combined with different assumptions about the stock recruit relationship. We focus on a set of OM based on the current assessment view (CAV) OMs used in the Greenland halibut MSE (Shelton and Miller, 2009; NAFO, 2010b). CAV is most closely consistent with the 2010 NAFO Greenland halibut accepted assessment model (Healey *et al.*, 2010). We test the HCR using alternative stock recruitment functions with different RP indices which vary in their level of biological complexity (incorporating sex-ratio and fecundity).

2. Material and methods

To allow the direct comparison of our results with those obtained in the 2010 NAFO Greenland halibut MSE (NAFO, 2010b), the simulations run in this analysis were conducted precisely as were done in 2010 and all the data used with the exception of the RP indices used in determining future recruitment were the same.

2.1. The simulation algorithm

The simulation algorithm used in this document is the same used in the development of the NAFO Greenland halibut Management Strategy Evaluation (Miller et al., 2007; Miller et al., 2008; Shelton and Miller, 2009) adopted by the NAFO Fisheries Commission in 2010 (NAFO, 2010a). The conceptual framework for MSE, adapted from Kell et al. (2007), comprises an operating model and a management strategy/procedure model. The operating model (OM) simulates the 'real or true system' (i.e. the biological population and the fishery, their interaction and the implementation of the management advice) and the Management Strategy (MS) simulates how the management advice is determined through the HCR. This simulation algorithm explicitly or implicitly acknowledges different sources of uncertainty in both the "real" system and the management procedure (Rosenberg and Restrepo, 1994; Francis and Shotton, 1997; Kell et al., 2007). The real biological population and fishery are projected, in yearly time steps, using the OM, and the MS is applied annually to produce the management advice (total allowable catch) for the next year. The Greenland halibut MSE takes into account historical uncertainty in the form of observation error through an XSA bootstrap procedure (Miller and Shelton, 2007). Process error (variation in weights at age, partial recruitment at age and number of recruits) was also taken into account. In the Greenland halibut MSE, no management implementation error (*i.e.* TAC over/under-runs) was considered after 2010, the start of the simulation.

2.1.1. The initial population

The initial random population is generated based on the 2010 assessment carried out with XSA (Healey *et al.*, MS 2010) but replacing the observed abundance indices by a set of 500 bootstrapped abundance indices. To generate abundance indices from the XSA for each bootstrap iteration, a nonparametric bootstrap resampling within each age and index was conducted (Miller and Shelton, 2007).

Greenland halibut matures at an old age (>10), and as a slow growing species, they likely live well beyond age 14, the plus group age in the assessment. Given that most of the reproductive potential was included in the 14+ plus group and all the fish are mature by age 20, it was decided to expand the age structure of the "true" population in the OM to age 20 (age 20+ as a plus group). The plus group numbers for each year estimated in the assessment were then expanded out to age 20+ based on the assumption that the PR (selectivity to the commercial fishery) for the older ages is equal to that of age 13 (Miller et al., MS 2008). Natural mortality was assumed constant for all ages and years and equal to 0.2. The weights at age matrix for years 1975 to 2009 was the same used in the in the 2010 NAFO Greenland halibut MSE. The weights at age for years 1975 to 2009 (up to age 13) were taken from the XSA inputs (based on commercial catch data) in Healey et al. (MS 2010). The weights at age (1975-2009) for ages older than 13 years old were calculated by Miller with the method explained in Miller et al. (MS 2007).

2.1.2. The operating models

The Operating Models (OMs) tested in this study were based on three different Stock/Recruitment (S/R) relationships: segmented regression, the Ricker S/R model, and a modified Ricker. The S/R relationships were fitted using the numbers at age 1 in the initial population and the different RP indices (as calculated in section 2.1.3) for the period 1975-2006 in each of the iterations to avoid the uncertainty in the last years XSA recruitment results, as it was made in Miller et al. (2008). Best fits for all S/R relationships were calculated by minimising the log residual sums of squares (SS). The Ricker S/R model led to very low recruitment at high values of RP causing extreme fluctuations at high stock size as a result of strong density dependent compensation. Therefore it was decided to implement the modified Ricker S/R OM where the recruitment does not decline below a specified level at high indices of RP. In the modified model, for estimates of RP above the maximum historically observed, recruitment

is set as the recruitment estimated by the Ricker function (plus an error term) for the highest observed RP. Similar to Shelton and Miller (MS 2009), the OM based on the segmented regression was called Current Assessment View (*CAV*), the OM based on the Ricker function was called *CAV_Ric* and the OM based on the modified Ricker model was called *CAV_mRic*. *CAV* is most consistent with the accepted assessment model and is the same XSA *CAV* OM tested in the Greenland halibut MSE (Shelton and Miller, 2009).

Twelve OMs, resulting from the combination of four RP indices (see below) with the three S/R described above, were tested. These OMs consist of an age-structured biological population and a single fishery inducing fishing mortality during the harvesting process. Each OM starts in 2010 and for this year the population numbers of age two and older are calculated using the numbers and fishing mortalities obtained in the generation of the initial population while the recruits at age one are estimated using the different S/R relationships described above with a lognormal multiplicative random error with autocorrelation. This error was bootstrapped each year and iteration from the observed errors of the best fit of each S/R relationship. The parametric forms of each S/R model to estimate the projections recruitment were the following:

Segmented regression:

$$\begin{cases} R = \alpha * RP * \varepsilon & \text{if } RP \le \beta \\ R = \alpha * \beta * \varepsilon & \text{if } RP > \beta \end{cases}$$

Ricker:

$$R = \alpha * RP * e^{-\beta^* RP} * \varepsilon$$

Modified Ricker:

$$\begin{cases} R = \alpha * RP * e^{-\beta * RP} * \varepsilon & \text{if } RP < maxObs (RP) \\ R = mxR * \varepsilon & \text{if } RP \ge maxObs (RP) \end{cases}$$

Where:

R is the estimated recruitment.

 α and β are the parameters of the functions.

maxObs (RP) is the maximum observed RP value for years 1975–2005

mxR is the recruitment estimated by the function for *maxObs (RP)* in the observed years.

 ε is the lognormal multiplicative random error with autocorrelation.

In subsequent years, the population numbers are carried forward using the exponential survival equation. Implementation error was only applied in 2010. For 2010 the catch level was the TAC (16 000 t) plus the observed TAC overrun resampled from the period 2004–2009.

$$C_{2010} = 16\,000\,\chi_y$$

$$\chi_y from U(1.27, 1.22, 1.27, 1.42, 1.32, 1.45)$$

For the other years projected, the TAC is caught exactly, unless there is not enough exploitable biomass to support such a TAC, in which case a value of 1 for the mean F for ages 1–20 is applied.

The selectivity of the fishery in the projected years is resampled from the selectivity observed in the period 1997–2006. Weights for projected years were resampled by year (all ages), from the period 2000 to 2009. Female maturity, sex ratio and fecundity in the calculated RP indices in the projections were taken without uncertainty and equal to the 2010 values as was done in the 2010 Greenland halibut MSE.

2.1.3. Indices of reproductive potential

Data on maturity, sex ratio and fecundity were collected from Canadian research vessel bottom trawl surveys conducted in autumn from 1978 to 2010. Survey data from Div. 2J and 3K only were used as these areas had the most consistent coverage of the deep water areas inhabited by Greenland halibut.

Proportion mature at age was estimated by cohort, using generalized linear models with a logit link function and binomial error. Age was treated as a continuous variable since in general it is not possible to have a lower proportion of adults at age a+1 than at age a, that is once a fish becomes an adult it will always be an adult (Morgan and Colbourne, 1999). All ages were used in the fitting. There were significant model fits for cohorts 1966–1983, 1985–1986, 1988–1992, 1994 and 1996–1998. For cohorts where there was no significant model fit to the data, the averages of estimates from adjacent cohorts or from the three closest cohorts were used.

Sex ratio (proportion female) at age was also estimated using generalized linear models with a logit link function and binomial error. These models had the form *sex ratio* = age + cohort, where age and cohort were both class variables. In this case age was treated as a class variable since there is no *a priori* reason to believe that sex ratio would change continuously across age (Morgan and Brattey, 2005). In order to produce reasonable estimates of proportion female for a particular age and cohort, a sufficient number of age samples were required. For example, if there were only two observations for a cohort at a particular age, then the proportion female could only be 0, 0.5 or 1. Therefore, we used only ages 3 to 14 in the model fitting and only included an age/cohort combination if there were at least 5 observations. Sufficient data were available to fit the model to cohorts from 1969–2001.

Fecundity data were limited. A fecundity/length relationship based on data collected in 1976–77 (Bowering, 1980) was used for those years. For 1986 unpublished data were used ($r^2=0.43$ for fit of model to data) and for the other years a combination of these two relationships was used. The relationships were:

- For 1976–1977: *F*=0.0623*(Length^3.082)
- For 1980: F= 0.0018*(Length^3.8263)
- For all other years: *F*=0.01064*(Length^3.454)

The fecundity length relationships were applied to mean length at age to produce egg production at age. The lengths at age used are the same as in the 2010 assessment and previous MSE work and are based on commercial samples which in most years come from a winter fishery. However, they were for sexes combined and thus could deviate from true female weight or length. Fecundity was determined mostly by size so age was not included in the modeling (Lambert *et al.*, 2003).

These estimates of maturity, sex ratio and fecundity were used along with the weights and numbers at age to produce four different Reproductive Potential (RP) indices. The different RP indices were:

 $B10^+$, the biomass for ages more than 9 years old as proxy of SSB where N_{ay} is the population number-at-age a in year y and W_{ay} the weight-at-age a in year y. This index has been used in the past as proxy for SSB in the assessment of this stock.

$$B10 + = \sum_{a=10}^{20} Nay * Way$$

SSB, the spawning stock biomass using maturity ogives estimated by cohort applied to the total biomass where M_{av} is the proportion mature-at-age *a* in year *y*.

$$SSB = \sum_{a=1}^{20} Nay * Way * May$$

FSB, the female spawning biomass estimated using maturity ogives estimated by cohort applied to female biomass where R_{ay} is the proportion of female-at-age *a* in year *y*.

$$FSB = \sum_{a=1}^{20} Nay * Way * May * Ray$$

TEP, the total egg production, incorporating a proxy for realized fecundity-at-age where E_{ay} is the egg production at age *a* in year *y* calculated as described above.

$$TEP = \sum_{a=1}^{20} Nay * May * Ray * Eay$$

2.1.4. The management strategy

The MS was first applied in 2010 and led to the first TAC advice for 2011 based on the Harvest Control Rule (HCR) approved by the Fisheries Commission in 2010 (NAFO, 2010a). The same HCR is applied every year up to 2030. The MS model is divided in two steps: (i) the OM which simulates the data collection (the surveys indices) (ii) the management decision model which uses a HCR based on the surveys indices to derive management advice. In the OM the abundance indices for all ages are generated with a multiplicative random error assuming a linear relationship between survey abundance at age and abundance at age in the true population (constant q):

$$\ln(I_{y,a}) = \ln(q_a) + \ln(N_{y,a}) + \varepsilon$$

Where: $I_{y,a}$ is the simulated survey index for a particular survey, age and year

 q_a is the estimated catchability for a particular survey and age

 $N_{y,a}$ is the OM abundance for a particular age and year.

 ε is the bootstrapped observed catchability error from each particular survey, age and period.

The TAC for year y+1 is set based on the survey indices observed in the period y-5 to y-1 with the HCR based on a simple TAC adjustment strategy that uses the change in perceived status of the stock (from research surveys) to adjust the TAC:

$$\text{TAC}_{y+1} = \text{TAC}_{y} (1 + \lambda * slope)$$

Where: *slope* = average slope of log-linear regression lines fit to the last five years of each of the three survey biomass indices (equally weighted).

The λ values are: 2 if the slope is negative and 1 if the slope is positive.

The HCR includes a constraint such that the TAC from 2012 onwards does not change by more than 5% from

the previous year. The starting value for the TAC was set at 17 500 t.

2.1.5. Performance Targets

The HCR was evaluated using several performance targets (PT)

- 1. The probability of the decline of 25% or more in terms of exploitable biomass from 2011 to 2016 is kept at 10% or lower.
- 2. The magnitude of the average TAC in the short (2015), medium (2020) and long (2030) term should be maximized.
- 3. The probability of failure to meet or exceed a milestone within a prescribed period of time should be kept at 25% or lower. Milestone means the average exploitable biomass for the period 1985–1999 (106 000 t.) to be compared with the exploitable biomass in 2031.

The PTs and their correspondent performances statistics (PS) were established in the Greenland halibut MSE (NAFO, 2010b). In this study a fourth PS is included related to fishing mortality. Although there are currently no precautionary approach fishing mortality reference points for this stock, the annual probability of the *F* being greater than the annually estimated F_{max} was included as a proxy for $P(F > F_{lim})$. There is no approved Fisheries Commission target for this statistic but less than 10% probability is considered a very low probability in the NAFO Precautionary Approach framework and we take this probability level as our target.

3. Results

3.1. Biological variables by age

Variation in female maturity at age by cohort was evident (Fig. 1) with a clear pattern over time with cohorts from the 1980s on generally maturing at a younger age than those of the 1970s. There was a trend of increasing proportion of females over time, although most of the change was in age classes at which very few females are mature (less than age 14). Fecundity has also varied over time, with some trend to lower fecundity since about 2000. Since fecundity data are limited, most of the change in fecundity actually reflects changes in mean length at age. The low egg production for an age 12 individual in 1980 is the result of the small length of age 12 individual in that year.

The proportion female at age is more or less constant around 0.5 until age 7 (Fig. 2). Proportion female then clearly increases from age 8 to age 12 and for older ages the proportion female is almost 1. This reflects differential





Fig. 1. Trends over time in biological inputs to the indices of Reproductive Potential. Age at 50% maturity estimated by cohort (along with 95% confidence limits), proportion female for ages 10 and 11 and number of eggs produced in thousands for an age 12 fish.

longevity and probably growth, maturity and mortality patterns between females and males. The variability in the proportion female is low for all ages in absolute terms but was as much as 20% for some ages. The estimated proportion mature at age is essentially zero for ages younger than 10, and increases to one by about age 18. The ages over which the fish mature (mainly 11–17) show substantial variation. Fecundity at age shows a clear increasing trend from age 5 onwards. This is the result of the increase in fecundity with length. The variability by age is quite low until age 15 and increases from age 16 to 20.

3.2. Indices of Reproductive Potential

The trends in RP indices are very similar with a decline to 1980 followed by a rapid increase to the early 1990s after which they all drop to 2006 before increasing to the end of the time series (Fig. 3). The main difference is that 10+ biomass reaches its maximum in 1991 while the other have their maximum in 1992. The main reason for this gap is that population numbers at 10+ were relatively high from the late 1980s to the mid 1990s, peaking in 1991 when the 10+ biomass has its maximum. However, the 1980 year class has a very steep increase in proportion mature at age and is estimated to be 97% mature at age 12, in 1992. This is in contrast to other cohorts that have mostly 10-25% mature at age 12. This results in indices of RP using proportions mature at age having their peak in 1992. SSB and FSB are very similar because most of the mature females are older than 13 years, where the proportion of females is almost 1, so that the inclusion of sex ratio does not result in much change. The TEP time series shows some deviation from the trends in SSB and FSB but is still very similar overall.





Fig. 2. Estimated proportion mature, proportion female and fecundity at age. The box represents the 25th to 75th percentile, the horizontal line the median, the whiskers the 10th and 90th percentile and the dots the outliers.

3.3. Stock recruitment relationships

The fits of the segmented regression to all the RP indices are very similar (Fig. 4). For all indices their level at the start of the projection (2010) is greater than the segmented regression break point (" β " parameter). For the Ricker S/R all the indices show a very similar fit with a strong compensation effect (Fig. 5). This strong compensation effect in the Ricker S/R function is driven by a small number of S/R pairs. The levels of all RPs at the start of the projection are close to those that produce the maximum recruitment.

Based on the Mean Absolute Error (MAE) and the Akaike Information Criterion (AIC), the Ricker S/R has a better fit to the data for 10+ biomass, SSB and FSB. For TEP the segmented regression and Ricker AIC and MAE values are very similar. In both segmented regression and Ricker the best fits were to the 10+ index followed by SSB, FSB and TEP (Table 1 and 2).

3.4. Stochastic results of the Operating Models using different Reproductive Potential (RP) indices

3.4.1 Operating Models based on the segmented regression (CAV)

The HCR has similar results for all RP scenarios in the *CAV* set of OMs, with their medians, 5^{th} and 95^{th} percentiles for biomass, fishing mortality, catch and recruitment showing very similar trajectories (Fig. 6). 5+ Biomass in the projected years shows a clear increasing trend reaching maximum values in the last year (2031) in all cases. All the RP scenarios show an increase in exploitable



Fig. 3 Reproductive Potential indices for ages 1 to 20+: 10+ biomass (10+), spawning stock biomass (SSB), female spawning biomass (FSB) and total egg production (TEP). All indices are normalized to the 1975–2010 period.

biomass (5–9) in the short term (2011–2016) reaching the exploitable biomass objective in 2017 for all the RPs. Table 3 presents the PS1 and PS3 results for each RP. The probability of the 2016 biomass being higher than the 2011 biomass (PS1) is very high (greater than 0.99) for the HCR in all of the RP scenarios. The probability of reaching the exploitable biomass objective in 2031 (PS3) is very high in all RP scenarios at more than 0.99. The exploitable biomass (5–9) time series shows an increasing trend from 2012 to 2018 after which it is more or less stable in all RP scenarios.

Fishing mortality shows a decreasing trend from 2012 to 2018 and after that is quite stable around 0.1 in all the scenarios under this stock recruitment assumption. The probability that the annual F is greater than the annual F_{max} (PS4) is less than 0.1 in all projected years for all the RP scenarios (Table 4). All the RP scenarios also have very similar catch results in the short, medium and long term (Figs. 6 and 7); showing a slight increase until 2024 with stability after that.

3.4.2. Operating Models based on the Ricker S/R function (CAV_Ric)

All of the RP scenarios show a major decline in biomass over the projection period under the assumption of a Ricker S/R relationship, however the timing of the decline varies. All results for SSB and FSB are very similar (Fig. 8). Exploitable biomass (5–9) increases until about 2019 before declining, while 5+ biomass increases to 2023 and then declines. F_{bar} declines and then remains at a low level for most of the time series, while recruitment increases to about 2014 and then declines. The 10+ RP index results are similar to those for SSB and FSB particularly for F_{bar} and catch. Biomass and recruitment decline later in the projection period for 10+ biomass than for SSB and FSB.

The results for TEP are very different from the others. Recruitment rapidly declines to very low levels because the TEP index grows much faster than the other RP indices. This causes the recruitment to drop in a short period close to zero as the Ricker S/R model leads to very low recruitment at high values of RP. This causes extreme fluctuations at high stock size as a result of strong density dependent compensation. The recruitment remains at very low levels for a long period causing a collapse in biomass (Fig. 8). The subsequent increase in the recruitment is probably because some of the runs do not collapse completely and then when the TEP reduces significantly, high recruitment is observed. F_{har} increases rapidly till the maximum imposed in the simulations and catch declines to zero. Catch for TEP in the medium and long term is much lower than for the other OMs under this S/R assumption (Fig. 9).

The probability that the 2016 exploitable biomass (5–9) is higher than the 2011 biomass (PS1) is very high for all RP scenarios, more than 0.99, except for TEP where this probability is only 0.2 (Table 3). The probability of reaching the exploitable biomass objective in 2031 (PS3) is very low, less than 0.01 for all RP indices under the Ricker function (Table 3). The probability of the annual *F* being larger than the annual F_{max} (PS4) is less than 0.01 for 10+ biomass in all projected years (Table 4). For SSB and FSB it is less than 0.05 in almost all years, except the last projected years where it is 0.07 and 0.1, respectively. For TEP it is less than 0.01 in the short term (until 2017), starts to increase in the medium term period from 2018–2021 and from then to 2031 in all years is higher than 0.7.

3.4.3. Operating Models based on the modified Ricker S/R function (CAV_mRic)

As in OMs based on the other S/R functions, the results for the SSB and FSB scenarios are very similar (Fig. 10). 5+ biomass increases to the early 2020s before leveling off, while 5–9 biomass increases and then declines, levelling off below the management objective in the last 15 years of the projection. Early in the projection period recruitment is at a higher level and then declines to a lower level by 2020. Biomass and recruitment trends for the 10+ biomass OM are similar to those for FSB and SSB but at a higher level. Recruitment for TEP reaches a stable level very early in the projection period, 5+ biomass shows



Fig. 4. Deterministic segmented regression stock recruit fit for the different Reproductive Potential indices. Vertical line shows the 2010 reproductive potential index level. 10+, SSB and FSB are in tons while TEP is in 10⁶ eggs.

an increasing trend over the period while 5–9 biomass levels off below the management objective around 2017. The probability of the 2016 biomass being more than the 2011 biomass (PS1) is very high for all the RP indices at more than 0.99 except for TEP where this probability is 0.82 (Table 3). The probability of reaching the exploitable biomass objective in 2031 (PS3) is very low for all RP indices under the modified Ricker function. It is less than 0.05 for the 10+ biomass and TEP scenarios, and less than 0.10 in the SSB and FSB cases.

Fishing mortality shows a slight decreasing trend from 2012 to 2031 in all the scenarios. The probability of the annual F_{bar} being larger than the annual F_{max} (PS4) is less than 0.01 in all scenarios from 2012 onwards (Table 4). All the RP indices scenarios in the short term have very



Fig. 5. Deterministic Ricker stock recruit fit for the different Reproductive Potential indices. Vertical line shows the 2010 reproductive potential index level. 10+, SSB and FSB are in tons while TEP is in 10^6 eggs.

similar mean catch results (Fig. 11). In the medium and longer term the catch for TEP is slightly lower than for the other scenarios.

4. Discussion

Choice of S/R function had a major impact on the results of Greenland halibut MSE. The HCR performed well on all OMs based on the segmented regression for all performance statistics, implying that the HCR is robust to the choice of RP used for this S/R model. The HCR failed to meet the long term target for exploitable biomass in the OMs based on the Ricker or modified Ricker function. The population dynamics in projected years is determined by the stock recruitment function and, thus, the selection of the stock recruitment form greatly affects the perceived robustness and performance of the HCR. The OMs based on the segmented regression assume constant recruitment above some level of the RP indices. The level of constant recruitment is similar, and high, for all the RP indices. Therefore, all OM reach the level of RP giving maximum recruitment early in the projection period, leading to similar results with a stable healthy population in all cases. However, in the Ricker based OMs the S/R function assumes that recruitment increases with increasing RP index to a maximum followed by a decline in recruitment due to compensatory mechanisms. For Greenland halibut this model leads to very low recruitment values at high values of RP which causes extreme population fluctuations at high RP. This large decline in recruitment is the cause of the drop in 5+ and exploitable biomass in all scenarios in the long/medium term. This scenario is not biologically reasonably because most the iterations collapse in the medium term and the posterior recovery

Table 1.Estimated segmented regression and Ricker deterministic
parameter values, as well as the Mean Absolute Error (MAE)
and the Akaike information criterion (AIC) for the analyzed
reproductive potential indices.

a b AIC 10+ 7.4211 17123 -68.98 SSB 24.091 5179 -67.10	MAE 0.1940 0.2010 0.2171									
10+ 7.4211 17123 -68.98 SSB 24.091 5179 -67.10	0.1940 0.2010 0.2171									
SSB 24.091 5179 -67.10	0.2010									
	0 2171									
FSB 26.706 4723 -62.61	0.21/1									
TEP 0.0037545 32311000 -58.97	0.2295									
Ricker										
a b AIC	MAE									
10 + 1.28E+01 3.34E-05 -82.87	0.1660									
SSB 4.41E+01 1.16E-04 -74.97	0.1890									
FSB 4.40E+01 1.16E-04 -71.20	0.1964									
TEP 0.005293 1.4422E-08 -57.43	0.2283									

Table 2.Segmented regression and Ricker deterministic parameter estimates and the 5%, 50% and 95% percentiles of
the stochastically estimated parameter values.

			Se	gmented r	egression							
	a	5%	50%	95%	b	5%	50%	95%				
10+	7.421	6.762	7.467	9.068	17123	13545	16941	18791				
SSB	24.091	22.173	26.233	34.331	5179	3576	4644	5608				
FSB	26.706	25.697	29.536	38.152	4723	3118	4222	4921				
ТЕР	0.00375	0.00354	0.00421	0.00509	32311000	23259857	28770605	34531810				
Ricker												
	a	5%	50%	95%	b	5%	50%	95%				
10+	12.78	11.22	12.10	13.08	3.34E-05	3.05E-05	3.24E-05	3.44E-05				
SSB	44.08	35.16	39.33	45.78	1.16E-04	9.58E-05	1.07E-04	1.21E-04				
FSB	44.03	39.02	42.80	48.44	1.16E-04	1.02E-04	1.14E-04	1.25E-04				
ТЕР	0.0053	0.0050	0.0055	0.0062	1.4422E-08	1.31E-08	1.46E-08	1.72E-08				



Fig. 6. Median, 5th and 95th percentiles values of the time series for 5+ biomass, exploitable biomass (5–9), F_{bar} (5–10), catch, the normal(0,1) standardized for the 1975–2031 period RP indices and recruitment for the 10+ biomass, spawning stock biomass (SSB), female spawning biomass (FSB) and Total Egg Production (TEP) RP indices used in the segmented regression. 2009 and 2010 are from the assessment while 2011–2031 are the results of the projections. The horizontal line on the 5–9 biomass plot is the management target of 106 000 t.

is probably because some runs do not collapse completely and high recruitment will be observed when the TEP level decreases. Results in this case are mainly model artifacts. The compensatory reduction in recruitment should have a limit bigger than zero, but existing data do not allow this limit to be estimated. To solve this problem the modified Ricker function was developed. In the modified Ricker model used here, recruitment does not decline below a specified level at high indices of RP. However, it still has a strong density dependent compensatory mechanism resulting in low biomass at the end of the projected period.

Understanding the basis of uncertainty in the S/R relationships is generally the most difficult outstanding

Table 3.	Probability of exploitable biomass in 2016 will be higher than the exploitable
	biomass in 2011 (PS1) and the probability of exploitable biomass in 2031 will
	be more than the target exploitable biomass (PS3) for 10+ biomass, SSB, FSB,
	and TEP Reproductive Potential indices under the segmented regression (CAV),
	Ricker (CAV_Ric) and modified Ricker (CAV_mRic) operating models.

PS 1	10+	SSB	FSB	ТЕР
SR	1.00	1.00	0.99	0.99
Ricker	1.00	1.00	1.00	0.20
Ricker Modified	1.00	1.00	1.00	0.82
PS 3	10+	SSB	FSB	TEP
SR	1.00	1.00	0.99	0.99
Ricker	0.00	0.00	0.00	0.00
Ricker Modified	0.00	0.07	0.08	0.03

Table 4.Probability of the annual F_{bar} (5–10) will be higher than the annual F_{max} (PS4) in the projected years for
the different Operating Models. In bold values more than 0.10 (10% of probability). Less than this level is
considered a very low probability in the NAFO Precautionary Approach framework.

	CAV			CAV_Ric				CAV_mRic				
Year	10+	SSB	FSB	TEP	10+	SSB	FSB	TEP	10+	SSB	FSB	TEP
2010	0.04	0.05	0.04	0.03	0.03	0.03	0.03	0.03	0.04	0.04	0.04	0.04
2011	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
2012	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2013	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
2014	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2015	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2016	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2017	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2018	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00
2019	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00
2020	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00
2021	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.51	0.00	0.00	0.00	0.00
2022	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.80	0.00	0.00	0.00	0.00
2023	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.94	0.00	0.00	0.00	0.00
2024	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.00	0.00	0.00	0.00
2025	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
2026	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
2027	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
2028	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
2029	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.96	0.00	0.00	0.00	0.00
2030	0.00	0.00	0.00	0.00	0.00	0.02	0.04	0.88	0.00	0.00	0.00	0.00
2031	0.00	0.00	0.00	0.00	0.00	0.07	0.10	0.73	0.00	0.00	0.00	0.00



Fig. 7. Box plot for short, medium and long term expected yield for the different RP indices under the segmented regression function. The box represents the 25th to 75th percentile, the horizontal line the median, the whiskers the 10th and 90th percentile and the dots the 5th and 95th percentiles.

problem in fisheries assessment and management (Hilborn and Walters, 1992) and it is a key problem in the MSE. The Ricker S/R function fits the Greenland halibut data better than the segmented regression for all the RP indices, except for TEP where the fit statistics were very similar. The data clearly seem to follow a Ricker curve, with a decline in recruitment at high levels of RP. With the current adopted HCR, this may pose a problem for the provision of advice because high population biomasses lead to low recruitment and, thus, unexpected rapid deterioration of population status and level of catches when population biomass is high. As such, it seems to indicate that the population should not be allowed to increase above the level corresponding to maximum recruitment at around an RP level (30 000 tones for 10+). However the better fit of the Ricker to the data is driven mainly by 3 or 4 stock recruit pairs at high stock size. The exact form of the S/R function is uncertain. Thus, it would be prudent to allow the population to increase until the shape of the S/R function is confirmed. If the Ricker is confirmed, where recruitment decreases above a specific level of RP, the current HCR adopted for GHL will be overly optimistic and a deterioration of population status, and decrease in yield, will be expected in the short term. The results in all OMs should be interpreted with some caution as they rely on recruitment obtained from the extrapolation of the fitted stock-recruit curves well beyond the maximum observed RPs indices values. In all OMs, all the RP indices, except the TEP under the Ricker function, reach the maximum observed (1975-2010) RP value in 2020 and grow until the end of the forecast period. Recruitment levels after 2020 are therefore more uncertain and in consequence the long term results of the management strategies obtained should be interpreted with caution. Despite this, it can be concluded that the current adopted HCR is not robust to the selection of different S/R relationships, which have a great impact on the performance of the HCR, and, thus, this issue should be explored further in the next revision of the HCR of GHL.

The results show that for Greenland halibut data the inclusion of more biological information when estimating the reproductive potential does not improve the S/R fit either for the segmented regression or the Ricker. The best fits in both cases were inversely related to the degree of biological complexity being best for 10+ biomass followed by SSB, FSB and TEP. These results are similar to those found by Marshall et al. (2006), Morgan (2008) and Murua et al. (2010), who showed that alternative and more complex RP indices did not always significantly improve the S/R relationship. Although there was variation in the biological inputs there were no strong trends over time. In addition, there are limitations with some of the data used to build the RP indices. Age determinations of Greenland halibut have long been considered highly uncertain (ICES, MS 1997; Alpoim et al., MS 2002; Treble and Dwyer, 2008) and recent results indicate a tendency to underestimate the age of older individuals (Gregg et al., 2006; Treble et al., 2008). There are many examples from other species where systematic underestimation of age has resulted in failure to realize the stock's vulnerability to exploitation (Campana, 2001), and for many deepwater species this has led to sudden declines of stocks as well as the fishery that they supported. Maturities were



Fig. 8. Median, 5th and 95th percentiles values of the time series for 5+ biomass, exploitable biomass (5–9), F_{bar} (5–10), catches, the normal(0,1) standardized for the 1975–2031 period RP indices and the recruitment for the 10+ biomass, spawning stock biomass (SSB), female spawning biomass (FSB), and Total Egg Production (TEP) RP indices used in the Ricker S/R function. 2009 and 2010 are from the assessment while 2011–2031 are the results of the projections. The horizontal line on the 5–9 biomass plot is the management target of 106 000 t.



Fig. 9. Box plot for short, medium and long term expected yield for the different RP indices under the Ricker function. The box represents the 25th to 75th percentile, the horizontal line the median, the whiskers the 10th and 90th percentile and the dots the 5th and 95th percentiles.

determined macroscopically; based on a classification scheme that likely over estimates maturity at age (Rideout *et al.*, 2012) and that may not detect trends. Fecundity data are limited so that variation in fecundity at age is really mainly driven by variation in mean length at age. Further it is often assumed that iteroparous fishes spawn annually once reaching sexual maturity, but this is not always the case. Skipped spawning has been reported for Greenland halibut by Walsh and Bowering (1981). There are also indications that ovarian development in Greenland halibut could last more than one year, which also implies that the Greenland halibut does not spawn every year (Albert *et al.*, 2001; Junquera *et al.*, 2003). All of these factors may affect the quality of the indices of RP making them less useful to improve the S/R relationships (Morgan *et al.*, 2011). In addition, variability in maturity, sex ratio and fecundity was not included in the projections. This, combined with quality issues related to the biological inputs, makes the use of different indices of RP less likely to impact the MSE (DeOliveira *et al.*, 2006, 2010).

All the OMs based on the segmented regression have very similar results and seem to be robust to assumptions about RP. However, there was variability in the results of the different indices of RP in the Ricker and modified Ricker OMs and some impact on whether performance statistics were met. In particular, TEP had a higher probability of failing to maintain F_{bar} below F_{max} than the other OM under the Ricker S/R function. In general though, the choice of S/R function had a greater impact than the inclusion of more biological information in the index of RP. Murua et al. (2010) also found little impact of using more complex indices of RP on the MSE for Northern European hake. In that case, stock biomass was at a high level and any variation introduced by using different indices of RP had little impact. In the case of Greenland halibut the projection period began when the population was at a relatively low level. However, recruitment at the starting biomass level was at or near maximum for the segmented regression and near the peaks of the Ricker curves due to the rapid increase in recruitment at low levels of the RP indices for all assumed S/R functions. This resulted in near maximum recruitment at the start of the projections for most OMs. The inclusion of alternative indices of RP is likely to have more impact in stocks with depleted reproductive capacity and/or where alternative indices have a greater effect on the S/R relationships.

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Fig. 10. Median, 5th and 95th percentiles values of the time series for 5+ biomass, exploitable biomass (5–9), F_{bar} (5–10), catches, the normal(0,1) standardized for the 1975–2031 period RP indices and the recruitment for the 10+ biomass, spawning stock biomass (SSB), female spawning biomass (FSB), and Total Egg Production (TEP) RP indices RP indices used in the modified Ricker S/R function. 2009 and 2010 are from the assessment while 2011–2031 are the results of the projections. The horizontal line on the 5–9 biomass plot is the management target of 106 000 t.



Fig. 11. Box plot for short, medium and long term expected yield for the different PR indices under the modified Ricker function. The box represents the 25th to 75th percentile, the horizontal line the median, the whiskers the 10th and 90th percentile and the dots the 5th and 95th percentiles.

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Opportunistic Sightings of Cetaceans in Nearshore and Offshore Waters of Southeast Florida

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Abstract

The majority of cetacean research pertaining to the western North Atlantic Ocean has focused on the waters between North Carolina in the United States and the Scotian Shelf in Canada; little is known about cetacean occurrence and distribution in the waters off southeast Florida (FL) where the subject study was conducted. Our study describes opportunistic, ship-based sightings of cetaceans during 1989–2006 in nearshore and offshore waters located in the Gulf Stream between the Bahamas and Palm Beach, FL. Nine species were observed during 60 sightings. For two of the documented species (false killer whale, *Pseudorca crassidens*, and Fraser's dolphins, *Lagenodelphis hosei*), very little existing information was available with respect to sightings and distributions, based on sightings data from dedicated surveys conducted along the US East Coast, but which only extended to central FL. We documented distinctive physical attributes of offshore ecotype bottlenose dolphins (*Tursiops truncatus*) and described foraging behavior of false killer whales. Our opportunistic observations highlight the importance of conducting regular surveys in this little-researched region. Data gathered during our study may have important implications for cetacean stock assessments and conservation strategies.

Keywords: cetaceans, sightings, bottlenose dolphin ecotypes, false killer whale, western North Atlantic Ocean, Florida, Gulf Stream.

Introduction

The ecology of pelagic tropical cetacean communities is largely unknown for most areas around the world (Mullin and Fulling, 2004). The distribution of marine mammals may be affected by environmental variables and their behavioral needs (*e.g.*, foraging, mating, socializing), however, data pertaining to these factors for pelagic cetacean communities are hard to obtain due to the high mobility of the animals and the logistical difficulty of gathering data at sea (Schick *et al.*, 2011). Thus, in some areas, very little information is known about cetacean populations. One such area is the offshore waters of southeast Florida (FL), which has very little cetacean survey coverage compared to other cetacean habitats in the western North Atlantic Ocean (Hamazaki, 2002; Jefferson and Schiro, 2008; Schick *et al.*, 2011; Waring *et al.*, 2015).

The majority of western North Atlantic cetacean surveys and research focus on the waters between North Carolina (NC) in the United States (US) and Nova Scotia in Canada (*e.g.*, Hamazaki, 2002). Stock assessments are updated regularly (annually for "strategic stocks" and every three years, or when new information is available, for nonstrategic stocks) by the National Marine Fisheries Service (NMFS) for most cetacean species inhabiting the US East Coast, with the most recent Stock Assessment Reports (SARs) updated in 2014 (Waring et al., 2015). The SARs include data from many different studies covering various coastal and offshore areas, cetacean species, time frames (e.g., seasonal, annual) and methods (e.g., plane-vs. shipbased surveys), but dedicated surveys of the waters south of central FL are lacking. Even when considering data from the broad-based Ocean Biogeographic Information System - Spatial Ecological Analysis of Megavertebrate Populations (OBIS-SEAMAP) database (Halpin et al., 2009), cetacean surveys conducted south of Cape Hatteras, NC are relatively scarce (Mullin and Fulling, 2003; Garrison et al., 2010; Schick et al., 2011).

The waters off of southeast FL provide a different cetacean habitat compared to the waters north of Cape Hatteras, due to the influence of the Gulf Stream, which varies in width and proximity to shore along the US East Coast. The Gulf Stream is a strong, warm ocean current that originates in the Gulf of Mexico as the Florida Current, then flows along the southern tip of FL and northward until it is deflected northeasterly and further offshore at Cape Hatteras, NC (Groves and Hunt, 1980). Oceanic features, such as fronts and eddies, are often associated with the Gulf Stream and such features can produce ecological effects (*e.g.*, on food web stability and phytoplankton production) that can affect animal abundance and distribution (Owen, 1981).

In the western North Atlantic, groupings of cetacean species have been classified by habitat use correlated with depth, temperature range and distance from the coast (Hamazaki, 2002; Schick et al., 2011). Moore (1953) reported the occurrence of 21 marine mammal species in FL waters and suggested that the Gulf Stream may induce some tropical species to visit FL waters and that the southward counter-current flow may be influential in bringing marine mammals from the north into FL waters. For example, the occurrence and distributions of sperm whales (Waring et al., 1993) and sea turtles (Hoffman and Fritts, 1982) have been associated with features of the Gulf Stream. The distribution of pelagic odontocetes in waters off the US East Coast, are also likely associated with the Gulf Stream, its distance from shore and associated fronts and eddies, as noted in the high biodiversity of species from northern and southern regions and coastal

and pelagic habitats recorded during stranding events off Cape Hatteras, NC (Byrd *et al.*, 2013). The location of the west wall of the Gulf Stream varies along the US East Coast, but is located closest to shore, <16 km (Gyory *et al.*, 2013), in our study area off the southeast coast of FL (Fig. 1). Thus, cetacean abundance and distribution in southeast FL waters may differ from the more northern waters of the western North Atlantic due to the variations in the width of the Gulf Stream and its close proximity to shore. However, research on this topic is lacking in our study area.

Our study describes the cetaceans sighted opportunistically by staff from the Wild Dolphin Project (WDP) while crossing the Gulf Stream in southeastern FL waters en route to two study sites in the Bahamas. In addition, we describe in more detail, information from sightings of the bottlenose dolphin (*Tursiops truncatus*) and the false killer whale (*Pseudorca crassidens*). The bottlenose dolphin occurs as two ecotypes (Hersh and Duffield, 1990; Mead and Potter, 1995; Hoelzel *et al.*, 1998; Torres *et al.*, 2003). We describe the physical difference in appearance of the offshore ecotype compared to the coastal ecotype in our study area because this difference may also occur in other areas of the western North Atlantic. We also describe our observations of the foraging behavior of the false killer whale, which is primarily oceanic and has been



Fig. 1. Map of opportunistic cetacean sightings in nearshore and offshore waters of southeast Florida out to the western edge of Little Bahama Bank during 1989–2006. All Atlantic spotted dolphin sightings occurred near the Palm Beach Inlet, labeled "PB inlet" (the one marker on the map for these sightings is slightly obscured by a bottlenose dolphin sighting marker in the same area). The Gulf Stream flows northward along the US East Coast, close to shore in our study area and is located farther offshore as it flows north.

sighted in the northern Gulf of Mexico (Maze-Foley and Mullin, 2006) and in the western North Atlantic from Cape Hatteras, NC to Tierra del Fuego, Argentina (Stacey *et al.*, 1994). However, false killer whales have rarely been documented off the coast of FL (Waring *et al*, 2015) and sightings compiled in the OBIS-SEAMAP database, as of 2 May 2016, show only two sightings off northern FL (Garrison, 2013a; Halpin *et al*, 2009).

Materials and Methods

Since 1985, staff from WDP have studied a resident community of Atlantic spotted dolphins (*Stenella frontalis*) located on Little Bahama Bank (LBB) (Herzing, 1997; Elliser and Herzing, 2012; 2014). Every year during 1989–2006, WDP staff made regular trips (8–10 trips per year) during May through September between Palm Beach, FL and the primary study site on Little Bahama Bank (LBB) (Fig. 1), crossing the Gulf Stream aboard a 19 m catamaran research vessel. During 1998–2004, one trip per year was also made during January–March to a secondary study site and spotted dolphin community on Great Bahama Bank (GBB), south of LBB.

Trip durations lasted between 6 and 12 hours each way depending on weather and oceanic conditions. There were one to five observers (*i.e.*, crew and volunteers) on watch for the duration of each trip. Observers watched for any cetacean activity by scanning ahead of the vessel across a 180° radius, with the naked eye, during daylight hours (0700–1900) from a height of 23 ft above the waterline. When observed, cetacean species were recorded by the crew and verified by scientific observers from WDP with expertise in cetacean identification. When a group or individual was observed, vessel speed was reduced to less than 7 knots, the boat's course was redirected from

the planned route and the group was approached. The boat was slowly and carefully driven to within roughly 100 m of the group, being careful to avoid sudden turns, accelerations, decelerations, and approaching the group head-on or quickly from behind, following general NOAA viewing guidelines for the region (NOAA, 2012). The cetaceans were identified to the lowest taxonomic level that researchers were confident in assessing. Group size was recorded and photographs were taken of as many individuals of each group as possible (using various Canon film and digital cameras over the years). For every sighting, the goal was to obtain two to three photographs of each individual, however, this was not always possible due to weather conditions and behavior of the animals. Sightings also entailed ad libitum (Altman, 1974) descriptions of behavior which were categorized as either social, travel, foraging or unknown. Once documented, the captain resumed the boat's prior route towards either Little Bahama Bank or FL. The exception to this protocol occurred during a single occasion when the boat remained idle with a group of false killer whales while their behavior was documented and photographs were taken. After about two hours, we ended the sighting due to reduced light levels and time constraints.

Results

For each crossing, routes were 110° ESE from the Palm Beach Inlet, covering a total estimated distance of 34 360 km and 2 084 hours of observation effort during the course of the study (Table 1). Roughly the same amount of sampling effort occurred on the return trips to FL from the Bahamas. A total of 60 opportunistic sightings of nine different types of cetaceans occurred, including eight species and a beaked whale only identifiable as a member of the Ziphiidae family (Table 2). Ranges for total group

Table 1. Estimated sampling effort, distance traveled (km) and observer time (hrs), for opportunistic sightings of cetaceans off the southeast coast of Florida (Little Bahama Bank) during trips to Little Bahama Bank and Great Bahama Bank during 1989–2006 (May–September) and 1998–2004 (January–March), respectively. A crossing is defined as a one-way trip to or from FL to Little Bahama Bank or Great Bahama Bank.

Sampling Effort	FL to Little Bahama Bank	FL to Great Bahama Bank
Average number of crossings per year	18	2
Average observer time per crossing (hrs)	6	10
Average observer time per year (hrs)	108	20
Distance per crossing (km)	100	140
Total observer time (all years, hrs)	1 944	140
Total distance traveled (all years, km)	32 400	1 960

		Number of	Group size range (mean		
Common name	Scientific name	sightings	±1 SD)	Latitude range	Longitude range
Beaked whale ¹	Ziphiidae	-	2 (NA)	NA	NA
Bottlenose dolphin ²	Tursiops truncatus	25	2 to 15 (7.7 ± 3.6)	26°16'08"–27°44'23"	79°16'57"–80°03'90"
False killer whale	Pseudorca crassidens	4	1 to 20 (9.5 \pm 9.4)	26°39'08"–27°06'46"	79° 11' 27"–79° 16' 19"
Fraser's dolphin	Lagenodelphis hosei	2	3 to 10 (6.5 \pm 4.9)	26°41'09"–27°01'69"	79°43' 90"–79°47' 75"
Pantropical spotted dolphin	Stenella attenuata	14	7 to 150 (56.9 \pm 44.9)	26°05'81"–26°46'77"	79° 16' 45"–79° 46' 44"
Short–finned pilot whale ³	Globicephala macrorhynchus.	5	8 to 15 (11.0 \pm 4.7)	26°29'49"–26°59'00"	79° 18' 00"–79° 47' 57"
Risso's dolphin	Grampus griseus	б	8 to 20 (13.3 \pm 5.8)	26°44'98"–26°50'24"	79° 19' 00''–79° 49' 45''
Sperm whale	Physeter macrocephalus	7	1 to 2 (1.5 \pm 0.7)	NA	NA
Atlantic spotted dolphin	Stenella frontalis	4	1 to 6 (3.5 ± 3.5)	NA	NA

Number of sightings, group size range (mean numbers of individuals per group \pm 1 SD) and location data, by species, for opportunistic sightings of cetaceans in waters off the southeast coast of Florida during May–September, 1989–2006. NA = not enough information, either due to inadequate sample size for determination of SD or lack of location data. Table 2.

¹ Possibly mother/calf pair.

² Bottlenose dolphin sightings include both Coastal and Offshore ecotypes.

³ Visual identification of short- and long-finned pilot whales at sea is extremely difficult (Rone and Pace, 2012), but based on known distributions of the two species, they were most likely short-finned pilot whales (Globicephala macrorhynchus) and are reported as such.

J. Northw. Atl. Fish. Sci., Vol. 48, 2016

size (Table 2) should be viewed with caution because they may not be fully representative of the true group size variation for species with fewer than four sightings. Visual identification of short- and long-finned pilot whales at sea is extremely difficult (Rone and Pace, 2012), but based on known distributions of the two species, they were most likely short-finned (*Globicephala macrorhynchus*) and were reported as such. Bottlenose dolphin sightings included both coastal and offshore ecotypes.

Bottlenose dolphins were the most commonly sighted cetacean, followed by pantropical spotted dolphins. Only bottlenose dolphins, pantropical spotted dolphins (*Stenella attenuata*) and Risso's dolphins (*Grampus griseus*, seen twice on one day) were seen more than once in a given year. All sightings occurred during May–September, except for one sperm whale (*Physeter macrocephalus*) and one pantropical spotted dolphin sighting which each occurred during January of 1991 and 2001, respectively. The two sightings of Fraser's dolphins (*Lagenodelphis hosei*) occurred in July during 1991 and 1993 and the five pilot whale sightings occurred in either May or September during 1990–1992, 1995 and 1999. During all but one sighting, the documented behavior was travel; for one of the false killer whale sightings, the animals were foraging.

Fig. 1 shows the distribution of the cetacean sightings (excluding one sperm whale sighting due to lack of latitude/longitude data). Only two species were sighted shoreward of the 200 m isobath (i.e., on the continental shelf), the bottlenose dolphin and the Atlantic spotted dolphin. All Atlantic spotted dolphin sightings occurred near the Palm Beach Inlet. Fraser's dolphins were only seen at depths between 200 m and 500 m. The bottlenose dolphin, Risso's dolphin, pilot whale and pantropical spotted dolphin were seen in many different locations across the Gulf Stream, in waters east of and deeper than the 200 m isobath. The larger odontocetes, including the sperm whale, false killer whale and beaked whale, were only sighted at depths greater than 500 m. Interestingly, false killer whales were only seen on the east side of the Gulf Stream, closer to Little Bahama Bank, north of Grand Bahama Island. Other than two sightings off northern FL (Garrison, 2013a), the only other false killer whale sightings near our study area were in waters east of the Abacos, Bahamas (Dunn, 2013b).

Bottlenose dolphins: coastal vs. offshore ecotypes

Definitive identification of bottlenose dolphin ecotype was not always possible. Four of the sightings were determined to be offshore ecotype bottlenose dolphins, sighted east of 79°46'00" at 26, 52, 56 and 75 km from the FL coast near the 500–600 m isobath. These bottlenose dolphins were distinctively larger in size and very robust as compared to the coastal ecotype, the latter which can easily be identified from a boat. Many, if not all, of the offshore ecotype bottlenose dolphins that we saw had a unique feature; a characteristic white saddle mark on the peduncle posterior to the dorsal fin. A coastal ecotype bottlenose dolphin (with no white saddle marking) is shown for comparison with the offshore ecotype (Fig. 2a,b). A total of 28-38 (based on size ranges tallied for each sighting) offshore individuals were documented. Photographs of sufficient quality to document identification/coloration marks were compared with those of coastal ecotypes from the sightings during crossings, as well as the long-term catalogue of over 300 resident coastal ecotype dolphins at the main study site in the Bahamas (Rogers et al., 2004). No obvious white saddle markings were evident in any of these coastal ecotype dolphins.

False killer whale foraging

At 1514 on May 24, 2006, 12 individually identifiable (through nicks, scars and shape of the dorsal fin) adult false killer whales were documented at 27°01′01″ N, 79°15'24" W (Fig. 3a). Most of the group remained at the surface, milling and surfacing slowly, while one or two animals dove. One of the diving animals returned to the surface with a large bloated fish (Fig. 3b). We could not get close enough to identify the species of the fish, however, it appeared to be a demersal species from the snapper or grouper family (Fig. 3c). The false killer whales at the surface then took turns biting chunks off the fish, and left only the gills. We observed three fish catch and consumption bouts within a two-hour observation period. We also observed social behavior occurring at the surface in-between feeding bouts, including two breaches and multiple spy-hops.

Discussion

All nine cetacean species documented in our study were also found in other western North Atlantic surveys (Kenney *et al.*, 1997; Hamazaki, 2002; Schick *et al.*, 2011). The NMFS stock assessments, as of 2014, identified 30 cetacean species inhabiting the Western North Atlantic stock areas which include waters off the East Coast of the US (Waring *et al.*, 2015). However, almost all the surveys that included waters off FL did not extend south of Central FL, and thus did not encompass our study area. Similarly, based on limited sighting data from OBIS-SEAMAP, 14 species were observed south of Cape Hatteras, though most sampling off the eastern FL coast was concentrated in Central and North FL waters (Schick *et al.*, 2011). Based on the most current sighting data available in the OBIS-SEAMAP database, as of



Fig. 2a. Offshore ecotype bottlenose dolphin sighted in the Gulf Stream off the southeast coast of Florida (June 3 2010.) Arrow indicates white saddle patch. Photographer: Cindy Elliser, Wild Dolphin Project.

Fig. 2b. Coastal ecotype bottlenose dolphin without white saddle patch sighted on Little Bahama Bank. This individual is part of a long-term resident population; to date no identified individual (over 300 documented) in this population has the white saddle marking seen on the offshore individuals. Photographer: Cindy Elliser, Wild Dolphin Project.



2 May 2016, only three of the nine species we observed have been documented by other research groups in our study area: the short-finned pilot whale (Dunn 2006; Halpin, 2009), sperm whale (Woolmer 2013; Halpin et al., 2009) and bottlenose dolphin (Garrison, 2013b; Josephson and Garrison, 2015a, 2015b). The other five species we observed (beaked whales were not considered for this comparison because we could not identify them to the species level) have only been seen to the north, east and/or south of our study area: Fraser's dolphin (Dunn, 2013b), false killer whale (Garrison, 2013a; Dunn, 2013b), pantropical spotted dolphin (Hyrenbach et al 2012; Dunn, 2013a; 2013b), Risso's dolphins (Dunn, 2013b), and Atlantic spotted dolphin (Garrison, 2013c; Dunn, 2013a, 2013b; Josephson and Garrison, 2015b.). It is important to note that each of the nine species we observed have stocks designated by NMFS in both the western North Atlantic and the northern Gulf of Mexico, and that the individuals we observed off southeast FL may be from either or both of these regions. Our results indicate that the ranges of the nine species we observed may extend south of north/central FL, or may indicate movement from the Gulf of Mexico, at least seasonally. In addition, for the false killer whale, Fraser's dolphin, pantropical spotted dolphin, Risso's dolphin, Atlantic spotted dolphin and beaked whale, our sightings are the first known sightings in southeast FL waters. Thus, the opportunistic sightings we report here are a significant addition to the cetacean literature and the results reinforce that there is a need for more dedicated research efforts in our study area.

Two of the species we observed, the false killer whale and Fraser's dolphin, were rarely seen in Western North Atlantic surveys conducted north of central FL based on the most updated SARs for each species Waring et al, 2007, 2015). In previous SARs, a false killer whale stock (or stocks) was only designated for the Gulf of Mexico, but this information was updated in the 2014 SAR with an initial abundance estimate for a separate Western North Atlantic stock (Waring et al, 2015). The survey used for the abundance estimate was conducted during June-August, in 2011, but did not cover waters south of central FL. As of 2 May 2016, no live sightings of false killer whales have been reported in NMFS SARs (Waring et al., 2015) or in the OBIS-SEAMAP database (Halpin, 2009) within our study area, however, strandings have been documented during the winter (Caldwell et al., 1970). We observed false killer whales on four different occasions (1992, 1997, 2004 and 2006) during May-August. These data indicate that our study area serves as false killer whale habitat at least during the summer.

Sightings of Fraser's dolphin in the western North Atlantic are scarce (e.g. single sighting of 250 individuals from a

1999 vessel survey off NC, which did not occur during the line-transect sampling effort), and thus population size and seasonal abundance are unknown for this stock, which is managed as a separate stock from that in the Gulf of Mexico (Waring et al., 2007). Although observed in all seasons in the more extensively surveyed northern Gulf of Mexico, they likely occur there in low numbers, but survey effort is not sufficient to precisely estimate their abundance (Waring et al., 2013). Data from OBIS-SEAMAP showed no sightings of Fraser's dolphins in our study area (Halpin, 2009), however, we documented two sightings during July of 1991 and 1993. Fraser's dolphins have also been documented as prey for killer whales (Orcinus orca) in the northern islands of the Bahamas, which is east of the Gulf Stream waters surveyed during our study (Dunn and Claridge, 2014). Thus, the sightings presented in our study represent the first reports of Fraser's dolphins in the western North Atlantic waters off southeast FL.

The sightings in our study primarily conform to the suggested distributions of deepwater versus coastal species (or ecotypes) in the Western North Atlantic where groupings of species tend to utilize particular habitats correlated with depth, temperature range and distance from the coast (Hamazaki, 2002; Schick *et al.*, 2011). For the few discrepancies (refer to the "Bottlenose dolphins (coastal versus offshore ecotypes)" section below), however, we cannot determine whether the variations observed were outliers or indications of true habitat preferences, due to the opportunistic nature of our study.

Bottlenose dolphins (coastal versus offshore ecotypes)

Much of what is known about offshore ecotype bottlenose dolphins has been determined from stranded animals (e.g., Hersh and Duffield, 1990; Mead and Potter, 1995), which does not allow for description of their coloration patterns. The coastal and offshore ecotypes (treated as separate management units under the US Marine Mammal Protection Act of 1972) are described as genetically separable, partially sympatric, but visually indistinguishable (Waring et al., 2001; Torres et al., 2005). In our study, we were able to document bottlenose dolphins with white saddle markings on the peduncles of the larger, more robust individuals. This could be a useful marker for identifying the ecotypes at sea and through photographs. However, due to the opportunistic nature of our study, it is unknown if this trait is common to all individuals of the offshore ecotype or if it is limited solely to the offshore ecotype. It is also possible that this feature is limited to animals in our study area, because the study that documented differences in western North Atlantic ecotypes (Torres et al., 2003) did not include waters south of Central FL. More research combining morphological,



Fig. 3a. False killer whale dorsal fin. Twelve unique individuals were documented through nicks, notches and scars on the dorsal fins, such as seen here. Photographer: Cindy Elliser, Wild Dolphin Project.



Fig. 3b. A false killer whale feeding on large, bloated demersal fish species brought to the surface. Photographer: Cindy Elliser, Wild Dolphin Project.



Fig. 3c. Large demersal fish species, from the Serranidae family, brought to the surface shortly before being eaten by false killer whales. Only the gills remained after feeding. Photographer: Cindy Elliser, Wild Dolphin Project.

photographic, genetic and water depth data collected during quantitative surveys is needed to determine if this white saddle pigmentation is a reliable diagnostic marker for ecotype differentiation.

Individuals we identified as the offshore ecotype were found greater than 34 km from shore, except for one sighting that occurred 26 km from shore. Our results were similar to a study off Cape Hatteras, NC where Torres et al. (2003) determined that there was a differentiation regarding depth and distance from shore between the two ecotypes: dolphins found beyond 34 km from shore (and in waters deeper than 34 m) were all of the offshore ecotype, whereas dolphins found within 7.5 km of shore were of the coastal ecotype. Torres et al. (2003) also found an overlap in the distributions of the two ecotypes, between 7.5 and 34 km from shore (and in waters less than 34 m deep), where both ecotypes were found, and identified this area as the "gray zone". It is known that the range of offshore bottlenose dolphins can extend (although in lower numbers) into the continental slope waters (Kenney, 1990). However, we cannot determine whether our sighting of offshore ecotype bottlenose dolphins at 26 km from shore (within the "gray zone") was due to an overlap in range with the coastal ecotype, because our sightings were not based on a quantitative survey. In addition, we used coloration patterns and Torres et al. (2003) used genetic analyses to distinguish between the two ecotypes. Furthermore, our method has not been verified quantitatively across region and ecotype. There is also the confounding fact of physiogeographic differences between the two study areas. In our study area, both deep water and the Gulf Stream occur closer to shore (the latter is often <16 km from shore during summer) than is the case further north (Gyory et al., 2013). The distribution of both ecotypes may also be affected by the fact that our study area is bracketed by shallow water on both sides of the Gulf Stream (i.e., the FL shelf to the west and Little Bahama Bank to the east). Thus, further research regarding the distribution patterns and abundance of bottlenose dolphin ecotypes, as well as other cetacean species, are warranted in our study area.

Stock delineation of bottlenose dolphin populations along the US East Coast are complex and include estuarine stocks, five coastal stocks (Northern Migratory, Southern Migratory, South Carolina/Georgia Coastal, Northern Florida Coastal and Central Florida Coastal, (Waring *et al.*, 2014) and one Western Atlantic Offshore stock (Waring *et al.*, 2015). There has been little study of coastal stock structure south of central Florida and the southern boundary of the Central Florida stock is uncertain (Waring *et al.*, 2014). The Offshore stock is based on surveys that do not extend south of central Florida (Waring *et al.*, 2014). 2014). Thus, information on stock structure in our study area is unknown, but it is clear that both ecotypes are present in southeast FL coastal and offshore waters, at least during the summer months (bottlenose dolphins were seen in every year from 1993–2005, except 2003, during May–September). In addition, there are multiple bottlenose dolphin stocks in the Northern Gulf of Mexico, including 31 bay, sound and estuarine stocks, the Gulf of Mexico Eastern Coastal stock, the Northern Gulf of Mexico Continental Shelf stock and the Northern Gulf of Mexico Oceanic stock (Waring et al., 2015). It is unclear whether the bottlenose dolphins observed in our study area should be considered as separate stocks or whether they are part of migratory or coastal stocks from the US East Coast and/or the Gulf of Mexico. Because many bottlenose dolphin stocks are migratory, it is important to understand the species' stock structure for management purposes, since movements of individuals or groups can involve intermingling between stocks and may vary with season. For example, off Cape Hatteras, NC there were definite seasonal changes in abundance and distribution of bottlenose dolphins. Abundance was greatest near shore (<3 km) during winter, but remained high out to 14 km (Torres et al., 2005). Combined with data from previous studies farther north, it is likely that the seasonal movement patterns along the US Atlantic coast are correlated, at least in part, with water temperature and prey availability (Torres et al., 2005). Similar results were found in the Gulf of Mexico for "Gulf" vs. "inshore" bottlenose dolphins, where "inshore" abundance increased and "Gulf" abundance decreased during the winter (Waring et al., 2015). Our opportunistic sightings reveal that more quantitative research is needed to determine the morphological and genetic characteristics of offshore bottlenose dolphins and for adequate stock management and conservation of both ecotypes in southeast FL waters.

False killer whale foraging

Most information about false killer whales, including prey, has been obtained from stranded animals in the Southern Hemisphere (Koen-Alonso *et al.*, 1999; Andrade *et al.*, 2001). Oceanic squid (*e.g.*, *Oregoniateuthis* sp., *Todarodes* sp., *Phasmatopsis* sp., *Gonatopsis borealis* or *Berryteuthis magister*) have been documented as prey for false killer whales around the world (Stacey *et al.*, 1994), and were the primary prey species found in Southern Hemisphere animals (Koen-Alonso *et al.*, 1999; Andrade *et al.*, 2001). Fish prey species included the Patagonian grenadier (*Macruronus magellanicus*), kingclip (*Genypterus blacodes*), as well as sciaenid species including whitemouth croaker (*Micropogonias furnieri*) and black drum (*Pogonias cromis*) (Koen-Alonso *et al.*, 1999). The gut contents of some individuals included only fish contents from the families Sciaenidae and Serranidae based on otoliths (Pinedo and Rosas, 1989).

The false killer whales we sighted were feeding on what looked like a grouper. We contacted fish biologists at NOAA's Beaufort Laboratory and from the pictures they identified it as possibly Epinephelus sp., but definitely a serranid species (Jennifer Potts, pers. comm.). The group of false killer whales seemed to be sharing the prey and possibly feeding cooperatively. Cooperative feeding by false killer whales was suggested by Koen-Alonso et al. (1999) due to the fact that the squid found in their stomachs usually form schools of restricted size range, indicating that the whales may have hunted cooperatively on the same schools. In Hawaiian waters, false killer whales prey mainly on large pelagic fish and are frequently observed sharing prey (Baird et al., 2008). Due to these facts and the species' tendency to carry prev items for extended periods, surface observations of prey items may be less biased than for other cetacean species (Baird et al., 2008). False killer whales can forage at depths up to 200 m (Koen-Alonso et al., 1999). Sighting rates for even the "island-associated" Hawaiian false killer whales, who regularly utilize shallow water (<200 m), reveal a preference for water deeper than 3,000 m (Baird et al., 2008). Although we do not have an exact depth for the foraging sighting in our study, it occurred at a depth greater than 200 m. False killer whale ecology, abundance and distribution are unknown in our study area, however, it is evident that they do utilize local food resources and serranid fish species appear to be a part of their diet.

In conclusion, little is known about the cetaceans inhabiting the offshore waters of southeast FL. Through opportunistic sightings, we have documented nine cetacean species that inhabit the area during at least part of the year. Some of these species have very little existing information available regarding sightings and distribution in southeast FL waters. We have documented new information about the morphological features of offshore ecotype bottlenose dolphins, which may be useful in distinguishing between the two ecotypes at sea, and described the foraging behavior of false killer whales. This area of the Western North Atlantic has different physiogeographic and ecological features than areas farther north and our sightings demonstrate that the Gulf Stream is an important habitat for many cetacean species. Our observations highlight the need to conduct regular quantitative surveys of the offshore waters of southeast FL to better understand the distribution, abundance, stock boundaries and ecology of cetacean species in the area and how they relate to other populations along the US East Coast and in the Gulf of Mexico.

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Continental shelf residency by adult Atlantic halibut electronic tagged in the Gulf of Maine

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Abstract

In the Northwest Atlantic, emerging evidence suggests that different stocks of Atlantic halibut (*Hippoglossus hippoglossus*) exist in Canadian and U.S. waters. To examine the movement of Atlantic halibut that occupy the Gulf of Maine in U.S. waters during the summer, two types of electronic tags were attached to large adult fish (n = 70) in 2007–2009. None of the recovered tags (n = 12) provided evidence that the fish occupied the relatively deep waters of the continental slope during the winter, where Canadian Atlantic halibut have been shown to spawn. This observation provides additional evidence for the hypothesis that different stocks of Atlantic halibut exist in Canadian and U.S. waters. Furthermore, this observation requires reexamination of the long-standing assumptions made by fisheries scientists that all Atlantic halibut spawn in deep water on the continental slope and that the majority of mature Atlantic halibut spawn annually. This information may be important for understanding the population dynamics of Atlantic halibut in U.S. waters.

Keywords: Atlantic halibut, *Hippoglossus hippoglossus*, PSAT, satellite tag, electronic tag, Data Storage Tag, Gulf of Maine

Introduction

Atlantic halibut (*Hippoglossus hippoglossus*) is the largest and longest-lived of the flatfishes, and its range extends across the entire North Atlantic Ocean. In the Northwest Atlantic, the species is found from as far south as the coast of Massachusetts to as far north as the Canadian Arctic Ocean. The Gulf of Maine (GOM; Fig. 1) has a long history of commercial harvest of this species and it was found there in such abundance prior to the 1830s that it was killed and discarded by Atlantic cod (*Gadus morhua*) fishermen who considered Atlantic halibut to be a nuisance (Grasso 2008). By 1880, its large size, tasty flesh and suitability to ice preservation had motivated such aggressive overfishing that the species was quickly driven to commercial extinction by the 1940s (Grasso 2008). Currently, the Atlantic halibut in the Northwest Atlantic is classified as a 'Species of Concern' in U.S. waters by National Marine Fisheries Service, 'threatened' by the American Fisheries Society and 'endangered' by the International Union for Conservation of Nature (NMFS 2009). Because recent stock assessments indicate that the Atlantic halibut in U.S. waters remains in a depleted state, there are only limited, size-restricted fisheries there (NEFSC 2012). However, Atlantic halibut abundance just across the Hague Line (the maritime border between the U.S. and Canada; Fig. 1) in Canadian waters on the Scotian Shelf and Grand Banks has rebounded, with high production and recruitment in recent years (Trzcinski and Bowen 2016). Today, Atlantic halibut from these Canadian waters are certified as sustainable by the Marine Stewardship Council (www.msc.org). Effective fisheries management plans, favorable ocean conditions, and reduced bycatch in other fisheries have all been speculated to be responsible for the recovery of the Canadian Atlantic halibut fishery (Trzcinski and Bowen 2016).

In the past, Atlantic halibut from the Northwest Atlantic in both Canadian and U.S. waters were assumed to come from a large, interbreeding stock (Stobo *et al.*



Fig. 1. Select areas and sea floor features in the northwest Atlantic occupied by Atlantic halibut.

1988). However, there is much uncertainty surrounding Atlantic halibut stock identity and structure (NEFSC 2012; Shackell et al. 2016; Trzcinski and Bowen. 2016), and several lines of evidence suggest that Atlantic halibut may have finer stock structure than originally assumed (Shackell et al. 2016). First, recent research has documented large differences in abundances of juvenile Atlantic halibut from U.S. and Canadian waters (1965-2014), despite there not being any detectible shortage of suitable rearing habitat in either area (Shackell et al. 2016). Second, while Atlantic halibut have been shown to make extensive migrations >3000 km, the majority of fish are thought to remain near (<50 km) their respective release sites (Kanwit 2007; den Heyer et al. 2012). This observation indicates that relatively long movements of a minority of fish, which tend to attract researchers' attention, masks the overall tendency for individual Atlantic halibut to reside in relatively small areas. Third, while genetic analyses have found no significant genetic differentiation among Atlantic halibut from the GOM, Scotian Shelf, Gulf of St. Lawrence and Iceland (Reid et al. 2005), recent research demonstrates difficulty in detecting genetic differences between stocks of marine fishes (Hauser and Carvalho 2008). These results provide evidence for the hypothesis that different stocks of Atlantic halibut exist in U.S. and Canadian waters (Shakell et al. 2016). If different stocks of Atlantic halibut exist, this may explain why U.S. Atlantic halibut populations have not recovered (Shakell et al. 2016) while geographically proximate Canadian populations have rebounded.

Additionally, little is known about the reproductive biology and behavior of Atlantic halibut. The species is iteroparous and is assumed to spawn annually upon reaching maturity (Neilson et al. 1993). Atlantic halibut are generally thought to follow the distribution patterns of their congeners Pacific halibut (Hippoglossus stenolepis), spending summer months in relatively shallow, near-shore waters to feed and, in the winter, moving into deeper water on the continental slope, where spawning is presumed to occur (Stobo et al. 1988; Sigourney et al. 2006, Kanwit 2007; Armsworthy et al. 2014). As group-synchronous batch spawners, Atlantic halibut from several summer feeding areas are thought to gather in large spawning aggregations at discrete deep water locations (Bowering 1986; Haug 1990). In the Northwest Atlantic, documented spawning areas are located offshore along the continental slope in depths >300 m, including the Scotian Shelf (Fig. 1; Stobo et al. 1988); on the southern flank of the Grand Banks (Fig. 1; Armsworthy et al. 2014); and on the continental slope off western Greenland (Godø and Haug 1988). In the Northeastern Atlantic, some Atlantic halibut spawning areas have been identified at inshore

locations, in Norwegian fjords (Devold 1938; Van Der Meeren *et al.* 2013), in depths >800 m, therefore, it is assumed that depth is an important habitat characteristic of spawning Atlantic halibut. The spawning season for Atlantic halibut in the Northwest Atlantic is a matter of some debate, but is thought to occur between late fall and spring, primarily from February to April in the Gulf of St. Lawrence (Fig. 1; Kohler 1967) and GOM (Fig. 1; Bigelow and Schroeder 1953; McCracken 1958), and November and December off the Scotian and Newfoundland coasts (Fig. 1; Neilson *et al.* 1993; Sigourney *et al.* 2006; Armsworthy *et al.* 2014).

In general, the goal of this study was to investigate stock identity, reproductive biology and behavior of Atlantic halibut in the Northwest Atlantic. To accomplish this, researchers from the Maine Department of Marine Resources conducted a multi-faceted, multi-year survey and tagging project in the GOM, part of which included attaching two types of electronic archival tags to Atlantic halibut during the summer. These tags measured and recorded environmental data at preprogrammed intervals while attached to the fish. In this paper, information obtained by the electronic tagging portion of the project was used to explore the hypothesis that Atlantic halibut in U.S. waters in the GOM do not intermingle with those from Canadian waters, and may comprise a distinct stock.

Methods

The Atlantic halibut tagged in this study were captured on longline gear at 65 stations along random grid transects of Maine's near-shore waters in 2007, 2008 and 2009 (Fig. 2 and Table 1). All of the tagged fish were weighed and measured, tagged quickly without anesthetic, and gently released head-first back into the ocean.

Sixty one Data Storage Tags (DST; Star Oddi, milli-TD, Gardabaer, Iceland) were externally attached to fish ranging in total length (TL) from 51 to 142 cm. Each tag was attached to the eyed side of the fish with stainless steel wires inserted through muscle tissue along the dorsal fin and secured to a plastic backing plate on the white side of the fish. The DSTs measured and recorded ambient water temperature and water pressure, which was converted to depth, at intervals ranging from every five minutes to every 24 hours. The recording interval and battery life determined for how long the tags collected data. The data from these tags were recovered only after the fish was recaptured in fisheries.

Nine Pop-up Satellite Archival Tags (PSATs; X-tag, Microwave Telemetry, Inc., Maryland, USA) were also



Fig. 2. Release (circles) and end locations (stars) of Atlantic halibut tagged with two types of electronic tags in the Gulf of Maine. End locations were considered as the Global Positioning System location where the fish was recaptured or the first message from Pop-up Satellite Archival Tags with an Argos Location Class 1, 2, or 3, resulting in a positional error of <1.5 km. Dashed lines are stylized paths traveled by each fish between release and end locations. The darkest gray shade denotes depths (>250 m) that none of the tagged Atlantic halibut occupied.

deployed. The fish selected for PSATs were generally larger, ranging from 92 to 148 cm (TL). These tags were attached to the fish with a tethered umbrella dart inserted through muscle tissue alongside the dorsal fin on the eyed side of the fish, in a location where the antenna would not interfere with the caudal fin during swimming. As with the DSTs, tagging was accomplished quickly and without anesthetic. These tags collected the same data as the DSTs, but had the additional benefit of being fisheries independent. Specifically, PSATs detached from a fish on a specified date, floated to the sea surface, and transmitted data to orbiting satellites (Argos satellite system). While transmitting to satellites, each tag's location was determined from the Doppler shift of successive transmissions to the passing satellite (Keating 1995). PSAT pop-up dates were staggered to provide different windows of time in which to view fish locations and occupied depths and temperatures. As such, some tags were scheduled to transmit data during the summer feeding season, while others were set to pop-up during the spawning season, purported to occur from November to January on the Grand Banks and Scotian Shelf (Neilson *et al.* 1993; Armsworthy *et al.* 2014). Still others were set to collect data for a full year. Because the satellites are limited in their ability to receive incoming data, data were sub-sampled by an onboard algorithm and then transmitted

to satellites, resulting in temporal resolution of varying intervals, ranging from every four minutes to every 60 minutes, depending on deployment duration.

For all fish, end locations were considered as the Global Positioning System location where the fish was recaptured (for DSTs or PSATs that were physically recovered) or the first message from PSATs with an Argos Location Class 1, 2, or 3, resulting in a positional error of <1.5km.. Horizontal displacement of each fish was measured as the great-circle distance between each fish's tagging and end locations, and represents the minimum distance each fish could have traveled during its time at liberty with the tag. Assuming that Atlantic halibut are demersal and they occupy the seafloor at least once a day, maximum daily depths were used to infer approximate locations for the tagged fish. Specifically, if maximum daily depths were <~250 m, a tagged fish was assumed to occupy the continental shelf while if maximum daily depths were $>\sim$ 250 m, a tagged fish was assumed to occupy either the continental slope or a deep basin in the GOM. This coarse geoposition approximation does not provide accurate locations; however, more importantly in the context of this study, it provides information on where the fish could not have been.

The depth time series data were examined qualitatively for evidence of spawning activity. The spawning behavior of many flatfish species is characterized by a series of abrupt vertical ascents and descents in the water column, termed 'spawning rises'. In Atlantic and Pacific halibut, the 'spawning rises' are typically 100-200 m in amplitude, a range that presumably allows the fish to release its neutrally buoyant eggs at the most advantageous depth for survival of progeny. These rises are followed by a resting period on the seafloor that approximately corresponds to the ovulatory interval necessary to hydrate another batch of eggs (Seitz et al. 2005). This behavior has been attributed to both Pacific halibut (Seitz et al. 2005; Loher and Seitz 2008) and Atlantic halibut (Armsworthy et al. 2014), always occurring on the continental slope from depths >400 m in the Pacific Ocean and >800 m in the Atlantic Ocean.

Results and Discussion

Data were recovered from seven DSTs and five PSATs (Table 1), with measurement intervals ranging from every four minutes to every 90 minutes. Time at-liberty of individuals ranged from just two weeks (Tag 34260, 14 days) to almost two years (Tag 8833, 709 days), while

Table 1.Electronic tagging information for 12 Atlantic halibut from the Gulf of Maine in the Northwest Atlantic. Tag 8808
was physically recaptured and subsequently redeployed on another fish (8808B). Recovery date is when tags were
physically recaptured or reported to Argos satellites. DST is Data Storage Tag, PSAT is Pop-up Satellite Archival Tag.
Tag resolution is the frequency of depth data provided by each tag. The unknown (UNK) horizontal displacement could
not be calculated because the end location of the tag was not provided. The discrepancy between a fish's time at-liberty
and days of data of its corresponding tag resulted from the memory of the tag reaching its capacity before the tag was
recaptured.

Tag #	Tag type	Tag resolution (minutes)	Total length (cm)	Tagging date	Recovery date	Days at-liberty	Days of data	Horizontal displacement (km)	Max depth (m)
8808	DST	5	99	25/06/2007	10/09/2008	443	42	24	138
8823	DST	5	142	02/07/2007	17/10/2007	107	57	211	189
8831	DST	5	113	12/06/2007	24/11/2008	531	72	UNK	207
8833	DST	5	107	12/06/2007	21/05/2009	709	72	17	192
9508	DST	60	113	21/06/2008	15/06/2009	359	359	7	177
9518	DST	60	104	21/06/2008	09/06/2009	353	353	57	248
8808B	DST	90	97	21/05/2009	14/06/2010	389	271	117	173
34251	PSAT	15	114	11/07/2009	11/01/2010	184	184	47	59
34256	PSAT	15	112	23/06/2007	22/07/2007	29	29	2	75
34260	PSAT	15	92	12/06/2007	26/06/2007	14	14	25	161
64487	PSAT	4	111	20/10/2009	20/11/2009	31	31	62	197
83721	PSAT	60	148	23/05/2008	20/05/2009	362	362	99	210

days of data for individual tags ranged from two weeks (Tag 34260, 14 days) to almost a full year (Tag 83721, 362 days). The discrepancy between a fish's time at-liberty and days of data of its corresponding tag resulted from the memory of the tag reaching its capacity. Nine of the tags provided data for summer months when the fish were presumably foraging and feeding in the nearshore waters. Six of the tags provided data from winter months when the fish presumably were spawning or migrating to offshore spawning locations.

Although some Atlantic halibut have been shown to undertake exceptionally long migrations >2500 km (Stobo *et al.* 1988), all but one of the fish in this study had end locations within the GOM (Fig. 2) and most of the horizontal displacement distances were relatively small (mean 60.7 km, range 2–211 km; Table 1). Some displacements were remarkably short, considering the length of time that the fish was at large. For example, a 113 cm fish (tag 9508) was recaptured only seven km from where it was tagged after being at liberty for 359 days. Another fish (tag 8833) was recaptured 17 km from where it was tagged 709 days earlier. Only one of the tagged fish (8823), the fish with the largest horizontal displacement (211 km), was recovered outside of the GOM, in relatively shallow coastal waters northeast of Browns Bank on the Scotian Shelf (Fig. 2). These results corroborate findings from previous studies in which a majority of Atlantic halibut appear to demonstrate limited movements (Jensen and Wise 1961; Kohler 1964; Stobo *et al.* 1988; Kanwit 2007; Col and Legault 2009; den Heyer *et al.* 2012). These limited movements may result in a lack of intermingling of Atlantic halibut from Canadian and U.S. waters on spawning grounds, potentially limiting gene flow among these areas and resulting in the existence of different stocks of fish in geographically proximate areas.

None of the tagged Atlantic halibut occupied depths >248 m (Fig. 3), implying that none left relatively shallow continental shelf waters for the deep basins of the GOM or the continental slope. From this observation, it is not possible to ascertain whether the tagged fish remained in the GOM while at liberty, as opposed to exiting the Gulf for the relatively shallow waters of the Scotian shelf, similar to one fish. However, it can be inferred that none occupied documented spawning grounds in the Northwest Atlantic in relatively deep water along the continental slope, where Atlantic halibut from the Scotian Shelf and Grand Banks have been shown to spawn (Armsworthy *et al.* 2014). This observation provides further evidence of a lack of intermingling of adult Atlantic halibut from the GOM and Canadian waters during the spawning season.



Fig. 3. Maximum daily depths occupied by 12 Atlantic halibut tagged with two types of electronic tags in the Gulf of Maine. The shaded area represents the purported spawning season of Atlantic halibut while the horizontal dashed line represents its minimum reported spawning depth.

None of the tagged fish demonstrated any abrupt vertical movements termed 'spawning rises' (Seitz *et al.* 2005), at any depth or any time of year, that could be considered evidence of spawning activity. Although it is possible that the tagged fish were immature and therefore did not participate in spawning migrations and activity, this is unlikely based on the size of the tagged fish. One caveat is that the temporal resolution of some tags may prohibit identification of individual spawning rises, as the intervals between their depth readings were greater than the duration of spawning rises (Seitz *et al.* 2005). Furthermore, it is possible that frequent changes in occupied depths masked spawning rises.

Nevertheless, the lack of evidence of spawning behavior (migration to spawning areas, occupation of spawning depths and spawning activity) challenges some commonly-held assumptions about Atlantic halibut in the Northwest Atlantic, including 1) all Atlantic halibut spawn in deep water on the continental slope and 2) the majority of mature Atlantic halibut spawn annually. The apparent violation of these assumptions clearly requires reconsideration of Atlantic halibut biology and ecology in the Northwest Atlantic. First, it is possible that Atlantic halibut have a spawning behavior on the continental shelf without an abrupt rise that is not observable by electronic tags, which has not been documented previously. Second, it is possible that Atlantic halibut do not spawn annually, commonly referred to as skip-spawning. A recent reanalysis of electronic tag data from the closely related Pacific halibut proposed that ~10% of mature fish do not participate in spawning migrations and of those that do, 10–15% may not actively spawn (Loher and Seitz 2008). It is possible that Atlantic halibut may have equal or even higher percentages of skip-spawning mature adults. A review of Kohler's (1967) size-at-maturity survey of Atlantic halibut determined that, of the largest (>91 cm) females surveyed (n = 26), only 50% were reproductively active (Burton 1999).

The observations in this study, taken together, suggest that adult Atlantic halibut that feed in the GOM during the summer may not commonly intermingle with fish from elsewhere in the Northwest Atlantic, potentially limiting gene flow of this species among geographically proximate regions. This observation provides further evidence that Atlantic halibut in Canadian and U.S. waters are not composed of a large, interbreeding population, as previously assumed (Stobo *et al.* 1988) and corroborates recent research suggesting that finer-scale stock structure exists for Atlantic halibut (Shakell *et al.* 2016). This fine scale stock structure may explain the disparity in abundance between U.S. and Canadian Atlantic halibut, and shed light on why the U.S. Atlantic halibut fishery

has not recovered since its collapse (Shakell *et al.* 2016). Similar examples of relatively isolated spawning components of adult fish have been proposed for Atlantic halibut in a Norwegian fjord (Seitz *et al.* 2014) and Pacific halibut in the Aleutian Islands (Seitz *et al.* 2011). Although this study was small in both sample size and geographic scope, it adds to the body of knowledge about Atlantic halibut and provides direction for future research. Given the precarious status of Atlantic halibut stocks in U.S waters of the Northwest Atlantic, a better understanding of the species' stock identity and reproductive characteristics in different parts of this species' range could, one day, contribute to sound international management policies that facilitate a stock recovery that has eluded fisheries scientists and managers for almost a century and a half.

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Perspectives provided by bottom trawl transect surveys conducted in the 1950s and 1960s on the dynamics of commercially exploited groundfish species on southern Grand Bank and St. Pierre Bank

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Abstract

Biomass estimates for Atlantic cod, haddock, American plaice and yellowtail flounder in NAFO divisions 3NO and Subdivision 3Ps were calculated from research vessel bottom trawl (RV) surveys conducted in the 1950s and 1960s using a transect survey design. Although these data are not currently included in resource assessment, they represent some of the earliest available data for these stocks and provide a means to examine population dynamics prior to the start of the stratified random surveys. Analyses of the survey data demonstrates that there was a deepening in the distribution of cod, haddock and American plaice, in 3Ps in response to changes in water temperatures during the late 1980s and early 1990s, and that this accounted for much of the reduction in biomass in shallow waters. Comparisons of RV estimates of population parameters with those from Sequential Population Analyses for cod in 3NO and 3Ps concluded that the latter provided valid measures of changes in population during the 1960s and 1970s.

Keywords: Grand Bank, groundfish, Saint Pierre Bank, transect surveys

Introduction

In the early 1970s, the International Commission for Northwest Atlantic Fisheries (ICNAF), the predecessor of the Northwest Atlantic Fisheries Organization (NAFO), adopted regulations that set limits on the catch that could be taken from each of the groundfish populations (stocks) that were of commercial importance. The Total Allowable Catch (TAC) from a particular fish stock was based on an estimate of its absolute size calculated using what were then new scientific methods, now referred to as Sequential Population Analyses (SPA). Time series of relative abundance indicators were required for the "calibration" of SPA estimates of stock abundance. Initially, fishing success (catch rate) of the commercial fleets was used to determine abundance, but it was recognized that commercial catch rates were influenced by a variety of factors other than abundance (Kulka *et al.*, 1996) and that the fishery-independent abundance estimates provided by standardized research vessel (RV) surveys were preferable. Consequently, series of bottom trawl surveys, based on a stratified-random (SR) sampling design, were initiated for all Northwest Atlantic fishing areas (Doubleday, 1981; Doubleday and Rivard, 1981). In NAFO Subarea 3, SR surveys were initiated by the Fisheries Research Board of Canada, Biological Station, St. John's, Newfoundland, (now Science Branch, Department of Fisheries and Oceans (DFO) Newfoundland Region), in Division 3N in 1971, Subdivision 3Ps in 1972 and in Division 3O in 1973. Research vessel surveys based on a fixed station transect sampling design had been conducted previously in these areas for about 20 years (Pitt *et al.*, 1981). However, the data from these were not directly comparable to those from the new SR survey series, and thus were not utilized in SPA calibrations.

These transect data are the earliest available for the stocks in question and therefore provide an invaluable means of examining early stock dynamics. They have been used previously, along with SR survey data, in a study of longterm fish community changes in 3Ps and 3NO by Casey (MS 2000), and her results were utilized by Myers and Worm (2003) in a study describing depletion of predatory fish communities worldwide. The conclusions of these authors were based on abundance estimates within a set of index strata extending to a depth of 275 m (150 ftms) in 3NO and of 365 m (200 ftms) in 3Ps. However, fishing was conducted at depths greater than these in all years, and it has been demonstrated that temporal changes in depth preferences of species do occur as a response to changes in abundance and/or temperature (e.g. Fréchet and Gagnon (1993), Kulka et al. (1995), Kulka et al. (1996) and Atkinson et al. (1997) for cod). Thus, there is a possibility that the results of Casey, and Myers and Worm, were confounded by temporal changes in species depth distribution. The present analyses investigate this possibility.

The primary commercial species, Atlantic cod (Gadus morhua), haddock (Melanogrammus aeglefinus), American plaice (Hippoglossoides platessoides) and yellowtail flounder (Limanda ferruginea), were utilized to obtain what the present authors considered to be the best estimates of population parameters for comparison with the estimates reported by Casey. These species comprised about 70% of the biomass of all the species considered by Casey in 3NO and about 35% of the biomass of those in 3Ps. Comparisons are made also with the results of SPAs conducted for the cod populations in these study areas as these extended back to the transect survey years. For these, the consistency of estimates of size/age structure and mortality from transect surveys with those calculated from these SPAs was evaluated, giving further indicators for evaluation of the consistency of transect survey population estimates with those from the subsequent SR surveys. The sensitivity of results to the decision-making criteria used by Casey and by the present authors for integration of the data series is examined. Also, the conclusions of Myers and Worm regarding progressive declines in Gadoid and Pleuronectid populations in Divisions 3NO and Subdivision 3Ps from the beginning of the 1950s are reviewed in light of present findings.

Methods

The data used in the present analyses were provided to the authors by DFO, Newfoundland and Labrador Region, as were those utilized previously by Casey. For 3NO surveys, these data extended from 1950 and, for 3Ps, from 1953. Although earlier surveys were conducted, the results of these were recognized as being biased (*e.g.*, Templeman *et al.*, 1978), or were no longer available. Since the stock area for American plaice and yellowtail flounder are 3LNO and the standard historical RV surveys were for 3NO only, the assumption is made that the proportion of the stock inhabiting 3L remained relatively constant over the period.

Transects extended from shallow to deep water (38–369 m) and fishing was conducted on each transect at standard depth intervals. An inventory of the data used from these surveys is in Table 1. In the SR period, fishing was conducted in waters much deeper than in the transect period (Table 2). When calculating biomasses, Casey adjusted for catchability of the research gear using factors proposed by Edwards (1968) but these factors are used in the present analyses only to derive estimates of the gadoid and pleuronectid biomasses that are directly comparable with those in Fig. 3 in Myers and Worm (2003). The geographic locations of transects, and of the strata used on subsequent SR surveys, are illustrated in Pitt *et al.* (1981).

On the survey vessel used initially, the Investigator II (INV II), fishing was conducted during daylight hours only. Thus, abundance data from surveys conducted subsequently by the A.T. Cameron (ATC) and the Wilfred Templeman (WT), on which sampling occurred on a 24-hr. basis, were standardized to INV II units by adjusting catches in night sets for diel variation in catchability, using conversion factors provided by Casey (2000). Catches by the ATC and WT were adjusted also for the greater area swept by the gears used compared to that used by INV II, again following Casey, rather than utilizing the results from the only comparative fishing experiment conducted during the period between these vessels (Gavaris and Brodie, 1984) as the reliability of such experiments is low (Halliday and Pinhorn, 2009). Distance towed was typically 3.3 km. Catches from the few sets that varied from that were prorated to this distance.

Transect survey data were standardized with those from SR surveys by assigning the sets in fixed transect

		Division	ns 3NO	Subdivis	ion 3PS	
Vessel	Year	Months	Sets	Months	Sets	
INV II	1950	4	29	NS	NS	
	1951	Division Months 4 3\4 4\5\6 5 5\6 5\6 4\5 5 4 NS NS 5 4\6 6 4\5\6\7 4\5 3\6 2\5 6\7 5\6 4\5 5\6 4\5 5\6 6 6 6 5\6 6 6 6 6 6 6 6 6 6 6 6 6 6	29	NS	NS	
	1952		73	NS	NS	
	1953		49	5\6	31	
	1954	5\6	45	6	28	
	1955	5\6	63	NS	NS	
	1956	4\5	27	5\6	30	
	1957	5\6	30	6\7	30	
	1958	4\5	29	5	32	
	1959	5	34	6	30	
	1960	4	18	6	37	
	1961	NS	NS	NS	NS	
	1962	NS	NS	NS	NS	
	1963	5	75	6	38	
	1964	4\6	54	6	7	
	1965	6	12	6	38	
ATC	1959	4\5\6\7	60	NS	NS	
	1960	4\5	42	6	38	
	1961	3\6	69	NS	NS	
	1962	2\5	83	5	12	
	1963	6\7	69	NS	NS	
	1964	5\6	82	6	31	
	1965	4\5	88	NS	NS	
	1966	5\8	68	NS	NS	
	1967	6	40	4\5	41	
	1968	5	44	5	20	
	1969	5\6	12	3	28	
	1970	6	31	2\3	28	
	1971	2\3	36	NS	NS	

Table 1. Inventory of transect surveys conducted in Divisions 3NO and Subdivision 3Ps

NS-Not surveyed

stations to the strata used in the subsequent SR surveys. Assignments were made on the basis of the position and depth of transect stations in relation to stratum boundaries, preference being given to depth as this was the more accurately measured parameter. Annual biomass estimates were then derived for each stratum by the swept area method (Doubleday, 1981) and summed to derive overall annual biomass estimates. This is the same procedure as that used by Casey (2000). The small numbers of cases where there was only one set per stratum were eliminated from the analyses. The number of sets per stratum ranged from 2 to 14 with a mean of 4.2 for 3NO and from 2 to 11 with a mean of 4.1 for 3Ps.

The area surveyed varied over time in both survey series but standardized time series of abundance estimates were obtained for each species in each of the study areas based on those area/depth strata that were most regularly fished. For 3NO populations, abundance estimates were obtained for a subset of 11 'index' strata, all shallower than 183 m (100 ftm) that were surveyed in at least 15 years during 1950–70, the transect sampling period. In Casey's analyses the strata utilized extended to 275 m (150 ftm). For 3Ps, the analysis was based on a subset of eight index strata, all shallower than 275 m that encompassed St. Pierre Bank in the eastern part of the Subdivision. These eight strata were surveyed in at least 12 years during the transect sampling period, 1953–70. In this case, the strata utilized in Casey's analyses extended to 365 m (200 ftm). Substantial numbers of sets were made in areas outside the index strata also, primarily in the stratified random period (Table 2), and biomass indices from all strata fished during this period are shown for comparison. The study period extended to 1995 to match that of Casey. This end date post-dates the collapse of the groundfish stocks in the area.

On almost all surveys, data collected were adequate to describe abundance, length composition and age composition of the study species. Visual examination did not indicate that there were discontinuities in RV parameter estimates at the time of transition between sampling methods.

Comparisons of estimates of population parameters from transect surveys with those from SPAs were restricted to

the cod stocks since no SPAs were conducted for haddock and, for plaice and yellowtail, the statistical areas used for stock assessment and the areas for which adequate survey data were available to the authors did not coincide. The SPAs used in comparisons were, in 3NO, that of Power et al. (2010) and, in 3Ps, that of Brattey et al. (2002). The results utilized were for the years 1959-1979 for 3NO, and 1959–1978 for 3Ps, thereby excluding those, more recent, years influenced by SPA calibration (Pope, 1972). The parameters compared were population size (ages 2+), recruitment (numbers at age 4 for 3NO, age 5 for 3Ps) and total mortality (Z). (The estimates of Z from survey data were obtained by fitting least square straight lines to log numbers per set for each year-class for ages 4-12 for 3NO cod and ages 5-12 for 3Ps cod.) Temperatures recorded were the bottom temperatures at the end of each research vessel tow.

The time-period used for summarizing the data in Table 2 and in Fig. 6 varied from 4 to 6 years to correspond to phases observed in the data as follows: 1970–75 - a period of low biomass, 1976–79 and 1980–85 - to cover the rebuilding phase, 1986–89 - to cover the beginning of the collapse, and 1990–95 - to cover the period of the collapse.

Divisions 3NO											
Period	Index	Strata			Outside Inde	ex Strata					
	Depth Range (m)	No.Sets	Depth Range	No. Sets	Depth Range	No. Sets	Depth Range	No. Sets			
1950s (T)	42-183	355	49–183	50	184–275	44	276-358	17			
1960s (T)	42-183	467	55-183	122	184-275	146	276-298	20			
1970–75 (T/SR)	42-183	124	57-183	106	184-275	52	276-353	22			
1976–79 (SR)	33-174	219	55-183	207	184–275	48	276-362	40			
1980–85 (SR)	38-156	298	36-183	261	184–275	77	276-357	60			
1986–89 (SR)	42-158	365	54-183	311	184-275	53	276-356	55			
1990–95 (SR)	43-140	448	56-183	342	184–275	74	276-351	81			
Subdivision 3Ps											
1950s (T)	38-256	147	59–293	33	NS	NS	NS	NS			
1960s (T)	38-274	249	59-318	39	NS	NS	NS	NS			
1970–75 (T/SR)	44–274	138	62-275	64	276-400	95	>400	13			
1976–79 (SR)	46-271	126	62-275	103	276-400	89	>400	19			
1980-85 (SR)	36–268	187	57-275	222	276-400	84	>400	93			
1986-89 (SR)	41-264	167	61–275	220	276-400	70	>400	113			
1990–95 (SR)	45-260	243	66–275	350	276-400	127	>400	222			

 Table 2.
 Numbers of sets in Index Strata and Outside Index Strata by Depth Zone.

NS=Not Surveyed

T=Transect Period

SR=Stratified Random Period

Results

Survey Estimates of Population Biomass

Survey estimates of biomass in the index strata for the four study species in each of the study areas, 3NO and eastern 3Ps correlated well with the estimates of Casey, R² ranging from 0.77 to 1.00. Biomass estimates for all strata fished, in the years after the introduction of stratified-random sampling in 1972–73, are compared with those for the index strata to confirm that the index strata provide satisfactory indicators of the populations overall.

3NO (Fig. 1)

Cod: Biomass increased from a low level in 1950–51 to a peak in the mid-1950s, but declined precipitously thereafter to an intermediate level maintained through most of the 1960s before declining again to a level comparable to that in 1950–51. Biomass remained low throughout the 1970s and into the 1980s, but then returned to about 1960s levels in the mid to late 1980s, before again declining to the lowest level in the time series by

the mid-1990s. Estimates from all strata were not greatly higher than those for the index strata and varied similarly.

Haddock: Biomass was low in 1950, but increased greatly immediately thereafter. It fluctuated at high levels in the 1953–60 period, then returned to, and remained at, very low levels. Indices from all strata and index strata were almost identical.

American plaice: Biomass was low in the 1950s but increased to a peak in the mid-1960s and generally remained at this level to the mid-1980s, before declining. In this case, estimates for all strata were approximately double those for index strata, indicating that a substantial portion of the population occurred outside the index strata. Nonetheless, both indices show a decline in biomass in the late1980s and early 1990s.

Yellowtail flounder: Biomass was very low in the 1950s, but increased greatly in the 1960s and reached its highest level in the late 1970s to early 1980s, declining thereafter ($R^2 = 0.74$ with Casey). The lower correlation with the results of Casey reflects a dichotomy in estimates after



Fig. 1. Biomass (000 MT) for the major species in Divisions 3NO. (Solid line - indices from Index Strata; Dashed line - indices from All Strata (after 1972).

1972, which can be satisfactorily explained if one assumes that Casey neglected to apply the catchability factor of 0.39 to 1973–95 data. Making such an adjustment to Casey's data improves the correlation with present estimates to R^2 =0.86. Estimates of biomass from all strata in the post-1972/73 period were almost the same as those for index strata, reflecting the shallow water distribution of this species (less than ~90 m).

3Ps (Fig. 2)

Cod: Biomass was high in the 1950s, but subsequently declined steadily to a minimum in the mid-1970s. It rebuilt to some extent in the early 1980s but declined greatly thereafter to very low levels, consistent with the results of Casey. Estimates for all strata varied similarly to those for the index strata until 1985, but then diverged substantially, indicating a change in the proportion of the biomass occurring outside the index strata.

Haddock: Biomass was high in 1953 and 1954 but by 1956 had declined to a very low level at which it remained. However, estimates for all strata detected a peak in abundance in years 1984–90 not observed in the index strata.

American plaice: Biomass estimates from index strata were highly variable, low values occurring in the 1950s, about 1970 and in the late 1970s and early 1990s. Estimates for all strata were substantially higher (about 160%) than those from the index strata but varied similarly.

Yellowtail flounder: Biomass was quite variable throughout the period with highs in the mid-1960s and mid-1980s and lows in the mid-1970s. The estimates from the index strata and all strata were almost identical because yellowtail are seldom found deeper than 90 m.

Survey versus SPA estimates of population parameters

3NO cod (Fig. 3)

Abundance: Both RV and SPA indices of age 2+ numbers show that abundance increased from low levels in the



Fig. 2. Biomass (000 MT) for the major species in Subdivision 3Ps (Solid line - indices from the Index Strata; Dashed line - indices from All Strata (after 1972).

1950s to a peak in the mid-1960s, then declined to a low level in the early 1970s.

Recruitment: SPA age 4 numbers and the RV age 4 numbers-per-set both show abundance of 4 year olds was low in the late 1950s increasing to a peak in the mid-1960s and then declining to a very low level in the early 1970s.

Mortality: Total mortality estimates (Z) for the year classes 1955–67 in the RV and SPA series are in broad

agreement, both showing Z to be low for the late 1950s year classes, increasing to higher levels for the mid to late 1960s year classes.

3Ps cod (Fig. 4)

Abundance: Both RV and SPA indices of age 2+ numbers show that a high level of abundance in the early 1960s was followed by a decline to a very low level in the mid-1970s where it remained in subsequent years.



Fig. 3. Comparisons of estimates of population parameters from research vessel surveys and from SPA for Divisions 3NO cod. (Solid line - research vessel estimates; dashed line - SPA estimates).



Fig. 4. Comparisons of estimates of population parameters derived from research vessel surveys and from SPA for Subdivisions 3Ps cod. (Solid line - research vessel estimates; dashed line - SPA estimates)

Recruitment: At age 5, the first age fully recruited to the fishery, survey data show sharp peaks in recruitment in 1960, 1968 and 1979 while the SPA data show peaks in 1960, late 1960s and late 1970s. Thus, estimates from the two sources were in general agreement.

Mortality: The Z-values calculated by year class from RV and SPA data were in close agreement, Z increasing steadily from the 1954 year-class to the early to mid-1960s year-classes.

Discussion

The present analyses evaluate biomass estimates derived by Casey (MS 2000) for cod, haddock, American plaice and yellowtail flounder using RV survey data from southern Grand Bank in 3NO and St. Pierre Bank in 3Ps in the period 1950–1995.

The biomass trends obtained proved to be in close agreement with those of Casey when the comparisons were restricted to a selected set of strata that were sampled consistently from the beginning of the 1950s to 1995. Inclusion of samples from a larger area, surveyed by the stratified random surveys conducted from the early 1970s, made little difference to the estimates obtained for the shallow-water species, haddock and yellowtail, but estimates for the more deeply-distributed cod and plaice were higher when all strata were included in the calculations. However, the pattern of inter-annual variation in abundance was similar between index-strata and all-strata estimates, except for cod, haddock and plaice on St. Pierre Bank from about 1985 onwards. This correspondence for most of the stocks verified the assumption that the biomass estimates from the Index Strata were representative of the area as a whole. The disparity for St. Pierre Bank, where all-strata estimates for these three species were much higher than those for index strata only, was brought about by their avoidance of an influx of very cold water in the 1986-89 and 1990-95 periods in the depths corresponding to the Index Strata (Fig. 6) by moving deeper, fish being found in abundance as deep as 550-730 m. This movement to deeper water outside the Index Strata was missed by Casey and, consequently, by Myers and Worm (2003), because their conclusions were based on Index Strata only. Thus, their conclusion that the cod biomass in 3Ps declined continuously from the 1950's was erroneous.

For cod, the population parameters of biomass, population numbers, recruitment and mortality estimated from SPA calculations in both 3NO and 3Ps were in good agreement with those from the transect surveys conducted in the 1960s and early 1970s, although in the case of St. Pierre Bank cod, the peaks in recruitment in 1968 and 1979 were less pronounced than in the survey data. For both populations, the comparisons indicate that the SPAs provided valid measures of changes in population during this period, despite the uncertainties in catch statistics and the deficiencies in biological sampling of catches at that time (Halliday and Pinhorn, 1996).

The results of Casey were used by Myers and Worm (2003) to describe trends in overall biomass of gadoid, and of pleuronectid, species in Div. 3NO and 3Ps. Estimates of biomass for these two families based on present results are in close agreement with those of Myers and Worm (Fig. 5) (R^2 =0.90 for Gadoid species and 0.85 for Pleuronectid species). This is to be expected, as the comparison is dominated by the present study species, and the close similarity of estimates reported here for these species with those of Casey has already been noted.

However, the difference between the present and previous studies lies in their interpretation of the data. Myers and Worm's interpretation of Gadoids in Fig. 5, after applying



Fig. 5. Gadoid and Plueronectid biomass for Divisions 3NO. (Dashed line - indices from Myers and Worm; solid line - biomass indices from present paper).

a local regression smoother, is a net decline in the biomass over the entire period in accordance with their hypothesis. However, considering the original data for gadoids, which is basically cod after the early 1960s, the biomass declined from a high in the mid-1950s to lows of less than 100,000 MT in the 1970s, in conjunction with several other species, but had rebuilt to over 700,000 MT by the late -1980s after which it declined precipitously. The pleuronectid biomass increased from very low levels in the early-mid 1950s to a peak of 550,000 MT by 1965. It then declined to a low of 300,000 MT by 1972, as noted above for the Gadoids, but had rebuilt to about 500,000 MT by the late 1970s to mid-1980s then declined precipitously.

Another important difference between the present analysis and that of Myers and Worm is the role of the data points for 1950 and 1951 in 3NO in the present study, which shows gadoid biomass to be much lower than in the immediately following years. This leads to a different interpretation of the status of these populations in the 1950s than that presented by Myers and Worm,



Fig. 6 Mean percentage of cod, haddock and plaice in deep strata (>274 m) (dashed line) and percentage of bottom temperatures < 0 0 C (solid line) in A. Index Strata (36–274 m) and B. Non-Index Strata with depths similar to those in the Index Strata for subdivision 3Ps. Period indicates the beginning of each period. See text for a list of periods used.

one that shows large increases in abundance of cod and haddock from very low levels at the beginning of the 1950's to very high levels by mid-decade. The increase in haddock abundance was due to recruitment of a very large 1949 year-class and subsequently by a large 1955 year-class (Templeman, 1966). For cod, data are scant, but Williamson (MS 1965) identified 1949, 1955 and 1958 year classes as being particularly strong in both 3NO and 3Ps. This suggests that the peak abundance of cod in the mid-1950s was supported substantially by the 1949 cohort and abundance in the late 1950s and the 1960s by those of 1955 and 1958. The first year of present data for 3Ps was 1953, and thus they do not show whether or not there was an increase in the initial years of the 1950s, but Williamson's data for cod indicate a similar pattern of year-class strengths in this area as in 3NO.

Myers and Worm (2003) fitted exponentially declining curves to their combined abundance estimates for Gadoid and Pleuronectid species for the St. Pierre Bank, and southern Grand Bank populations from about 1950, and attributed the declines to the effects of the development of industrialized fishing. However, a subsequent study (Halliday and Pinhorn, 2009) found the weight of evidence favoured environmental changes, associated with variations in the North Atlantic Oscillation, as the primary factor driving large scale variations in the productivity of Northwest Atlantic groundfish population.

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NAFO Scientific Council Studies

The Studies publishes papers which are of topical interest and importance to the current and future activities of the Scientific Council, but which do not meet the high standards or general applicability required by the Journal. Such papers have usually been presented as research documents at Scientific Council meetings and nominated for publication by the Standing Committee on Publications. Studies papers are not peer reviewed.

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The paper should be in English. The sequence should be: Title, Abstract, Text, References, Tables and Figures.

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The references cited in the text should be listed alphabetically. References should be mainly restricted to significant published literature. Unpublished documents and data, papers in preparation, and papers awaiting acceptance to other journals, may be cited with full contact addresses as unpublished or personal communications.

Examples:

- KING, M. 1995. Fisheries biology, assessment and management. Fishing News Books, UK, 341 p.
- CROWDER, L. B., and S. A. MURAWSKI. 1998. Fisheries by-catch: implications for management. *Fisheries*, 23: 8–16. doi:10.1577/1548-8446(1998)023<0008:FBIFM> 2.0.CO;2
- ÁVILA DE MELO, A. M., D. POWER, and R. ALPOIM. MS 2005. An assessment of the status of the redfish in NAFO Division 3LN, *NAFO SCR Doc.*, No. 52, Serial No. N5138, 19 p.

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