

# Using multivariate state-space models to examine commercial stocks of redfish (*Sebastes* spp.) on the Flemish Cap

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**Abstract:** There are three different species of redfish (*Sebastes* spp.) in the waters of the Flemish Cap (Division 3M, NAFO Regulatory Area): *S. fasciatus*, *S. mentella*, and *S. norvegicus*. Historically, *S. fasciatus* and *S. mentella* have been managed together as a single stock because of similar biology and difficulty in species identification. Here we use multivariate autoregressive state-space models to examine the abundance trajectories of the three species and to determine whether they can be treated as a single stock for management purposes or whether they should be treated separately. We also included covariates to evaluate relationships with climate, commercial catch, and the abundance of predators and (or) competitors and prey. We did two separate analyses: (i) a single-period analysis over the full time series and (ii) a blocked, two-period analysis over different regulatory periods. In both analyses, the best-fit model included separate trajectories for each species at each depth but one overall stock growth rate; both also included commercial catches as a covariate. These analyses suggest that a single assessment for the *Sebastes* complex is acceptable.

**Résumé :** Il y a trois espèces différentes de sébastes (*Sebastes* spp.) dans les eaux du bonnet Flamand (division 3M de la zone réglementée par l'OPANO), soit *S. fasciatus*, *S. mentella* et *S. norvegicus*. Par le passé, *S. fasciatus* et *S. mentella* ont été gérés ensemble en tant que stock unique en raison de leur biologie semblable et de la difficulté d'identifier ces espèces. Nous utilisons des modèles d'espace d'états autorégressifs multivariés pour examiner les trajectoires d'abondance des trois espèces et déterminer si elles peuvent être traitées comme un seul stock aux fins de la gestion ou si elles doivent être traitées séparément. Nous avons aussi inclus des covariables pour évaluer les relations avec le climat, les prises commerciales et l'abondance de prédateurs/concurrents et de proies. Nous avons réalisé deux analyses distinctes, à savoir : (i) une analyse sur une seule période pour toute la série chronologique et (ii) une analyse en blocs sur deux périodes distinctes du point de vue réglementaire. Dans les deux analyses, le modèle présentant le meilleur ajustement inclut des trajectoires distinctes pour chaque espèce à chaque profondeur, mais un seul taux de croissance global du stock; les deux analyses intègrent aussi les prises commerciales comme covariable. Ces analyses donnent à penser qu'une seule évaluation pour le complexe des *Sebastes* est acceptable. [Traduit par la Rédaction]

## Introduction

Given the complexity of ecosystems, it is important to understand the major processes determining fisheries dynamics. Three species of redfish (*Sebastes* spp.) are found in the waters around the Flemish Cap in the North Atlantic (Northwest Atlantic Fisheries Organization, NAFO, Division 3M; Fig. 1): Acadian redfish (*S. fasciatus*), deepwater redfish (*S. mentella*), and golden redfish (*S. norvegicus*) (Saborido-Rey 1994). Historically, *S. fasciatus* and *S. mentella* have been the dominant redfishes in Flemish Cap waters (Avila de Melo et al. 2015). Because of their high external similarity, the commercial catches are often not split into different species but instead lumped into “redfish” (Garabana 2005). As a result, management has treated the two species as a single stock with an assessment in 3M for a “beaked redfish” complex. From 2004 to 2006 there was a rapid increase of the third species *S. norvegicus*, and a new fishery started in 2005 (Avila de Melo et al. 2015). This species will be assessed for first time in June 2018 as an independent stock.

Commercial catches of redfish were very high at the end of the 1980s but then failed continuously through the 1990s. Catch increased again in the 2000s, but at a much smaller scale (Fig. 2a). Concomitant with changes in the redfish abundance and its fish-

ery were changes in Atlantic cod (*Gadus morhua*, a predator and competitor) and shrimp *Pandalus borealis* (prey). After a period of high fishing pressure in Flemish Cap, cod collapsed in the mid-1990s, and a moratorium was imposed in 1999. In 2010, the cod fishery reopened; the shrimp fishery entered into moratorium in 2011 (Avila de Melo et al. 2015; Casas 2014; González-Troncoso 2015).

While commercial catch has risen since 2000, the stock assessment, which is based in part on a fishery-independent trawl survey, shows a strong decline in redfish biomass on the Flemish Cap (Fig. 2b) from approximately 2006. Therefore it is important to evaluate the efficacy of current management strategies. We know that the redfish are different species. However, since they are closely related and have similar biology, we might ask whether the trends the abundance of individual species allow for treating them as a single complex or whether the individual species show different population trends through time, which might require separate management schemes.

Multivariate autoregressive state-space models (MARSS) have been used extensively to understand species interactions and the dynamics of freshwater plankton communities (Hampton et al.

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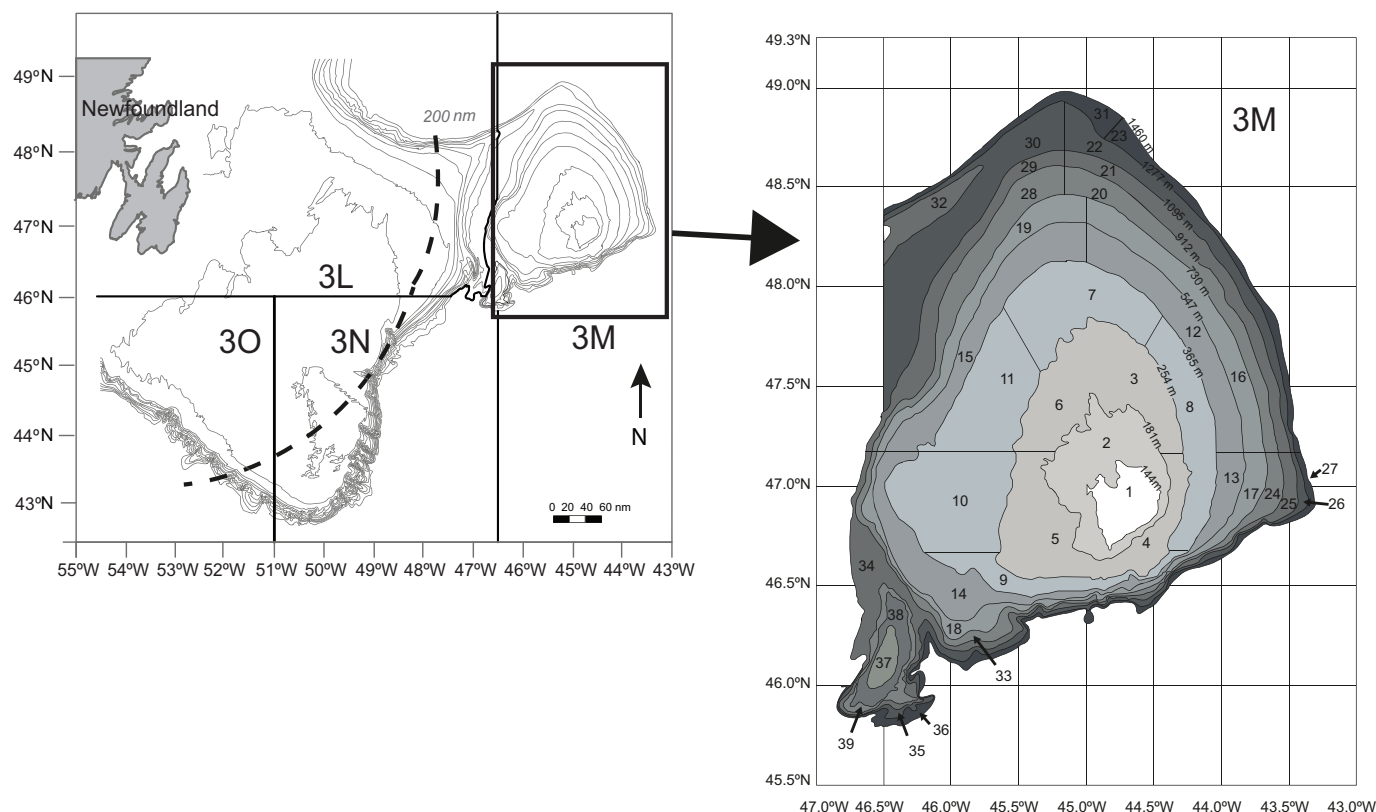
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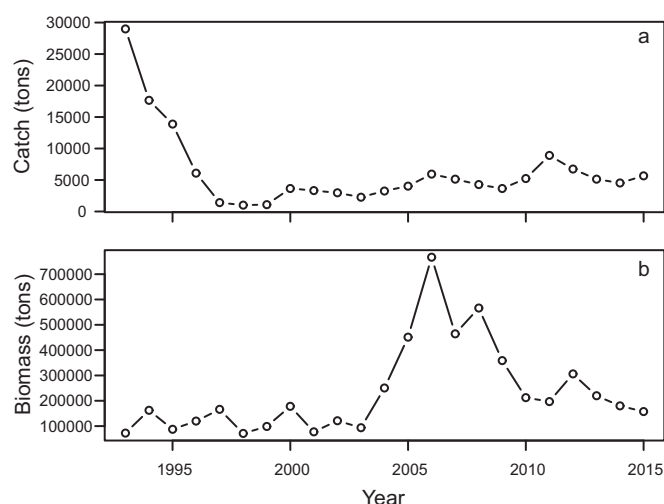
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**Fig. 1.** Chart of the NAFO Divisions 3LMNO. EU bottom trawl area in Flemish Cap (NAFO Regulatory Area, Division 3M) is marked by square.



**Fig. 2.** (a) Commercial catches of redfish (*Sebastes* spp.) from commercial fishing vessels in NAFO Division 3M for all countries from 1993 to 2015. (Data were based on information from STATLANT 21A, NAFO website.) (b) Data of biomass estimate in the EU bottom trawl survey for redfish (*Sebastes* spp.) from 1993 to 2015.



2013; Ives 1995; Ives et al. 1999, 2003a; Ives and Settle 1997). However MARSS models can also be used (through model fitting and selection) to ask questions about the spatial structure of populations and for population viability analysis (Tolimieri et al. 2017). For example, Ward et al. (2010) examined time series of sea lion abundance at four different haul-outs to determine whether there was evidence for separate populations or whether sea lions at the four locations were part of the same larger population (e.g., one population growth rate for all four combined). MARSS offers sev-

eral additional advantages: it is able to use time series with missing values; it allows one to combine multiple time series with potentially different scales (e.g., different vessels with different catchability); and can include covariates in the analysis. For example, Tolimieri et al. (2017) used MARSS models to combine gappy data from multiple surveys and regulatory periods to estimate long-term population growth rate of rockfishes in Puget Sound and to evaluate data support for population structure among different basins within the sound.

Here we use MARSS models to examine the spatial structure of redfish stocks on the Flemish Cap combining surveys from two different vessels: R/V *Cornide de Saavedra* (1993–2002) and the R/V *Vizconde de Eza* (2003–2015). The primary objective of this study was to evaluate if there is data support for treating multiple species as a single “stock” (complex) in terms of their trends in biomass, or whether they should be assessed separately because their abundance trends differ substantially. We also examine whether abundance trends differ between two depth zones and examine the influence of environmental covariates and commercial catch on redfish stocks. We then re-examine these relationships more closely in two different regulatory periods related to the cod moratorium. Each hypothesis was converted into an appropriate MARSS model, and the best model was chosen using model-selection criteria.

## Materials and methods

### Study species

Redfish (*Sebastes* spp.) are viviparous and slow growing with protracted life spans (more than 50 years). Although the genus is more speciose in Pacific waters (Love et al. 2002), three species of redfish are present on the Flemish Cap: *S. fasciatus*, *S. mentella*, and *S. norvegicus*. However, many aspects of their biology and ecology are poorly studied, mainly due to the lack of good species identification and a proper definition of the stock structure. The latter is

important because it prevents the correct definition of many population and biological parameters (Garabana 2005).

### The Flemish Cap

The Flemish Cap (Fig. 1) is a raised bank separated from the Grand Bank of Newfoundland by the Flemish Pass, a channel with depth in excess of 1100 m that hinders the migration of shallow demersal species to the adjacent banks (Konstantinov 1970; Morgan and Bowering 2004; Templeman and Fleming 1963). It is managed by the Northwest Atlantic Fisheries Organization (NAFO) as Division 3M.

There are three main communities of demersal fishes on the Flemish Cap: a shelf or shallow community ( $\leq 250$  m), an upper slope or mid-depth community (251–600 m), and a lower slope or deep community ( $\geq 601$  m) (González-Troncoso et al. 2006; Nogueira et al. 2017; Paz and Casas 1996). *Sebastes norvegicus* is primarily found in the shallow assemblage, while *S. fasciatus* and *S. mentella* are found in the mid assemblage. In the shelf assemblage, *S. norvegicus* is the most dominant species in terms of biomass (40%) with *S. fasciatus* the next most abundant (28%). Together the three species of redfish make up 80% or more of the total biomass in the mid-depth assemblage. Therefore, we summarized the catch data into two depth categories:  $\leq 250$  m and 251–600 m corresponding to the shallow and mid assemblages described by Nogueira et al. (2017) (15 strata, 3601 hauls). We excluded data deeper than 600 m because most of the biomass of the redfish is from the shallower two depth zones (99%) and because data for 730 m or deeper exist only for 2004–2015.

### Field methodology

Abundance data for the three redfish species come from bottom trawl surveys carried out by the European Union (EU) to estimate abundance and biomass of demersal fishes in the Flemish Cap. The survey was carried out only during daylight hours. The survey has used two main research vessels: the R/V *Cornide de Saavedra* (1988–2003) and the R/V *Vizconde de Eza* (2004–2015). Data exist for 1998–1991, but we exclude these data due to poor identification of the three redfish prior to 1993. The survey was divided into 19 strata (max depth 730 m) until 2003, after which the depth of the survey was extended (max depth 1460 m) resulting in 32 strata. A minimum of two randomly placed trawls were conducted per stratum (Bishop 1994). Trawls were towed for 30 min at a speed of 3.0 knots (1 knot = 1.852 km·h<sup>-1</sup>) using a Lofoten otter trawl gear (mesh size was 35 mm, mean horizontal opening = 14 m, vertical opening was 3.5 m) and monitored using a Scanmar net control system. Around 120–180 valid hauls were made each year. The mean of the initial and final depth was used to define the bottom depth of each haul.

Our data are abundance of the three stocks of redfish *S. mentella*, *S. norvegicus*, and *S. fasciatus* estimated using the swept area method (Cochran 2007) for years 1993–2015. Smaller redfish (juveniles, less than 16 cm) are separated as an independent category during the EU surveys. The average proportion of each redfish species found in the identified juveniles is then applied to the catches of unidentified juveniles to split them by species (Avila de Melo et al. 2003). We summed abundance estimates from each of the strata by depth bin to create separate time series for each species of the two depth bins ( $< 250$  m and 251–600 m).

### Covariates

We included several covariates in the modeling process to examine the potential effects of climate (and oceanography), predators and prey, and commercial catch on redfish abundance.

- (1) North Atlantic Oscillation (NAO): We include the moving average of the NAO index in the previous 1–4 years to analyze the effect of environmental conditions (Fig. 3a). NAO index data are available on the NOAA website (<http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml>). We used this range because redfish recruit to the survey primarily

at age 4, although younger individuals can also be caught. The NAO measures variability the difference in atmospheric pressure at sea level between the Azores high and Icelandic low. Positive NAO results in more and stronger winter storms crossing the Atlantic and colder conditions in the NW Atlantic (but warmer conditions in Europe) (Ottersen et al. 2001; Visbeck et al. 2001). This climate variability affects populations and ecological systems, for example, with warmer conditions under more negative NAO, resulting in higher cod size and year-class strength (Ottersen et al. 2001).

- (2) Predators and Prey: For Atlantic cod (Fig. 3b) and Northern shrimp (Fig. 3c), we use abundance estimates in the EU bottom trawl survey. Cod is both a predator on and a competitor of redfish. Shrimp is the most important prey in the diet of redfish. We used the conversion factor calculated by González-Troncoso and Casas (2005) to combine cod and shrimp time series (separately) from R/V *Cornide de Saavedra* and R/V *Vizconde de Eza* to create a combined time series 1993–2015.
- (3) Commercial catch: Commercial catches of redfish (numbers) from commercial fishing vessels in NAFO Division 3M for all countries come from Avila de Melo et al. (2015) to study the effect of fishing (Fig. 3d).

### Statistical methodology: MARSS

We used MARSS models to evaluate different stock structures and the influence of covariates (Hinrichsen and Holmes 2009; Holmes et al. 2014a; Holmes et al. 2012; Tolimieri et al. 2017). While this approach can also estimate population growth rates and separate process and observational variance, these parameters are not the focus of our analysis per se. We fit MARSS models in the following form:

$$(1a) \quad \mathbf{x}_t = \mathbf{x}_{t-1} + \mathbf{u} + \mathbf{C}_t \mathbf{c}_t + \mathbf{w}_t, \quad \text{where } \mathbf{w}_t \sim \text{MVN}(0, \mathbf{Q})$$

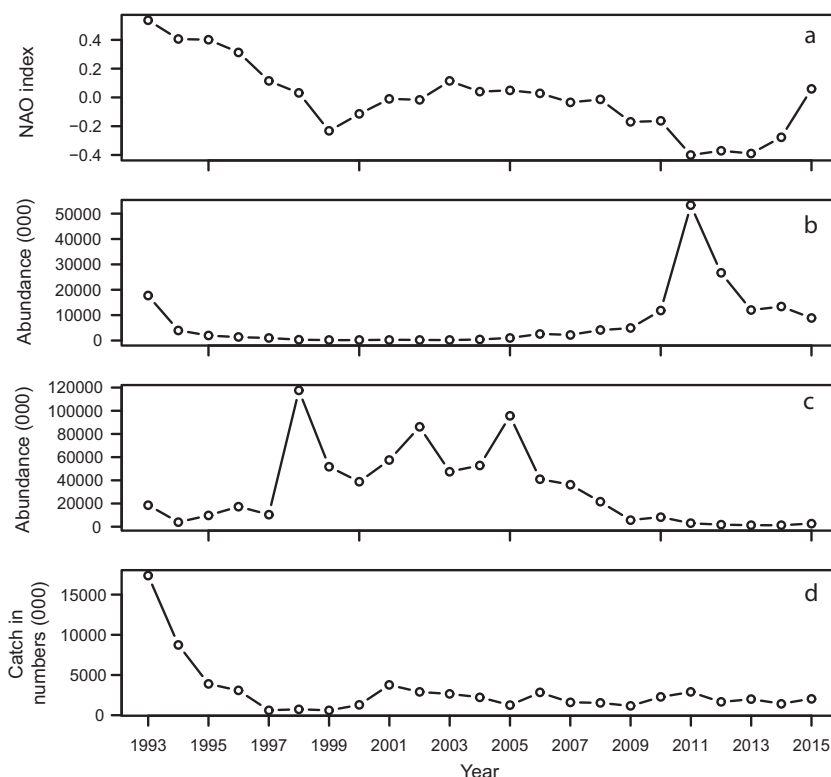
$$(1b) \quad \mathbf{y}_t = \mathbf{Z} \mathbf{x}_t + \mathbf{a} + \mathbf{v}_t, \quad \text{where } \mathbf{v}_t \sim \text{MVN}(0, \mathbf{R})$$

Equation 1a is the process equation, which models the set of true but unknown abundance trajectories (state processes). Here,  $\mathbf{x}_t$  is a column vector of the abundance (number of individuals) of each species (in our case, log(abundance) in year  $t$ ),  $\mathbf{u}$  is a column vector of the mean (long-run) growth rates for each trajectory (i.e., for each  $\mathbf{x}$  in  $\mathbf{x}$ ), and  $\mathbf{w}_t$  is a column vector of the multivariate normal (MVN) process errors or deviations from the long-term growth rate at year  $t$ .  $\mathbf{Q}$  is the process variance–covariance matrix with process variance on the diagonal and covariance on the off-diagonals. Here we assume correlated process errors (nonzero values on the off-diagonals) in all models, because ocean conditions are correlated at large spatial scales (Holmes et al. 2014a). The  $\mathbf{c}_t$  term allows the inclusion of covariates in the model such as the effects of environmental variables and fisheries catch (all covariates are standardized for the analyses).

Equation 1b is the observation equation. The term  $\mathbf{y}_t$  is a column vector of the observations (the data, log(abundance)) at year  $t$ .  $\mathbf{Z}$  is a 0,1 matrix that defines how the observations (the  $\mathbf{y}$  in  $\mathbf{y}$ ) relate to the underlying abundance trajectories (the  $\mathbf{x}$  in  $\mathbf{x}$ ). The parameterization of  $\mathbf{Z}$  determines whether the model estimates a different trajectory for each species of redfish (*S. fasciatus*, *S. mentella*, and *S. norvegicus*) and for each depth assemblage (shallow and mid), or one trajectory for all Flemish Cap. Within the  $\mathbf{y}$  eq. 1b,  $\mathbf{a}$  is a column vector of scaling terms for each observation time series  $\mathbf{y}$  in  $\mathbf{y}$ . It allows one to combine time series estimated on potentially different scales (e.g., with different catchability) — for example, to model the difference between the two vessels.  $\mathbf{v}_t$  is a column vector of the observation errors at year  $t$ , and  $\mathbf{R}$  is the variance–covariance matrix for the observation errors. The absolute scaling of the abundance trajectories is unknown, thus the estimated



**Fig. 3.** Covariates. (a) The moving average of the NAO index in the period between 1 and 4 previous years. (Data available at NOAA website.) (b) Data of abundance estimate in the EU bottom trawl survey for Atlantic cod (*Gadus morhua*). (c) Data of abundance estimate in the EU bottom trawl survey for Northern shrimp (*Pandalus borealis*). (d) Commercial catches in numbers of redfish from commercial fishing vessels in NAFO Division 3M for all countries. (Data were based on information from Avila de Melo et al. 2015.)



abundance trajectories (the  $\mathbf{x}$ ) are indices; they relate to the true abundances by an unknown scaling factor.

### Models tested

Changing the parameterization of  $\mathbf{Z}$  and  $\mathbf{u}$  allows us to specify different hypotheses about the stock structure. We tested seven different spatial structures for  $\mathbf{Z}$ . These models test combining all species into a single “stock” trajectory, treating each separately, or combining pairs of species. We also included depth as a factor since assemblages differ with depth and some species are more common in certain depth zones than in others. In terms of the parameterization of  $\mathbf{Z}$ , the models we tested included the following.

- (1) One trajectory for three species in all the depth ranges all same (1Z).
- (2) Different trajectories for each species in each depth zone (shallow and intermediate): Spp  $\times$  Depth (6Z).
- (3) Different trajectories for each species: Spp (3Z).
- (4) One overall trajectory for the three species within each depth zone: Depth (2Z).
- (5) Same trajectory for *S. fasciatus* and *S. mentella* but different for *S. norvegicus* in all the depth range: [S.f. & S.m.]  $\times$  S.n. (2Z).
- (6) Same trajectory for *S. norvegicus* and *S. fasciatus* but different for *S. mentella*: [S.f. & S.n.]  $\times$  S.m. (2Z).
- (7) Three different trajectories, one overall trajectory for *S. fasciatus* and *S. norvegicus* in the shallow zone, but different for *S. mentella*, and one overall trajectory for the three species in the mid zone: [S.f. shallow & S.n. shallow]  $\times$  S.m. shallow  $\times$  [S.f. mid & S.n. mid & S.m. mid] (3Z).

We also tested different levels of model complexity in the stock growth rate  $\mathbf{u}$ . We allowed  $\mathbf{u}$  to be the same (a single  $\mathbf{u}$ ) or different (multiple  $\mathbf{u}$ 's in  $\mathbf{u}$ ) across all trajectories specified in  $\mathbf{Z}$ .

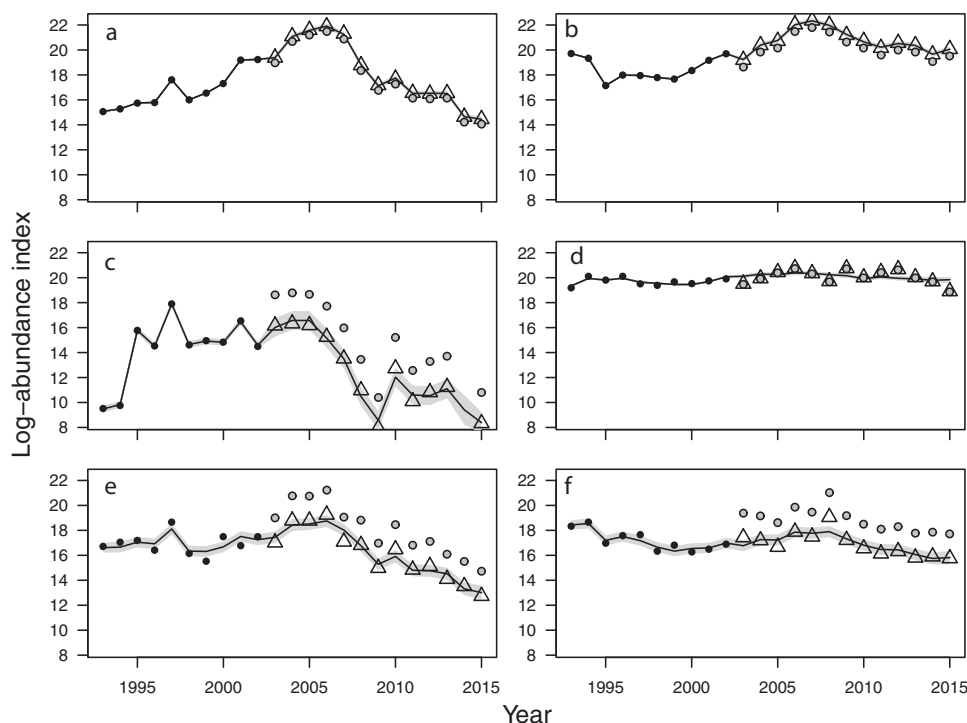
For the seven different spatial structures and the two different combinations of  $\mathbf{u}$ , we conducted two separate analyses.

- (1) Single-period analysis: Here we estimated  $\mathbf{u}$  and evaluated stock structure  $\mathbf{Z}$  across the full time series, 1993–2015.
- (2) Two-period analysis: We broke the time series into two time periods: 1993–2007 and 2008–2015 based on changes in management. We then set  $\mathbf{u} = \mathbf{0}$  and used dummy-coding in  $\mathbf{C}$  to estimate stock growth rates for each time period (for consistency, we report the population growth rates from these models as  $\mathbf{u}$ ). From 1993 to 2007, the shrimp fishery was open, and cod declined; the cod fishery was declared under moratorium in 1999. From 2008 to 2015, spawning stock biomass (SSB) of cod was above the limit reference point for SSB ( $B_{lim}$ ) for the first time since 1995. Although the fishery was not open until 2010, we choose that year as indicator of recovery of cod (González-Troncoso and Fernández 2009) and the potential for top-down predatory effects on redfish dynamics. These two periods also generally correspond to an initial period of increasing biomass followed by a period of decreasing biomass. This second analysis determines whether the three species responded differently to changes in regulations and estimate different population growth rates for each period. For example, it is possible that one species recovered more quickly or responded more strongly to re-imposition of commercial fishing.

We also included several covariates in the  $\mathbf{C}_t \mathbf{c}_t$  portion of the model that might be expected to affect the population dynamics of redfish.

- (1) Redfish predator: cod abundance.
- (2) Redfish prey: shrimp abundance.

**Fig. 4.** Estimate trajectories (process states) for the three species of redfish in each depth (solid line) and the observational process for each vessel, R/V *Cornide de Saavedra* (black circles) and R/V *Vizconde de Eza*, original data (grey circles), corrected for the scaling effect  $\alpha$  (triangles): (a) *S. fasciatus* in the shallow zone, (b) *S. fasciatus* in the mid zone, (c) *S. mentella* in the shallow zone, (d) *S. mentella* in the mid zone, (e) *S. norvegicus* in the shallow zone, (f) *S. norvegicus* in the mid zone. Grey envelopes indicate 95% confidence intervals.



- (3) Fishing effect: commercial catches of redfish in numbers.
- (4) Environmental effect: North Atlantic Oscillation (NAO) index. Note that other environmental variables were examined in preliminary analyses, sea surface temperature (SST), bottom temperature, cold intermediate layer (CIL). However, they were correlated with the NAO and were excluded.

We normalized our covariate data to easily compare the effects across different covariates. All analyses were repeated using all 15 different combinations of the covariates. We forced models to estimate the effect of covariates in different ways: (i) same effect for each stock, (ii) different effects for each stock, (iii) for 6Z, one covariate for each species or one covariate for each depth.

We used Akaike's information criterion corrected for sample size ( $AIC_c$ ) to select the most parsimonious model, ranked using  $\Delta AIC_c$  (Burnham and Anderson 1998). Models with  $\Delta AIC_c < 2$  were considered to be similarly supported. For similarly supported models, we chose the model with fewer parameters as the most parsimonious. Approximate confidence intervals (CI) on MARSS parameters were computed via numerical estimation of the Hessian matrix for the best-fit model or models. Confidence intervals and standard errors on  $u$  were computed using the parametric bootstrapping approximation. All analyses were run in R 3.2.0 (R Core Team 2016) using the MARSS package (Holmes et al. 2014a).

## Results

### Single-period analysis

We evaluated a total of 428 different models with and without covariates. The top 13 models without covariates (7 Z structures  $\times$  2  $u$  structures) are shown in the online Supplementary data, Table S1<sup>1</sup>. The best-supported model (lowest  $AIC_c$ ) included separate trajectories (six process states) for each species and in each depth zone,

suggesting that in each depth zone the abundance trajectories of each species behaved independently (albeit with some covariance). However, all populations had the same population growth rate with the best-fit model having one stock growth rate ( $u = 0.067 \pm 0.04$ ) across species and depth zones. Other models received substantially less data support with the next best model having a  $\Delta AIC_c$  greater than 6.0.

The best-fit model with covariates had the same population structure as above with separate species  $\times$  depth trajectories and a single  $u$  ( $u = 0.058 \pm 0.029$ , Fig. 4, Table S2<sup>1</sup>). In fact, all 15 top models included different trajectories for each depth zone and each species, which supports the results from the models without covariates. The best-fit model included a positive correlation between catch and redfish abundance ( $c_{\text{catch}} = 0.17$ ) and strong primarily positive covariance among the time series, especially within depths (Table 1). Its  $AIC_c$  (387.2) was over five  $AIC_c$  points lower than the best-fit model with no covariates ( $AIC_c = 392.1$ ), indicating that commercial catch was an important predictor. While the best-fit model included separate trajectories by species and depth, there was strong covariance among these trajectories in most cases (Table 1). The  $AIC_c$  for the second-place model was 1.8  $AIC_c$  points higher ( $AIC_c = 389$ ). The only difference was that the catch covariate had different effect in each depth ( $c_{\text{catchShallow}} = 0.142$ ;  $c_{\text{catchMid}} = 0.203$ ). We selected Model 1 as best model since it had fewer parameters. There was some evidence that shrimp abundance (prey) was also important. The third-ranked model included catch and shrimp, but its  $AIC_c$  was 2.3 points higher than the best-fit model with catch.

In the shallow depth zone, the trajectories of all three species were very similar (Fig. 4). Abundance increased until 2006 and then decreased with some fluctuation. In the mid zone, trajectories of the three species were also similar, but the variation in

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0435>.

**Table 1.** Model results for the best model, Model 1.

Species	Zone	Observational variance (R)	Process variance (Q diagonal)	Growth rate ( $\mu$ )	Catch	A Cornide	A Vizconde
S.f.	Shallow	0.000	1.220	0.058±0.029	0.170	0	-0.407
S.m.	Shallow	0.022	4.560			0	2.472
S.n.	Shallow	0.213	0.672			0	1.982
S.f.	Mid	0.013	0.573			0	-0.554
S.m.	Mid	0.261	0.025			0	-0.035
S.n.	Mid	0.244	0.251			0	1.960
		Covariance (Q off-diagonal)					
S.m. × S.f.	Shallow	1.554					
S.n. × S.f.	Shallow	0.807					
S.n. × S.m.	Shallow	1.217					
S.f. × S.f.	Shallow × mid	0.305					
S.m. × S.f.	Shallow × mid	-0.655					
S.n. × S.f.	Shallow × mid	0.164					
S.n. × S.m.	Shallow × mid	-0.010					
S.m. × S.f.	Mid × shallow	0.007					
S.m. × S.m.	Mid × shallow	-0.180					
S.n. × S.d.	Mid × shallow	-0.479					
S.n. × S.f.	Mid × shallow	0.083					
S.n. × S.n.	Mid × shallow	0.132					
S.m. × S.f.	Mid	0.051					
S.n. × S.f.	Mid	0.291					
S.n. × S.m.	Mid	0.042					

**Note:** One  $\mu$ , 6 state processes. Covariate: catch (commercial catches of redfish). S.f. (*Sebastes fasciatus*), S.m. (*Sebastes mentella*), S.n. (*Sebastes norvegicus*). Zones: Shallow (129–250 m) and Mid (251–600 m). Vessel: R/V Cornide de Saavedra and R/V Vizconde de Eza. **R** = Observational variance for observation error; **Q** diagonal = process variance (on the diagonal of the matrix);  $\mu$  = growth rate; **Q** off-diagonal = process covariance (on the off-diagonals of the matrix); A = scaling term for each observation time series.

abundance was less extreme. In fact, the trajectories for the three species in the mid zone showed little process variance.

### Two-period analysis

When we estimated different stock growth rates for the two different regulatory periods (1993–2007 and 2008–2015), the best-fit model was similar in structure to the best-fit model from the single-period analysis. It included different trajectories for each species in each depth zone but only one stock growth rate for all trajectories within a time period. Redfish showed positive population growth from 1993–2007 ( $\mu_{1993-2007} = 0.093 \pm 0.072$ ) but then declined strongly ( $\mu_{2008-2015} = -0.089 \pm 0.095$ ; Table S3<sup>1</sup>). Finally we included covariates in the two-period analysis. We ran 356 models that included all different combinations with and without covariates (Table S4<sup>1</sup>, top 15 models). The best-fit model included commercial catch, which was positively correlated with redfish abundance (catch = 0.176). Again, this model included trajectories for each species in each depth zone and positive population growth during the early period ( $\mu = 0.111 \pm 0.051$ ) but negative population growth ( $\mu = -0.176 \pm 0.078$ ) following cod recovery (Table 2). As with the single-period analysis, the model including catch fit better than the same model without catch ( $\Delta AIC_c = 6.6$ ).

### Discussion

Understanding population structure is important for conservation and management. While the three redfish are obviously separate species and populations, we can ask whether their abundance trends are similar enough to be treated as a single complex and (or) stock for assessment purposes, or whether they should be treated separately (Tolimieri et al. 2017). MARSS models allow us to combine multiple data sets while testing hypotheses regarding spatial structure and biotic and abiotic drivers in a formal statistical context (Tolimieri et al. 2017). Here we used MARSS to analyze the stock structure of three species of *Sebastes* spp. by combining data from two different vessels in two different periods. We tested multiple population structures to examine if

there is sufficient support combining the three species into a single complex for stock assessment, or whether there is data support for analyzing them separately.

Our results suggest that it is likely acceptable to treat the three species as a single multispecies complex for stock assessment. While the three species show independent abundance trajectories both among species and within species but between depth zones, these trajectories show substantial positive covariance, especially within depth zones, and share a single long-term population growth rate. Thus, although they are somewhat independent, the species tend to fluctuate in unison, suggesting similar responses to the effects of climate variation and fishing effort. This result makes sense given the strong ecological similarity among the three redfishes. Furthermore, the short length of the time series and strong covariance suggests that failure to combine the three species into a single time series may be the result of insufficient replication (Tolimieri et al. 2017). Additionally, the three species are largely sympatric with *S. fasciatus* and *S. mentella* inhabiting the same depth zones, although *S. mentella* is found in somewhat deeper waters. This distribution, combined with the commercial fisheries not distinguishing among the species, indicates that the three species likely experience similar fishing effort. Nevertheless, given that they are three distinct species, precautionary management should periodically re-evaluate the decision to manage the species as a single complex, and weak-stock management may be appropriate, especially at low population density.

Since the late 1980s, there has been some consensus amongst ecologists that management decisions are best guided by models that are grounded in ecological theory (Cuddington et al. 2013). We built models based on ecological assumptions and the available data. For example, in this analysis we assumed covariance between the three populations of *Sebastes* spp. We could have forced the populations to be independent (no covariance in the **Q** matrix), but since ocean conditions are correlated across large spatial scales and the species have similar biology, we forced the model to include covariance among abundance trends. All the top

**Table 2.** Model results for the best model, Model 29.

Species	Zone	Observational variance (R)	Process variance (Q diagonal)	Growth rate ( $\mu$ )	Catch	A Cornide	A Vizconde
S.f.	Shallow	0.001	1.122	Period 1993–2007	0.111±0.051	0.176	0
S.m.	Shallow	0.028	0.661				0
S.n.	Shallow	0.213	0.015				0
S.f.	Mid	0.015	0.541	Period 2008–2015	−0.073±0.078		0
S.m.	Mid	0.231	4.529				0
S.n.	Mid	0.232	0.223				0
		Covariance (Q off-diagonal)					
S.m. × S.f.	Shallow	1.486					
S.n. × S.f.	Shallow	0.756					
S.n. × S.m.	Shallow	1.200					
S.f. × S.f.	Shallow × mid	0.238					
S.m. × S.f.	Shallow × mid	−0.695					
S.n. × S.f.	Shallow × mid	0.132					
S.n. × S.m.	Shallow × mid	−0.054					
S.m. × S.f.	Mid × shallow	−0.070					
S.m. × S.m.	Mid × shallow	−0.250					
S.n. × S.d.	Mid × shallow	−0.432					
S.n. × S.f.	Mid × shallow	0.001					
S.n. × S.n.	Mid × shallow	0.086					
S.m. × S.f.	Mid	0.044					
S.n. × S.f.	Mid	0.250					
S.n. × S.m.	Mid	0.037					

**Note:** One  $\mu$ , 6 state processes. Covariate: commercial catches of redfish. Species: S.f. (*Sebastes fasciatus*), S.m. (*Sebastes mentella*), S.n. (*Sebastes norvegicus*). Zones: Shallow (129–250 m) and Mid (251–600 m). Vessel: R/V *Cornide de Saavedra* and R/V *Vizconde de Eza*. **R** = observational variance for observation error; **Q** diagonal = process variance (on the diagonal of the matrix);  $\mu$  = growth rate; **Q** off-diagonal = process covariance (on the off-diagonals of the matrix); **A** = scaling term for each observation time series.

models had the same structure with separate states for each species in each depth zone. However, there was strong covariance and a single population growth rate for all six states — either one for the whole time period or one within each time period for the two-period model.

Nogueira et al. (2017) found three depth assemblages in Flemish Cap waters, two of which (shallow and mid) we included in the analyses here. Depth is likely a proxy for other parameters like temperature, productivity, or oxygen levels (Tolimieri and Levin 2006), and it can be seen as a niche axis on which species occurrence is dependent (Heyns et al. 2016). We found separate but covarying abundance trajectories of the three species with depth (6Z). Differences between subpopulations could occur because of difference in size, recruitment, prey–predator relations, or different fishing effort in the two different zones. Interestingly, *S. mentella* showed negative covariance between shallow and mid-depth trajectories (Table 2). One potential explanation is that as fish move deeper with age, decreases in the shallow zone would be mirrored by increases in biomass in the mid-depth zone (Avila de Melo et al. 2015). Similarly, recruitment to the shallow zone would not necessarily result in immediate increase in abundance in the mid-depth zone.

In both the single-period and the two-period analyses, we found that one population growth rate (or one within time period) was sufficient to describe trends in the six trajectories. Thus, while the six trajectories may fluctuate somewhat independently from year to year (albeit with strong covariance), they follow the same increasing or decreasing trend over longer periods. Both *S. fasciatus* and *S. norvegicus* showed much more variable trajectories in the shallow zone versus the mid-depth zone as indicated by a comparison of the process variances for these species in each depth (Tables 1 and 2). Process variance measures the real variation in abundance due to processes like variable recruitment. Thus recruitment of these species to the shallow zone likely causes this increased process variance, while adult abundances in the mid-depth zone were more stable (Nogueira et al. 2017). *Sebastes mentella*

had similar process variance in the shallow and mid-depth zones, perhaps due to less variable recruitment. During the studied period, two important recruitment events above the mean have been documented, first at the beginning of the study period (1993–1994) and during a long period from 1999 to 2007 (Avila de Melo et al. 2015).

The models with highest data support in both the one-period and the two-period analyses included commercial catch, which was positively correlated with the abundance of redfish. This suggests that the increase of the stock size exceeds the catch, which is in line with the last advice from NAFO Scientific Council for this stock, which affirmed that the stock is above its historical level (NAFO 2015). One might expect the inverse relationship that catch would cause biomass to decline, but if the biomass dynamic exceeds the catch, the population will grow (Punt and Hilborn 1996). However, this relationship may simply mean that higher catches are both possible and allowed by management at higher biomass. In this case, catches would not affect the biomass (within years) but instead follow biomass from year to year even though the long-term effects might cause a decline due to fishing mortality.

We might expect a stronger relationship between redfish abundance and cod and shrimp via direct food-web dynamics. However these terms were not included in the best-fit models. Cod predation has been described as the main source of small redfish mortality (Lilly 1980; Perez-Rodriguez and Saborido-Rey 2012), and small redfish are prey of cod in years with successful redfish recruitment events (NAFO 2015). The lack of a relationship with cod may be the result of ignoring redfish size or age (e.g., length) in our analysis. A more detailed analysis focusing on smaller individuals (cod prey) might show a relationship. Pérez-Rodríguez et al. (2017) suggested that redfish predation on shrimp was the main driver in the decline of shrimp stock. It would be interesting to investigate models with different cohorts, but that is beyond the scope of the present paper. An alternate way to investigate the effects of cod and shrimp on redfish biomass would be to replace  $x_{t-1}$  in eq. 1 with  $Bx_{t-1}$  where the matrix **B** includes terms for density



dependence on the diagonal and species interactions on the off-diagonals (Hampton et al. 2013; Ives et al. 2003b). However, doing so requires the assumption that the community is stationary (fluctuating around equilibrium), which in a MARSS model means setting  $\mathbf{u} = 0$ , since one cannot estimate both  $\mathbf{B}$  and  $\mathbf{u}$  at the same time (Holmes et al. 2012, 2014b). We did investigate this route, but models clearly violated the stationarity assumption.

Many studies show that species respond to variability in the environment. On the Flemish Cap, cold periods were registered in the early to mid-1980s and early 1990s (Colbourne et al. 1997; Drinkwater 1996) followed by a warmer period starting in the late 1990s (Pérez-Rodríguez et al. 2012), where shrimp and cod had responded in the opposite direction to those changes. During the studied time period, the population size of redfish was not affected by changes in the NAO, probably because we analyzed adult populations, which would be less responsive to annual variation in climate conditions given that rockfishes are long-lived. It might be interesting to conduct a similar analysis using only data on recruits, but such data are not readily available since the survey does not effectively distinguish among recruits of the three species and because modeled recruitments by species from stock assessments are not available (two of the species are managed together).

A MARSS approach does not tell us what biological mechanisms or environmental factors cause the observed population structure, but the patterns of synchrony and correlation can help us infer which mechanisms and factors are likely important (Ward et al. 2010). We expected more correlation with other covariates, but the best-fit model only included catch. This result does not mean that other covariates do not affect the size of the population, only that they do not improve the fit of the model. If we look at other models that include cod, shrimp, or the NAO index, we observed correlation (parameters are different from 0), but these models had significantly poorer fits to the data than our best-fit models including only catch. It is important to realize that any modeling approach is a best-fit solution, not a perfect-fit solution (Stringham et al. 2003).

One advantage of MARSS is that it can combine different time series from different vessels and gear through the scaling parameter  $\alpha$ . The choice to combine time series via the  $\alpha$  parameter should be made with some care, however. Doing so requires the assumption that the multiple time series track the same underlying population process (Tolimieri et al. 2017). For example, here, we forced the model to combine the time series from the two vessels, which assumes that the two vessels differ primarily in the total abundance of the fish but do not sample radically different size classes of fish. The latter might cause the actual trends to differ since a smaller mesh size, for example, might better track trends in small fish, while larger mesh size would likely track trends in larger fish more closely. If the two vessels track the same population process, the  $\alpha$  parameter then acts as an estimate of the difference in catchability between the two surveys. While we did not do so, it is certainly possible to use model selection to determine whether combining the time series is reasonable — especially where time series overlap temporally (Tolimieri et al. 2017).

Two different ways of calibrating data from the two different surveys have been presented in the Scientific Council of NAFO (González-Troncoso and Casas 2005; Pérez-Rodríguez and Koen-Alonso 2010). The Scientific Council of NAFO (NAFO SC) accepted in 2005 the conversion factors calculated by González-Troncoso and Casas (2005). Alternative conversion factors between the two vessels on Flemish Cap were presented by Pérez-Rodríguez and Koen-Alonso (2010) in the Scientific Council of NAFO. The results of this study were different from previous studies in that there was no length effect for most fish species and the difference in the two vessels was generally greater. NAFO SC concluded that the results of this study point to a need to further investigate the conversion factors

for species in the EU Flemish Cap survey (NAFO SC Report 2010). Nevertheless, a comparison between both ways of calibration has never been performed mainly because of lack of time, and all stock assessments since 2005 until now (Alpoim et al. 2014; Avila de Melo et al. 2015; Casas 2014; González-Costas 2013; Healey 2011) have used the calibration of González-Troncoso and Casas (2005). MARSS could be useful tool to do a comparison between the two methods.

In conclusion, we used MARSS models to evaluate data support for different stock structures for redfish (*Sebastes* spp.) in the waters of the Flemish Cap. While the best-fit model included six different state processes (trends in abundance), one per species and in each different depth, all six states were best modeled with one combined stock growth rate (or one in each period for the two-period analysis). Thus, abundance for each species in each depth varied somewhat independently due their being separate species and having different size distributions with depth. However the unified stock growth rate supports treating the three species as a “complex” for management purposes. Nevertheless, further work could be done (i.e., analysis with different cohorts and the inclusion of recruitment data).

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