SPATIAL DISTRIBUTION, SPAWNING STOCK BIOMASS AND THE DEVELOPMENT OF SPATIAL REFERENCE POINTS

by

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For Jan Willem. My soulmate.

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ABSTRACT

The frequently observed positive relationship between fish population abundance and spatial distribution suggests that changes in spatial distribution can be indicative of trends in abundance. If changes in spatial distribution are significantly related to changes in spawning stock biomass (SSB), spatial distribution metrics (SDMs) can potentially serve as a proxy for changes in biomass. If changes are disproportional and SDMs can be indicative of rapid declines or increases in SSB per unit SDM, spatial reference points might complement SSB reference points. This applies especially in cases where changes in the SDM precede declines in SSB. Here, I examine the relationship between SSB and three SDMs: range, concentration, and density, using fisheries independent survey data for 10 demersal Northwest Atlantic populations (9 species). The results show that metrics of density, rather than range or concentration, offer the best correlate of spawner biomass. In addition, a decline in high density areas (HDAs) beyond a certain threshold is associated with disproportionately large SSB declines in 6 of 10 populations examined. According to density dependent habitat selection theory, HDAs might be indicative of highly productive areas. HDAs are also considered to have positive fitness consequences, enhancing the ability of individuals to locate prey, successfully spawn and evade predators. In the case of Eastern and Western Scotian Shelf Atlantic cod (*Gadus morhua*) HDA declines precede rapid SSB declines. Within the SSB-HDA relationships, there exist spatial thresholds. These are the points above which HDA declines faster per unit of SSB decline and below which SSB declines faster per unit of HDA decline. Spatial thresholds are generally situated between 0.2 and 0.3 HDA, indicating that when 70% to 80% of a stock's (maximum recorded) HDAs are lost, their relative importance increases and large SSB declines are likely to occur with further HDA decline. If stocks are above their spatial thresholds and at HDA levels associated with a healthy SSB, this would serve to enhance their recovery and reduce the probability of their collapse. For some stocks, the spatial threshold is positioned at levels of SSB and HDA significantly higher than those associated with overexploitation (0.5 SSB_{MSY}). Under these circumstances, waiting to take measures until 0.5 SSB_{MSY} is reached would mean accepting the risk of surpassing the spatial threshold. Development of an empirically derived spatial distribution indicator such as HDA could help indicate the status of a population's spatial structure and complement the use of SSB reference points as part of the precautionary approach to fisheries management.

LIST OF ABBREVIATIONS USED

AO	Area occupied
D90%	Minimum area containing 90% of the survey biomass
DDHS	Density-dependent habitat selection
DFO	Department of Fisheries and Oceans, Canada
ESS	Eastern Scotian Shelf
F	Fishing mortality
HDA	High density areas
HDA_T	HDA threshold
LDA	Low density areas
LRP	Limit reference point
MDA	Medium density areas
MSY	Maximum sustainable yield
NAFO	Northwest Atlantic Fisheries Organization
SSB	Spawning stock biomass
SDM	Spatial distribution metric
SSN	Spawning stock number
TRP	Target reference point
WSS	Western Scotian Shelf
ZDA	Zero density areas

ACKNOWLEDGEMENTS

CHAPTER 1   Introduction

A central theme in ecology is the study of the abundance and spatial distribution of organisms (Gaston 2003). Variation in spatial distribution can affect migration, reproduction and survival and consequently population abundance, resilience and persistence (Hsieh et al. 2010, Ciannelli et al. 2013). Positive relationships between the abundance of species and their spatial distribution have been documented for a wide range of terrestrial (Brown 1984) and marine species (MacCall 1990, Swain and Sinclair 1994, Fisher and Frank 2004). These positive abundance-spatial distribution relationships are considered one of the more pervasive macro-ecological phenomena (Gaston and Blackburn 1999, Gotelli 2008) and they suggest that changes in distribution can be indicative of trends in population abundance.

Knowledge about the trends of species abundance across space is needed to understand how human activities, such as fisheries, might adversely affect population spatial structure and population abundance (Hutchings 1996, Hsieh et al. 2010) and ultimately species persistence (Gaston 2003). The importance of considering spatial structure is increasingly recognized (Cadrin and Secor 2009, Guan et al. 2013), but not yet reflected by spawning stock biomass (SSB), the metric most often used in fish stock assessment and fisheries management to reflect population abundance (it reflects reproductive biomass) (Berkeley et al. 2004; Hsieh et al. 2010). Furthermore, spatial structures are not yet incorporated in biomass reference points currently used in fisheries management. For the purpose of conservation and resource management, it can be deemed important to have a comprehensive understanding of marine fish populations across space to ensure persistence throughout their geographic range (Berkeley et al. 2004).

The objective of this thesis is to address the following over-arching question: Is there value in creating spatial reference points that would complement currently used biomass reference points?

1.1   Thesis Structure

In Chapter 2, I discuss the theories about mechanisms underlying the relationship between biomass and spatial distribution. I then test for the presence of a relationship between four spatial distribution metrics (SDMs) and SSB, using fishery independent survey data. These four metrics reflect various aspects of the distribution characteristics of fish populations, including range, concentration and density. The SDM-SSB relationship is assessed for ten fish stocks on the Scotian Shelf, eastern Canada. The aim is to determine the potential utility of spatial reference points, for which I will assess whether any of these SDMs can be considered an indicator of turning-points in SSB, i.e. a threshold point indicating rapid change in the non-linear relationship between the SDM and SSB. A time series analysis is applied to those SDMs that have a non-linear relationship with SSB to determine whether the SDM precedes rapid changes in SSB in time.

Based on the results of the previous chapter, in Chapter 3 I focus on the SDM that exhibited the greatest potential, and that can be considered an indicator for a turning point in the SDM-SSB relationships, and assess where the threshold is positioned relative to existing biomass reference points. I discuss scenarios in which a spatial reference point could serve fisheries management in a manner complementary to existing biomass reference points.

CHAPTER 2   Spatial distribution and marine fish spawning stock biomass

2.1   Introduction

Fisheries managers establish abundance boundaries for commercially exploited fishes to ensure the maintenance of healthy and productive populations and enable the recovery of depleted populations. Scientists will often estimate the biomass of the reproductive part of fish populations or SSB as a measure of abundance, and recommend target and limit reference points (indicator benchmarks) for fisheries based on expected outcomes for SSB (Caddy and Mahon 1995). To date, however, many overfished populations have not rebuilt at forecasted rates (FAO 2012, Neubauer et al. 2013).

Total biomass is merely one aspect of the viability of a population and poor viability can be indicated by atypical spatial distributions (Cotter et al. 2009b). The spatial structure of fish populations is potentially equally as important in maintaining long-term sustainable fish populations as SSB, however spatial indicators are not typically used by fisheries management (Caddy and Agnew 2004, Berkeley et al. 2004). The absence of information about spatial structures in fisheries management can increase the probability of overexploitation (Ying et al. 2011). Hence, indicators that incorporate spatial distribution information have considerable potential for strengthening management and recovery plans (Caddy and Agnew 2004). The potential of spatial distribution indicators to signal changes in biomass has been recognized (Hutchings 1996) and efforts towards integrating spatial distribution indicators in assessment methods have been made (Cotter et al. 2009b, Woillez et al. 2009, Simmonds 2010). However, neither a comparative assessment of the functionality of various spatial distribution methods as indicators for SSB in groundfish fisheries management, nor an assessment of the potential utility and development of fisheries management reference points based on spatial criteria has been undertaken.

There is potential for the development of spatial distribution indices, based on the positive relationship between the abundance of populations and their spatial distribution, a pervasive macro-ecological pattern across a wide range of terrestrial (Brown 1984, Gaston and Blackburn 1999) and marine species (MacCall 1990, Swain and Sinclair 1994, Fisher and Frank 2004). Both density dependent and density independent factors

limit the spatial distribution of populations and species by altering living conditions and influencing survival, reproduction, vital rates and abundance (Gaston 2003, Shepherd and Litvak 2004). Consequently, positive abundance-spatial distribution relations have been explained by abundance-environment relationships (Perry and Smith 1994), abundance-occupancy relationships (Fisher and Frank 2004), as well as a combination of the two (Ciannelli et al. 2012).

In this thesis, the abundance-occupancy and density patterns across space are examined, which have been explained predominantly by meta-population (Levins 1970, Kritzer and Sale 2004) and density-dependent habitat selection (DDHS) theory (Fretwell and Lucas 1969, Myers and Stokes 1989). According to the former, a meta-population is partitioned into several interacting but spatially separated subpopulations that occupy distinct areas or patches (Levins 1970). Migration between patches decreases the probability of local extinction, thus serving as a 'rescue effect' for meta-populations of conservation concern (Brown and Kodric-Brown 1977). The rate of immigration per patch increases as the proportion of patches that are occupied increases, and this can generate a positive relationship between local abundance and the number of occupied patches (Gaston 2003). Ideal free distribution theory suggests that individuals are capable of choosing the most suitable habitat and are free to occupy that habitat, resulting in a population distribution that reflects available resources (Fretwell and Lucas 1969). Based on the ideal free distribution, DDHS accounts for a positive abundance - spatial distribution relationship resulting from the dispersal of individuals or populations into suboptimal habitats with increases in abundance. This association occurs because, at low abundance, individuals or populations occupy mainly optimal habitat. As abundance increases, competition for resources increases, eventually leading to a decrease in habitat suitability and in turn resulting in the spread of individuals or populations into suboptimal habitat (Fretwell and Lucas 1969, Myers and Stokes 1989).

A relationship between abundance and spatial distribution implies that changes in spatial distribution may impact population abundance and eventually persistence (Hsieh et al. 2010). The relationship between range size and extinction risk is generally negative and non-linear, with species of small ranges experiencing disproportionally higher rates of extinction than those with intermediate range sizes (McKinney 1997, Gaston 2003). A

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decline in population range size can decrease gene flow and dispersal to other populations, which may lead to a reduction of population abundance and increase the probability of population and meta-population extinction (Lawton 1993, Wilson et al. 2004). According to DDHS theory, a population at low abundance that contracts to a smaller, potentially more optimal habitat, might be more sensitive to environmental (Hanski 1992), demographic and genetic stochasticity (Lande 1993), as well as overexploitation. Fishing in an area of high density can cause local depletion when recolonization rates are low relative to the intensity of fishing (Shackell et al. 2005). Fisheries have caused contractions in fish spatial distribution (Garrison and Link 2000, Fisher and Frank 2004) and can reduce the spatial heterogeneity of populations, an important component of their bet-hedging or risk-spreading strategies to withstand environmental variability. For example, fishes exhibit spatial variation in reproduction traits (Hsieh et al. 2010) and it may be that only a small fraction of spawners, that spawns at the appropriate time and place – which can vary annually - successfully contributes to each new cohort (Larson and Julian 1999). Given that, a reduction in (density across) spatial distribution has considerable potential to reduce recruitment and abundance, and to increase population variability.

The impacts of fisheries on spatial distribution and persistence of fish populations are not well known, and potential impacts might not always be well-reflected by population abundance data (Berkeley et al. 2004, Hsieh et al. 2010). Thus, for the purpose of conservation and resource management, it can be deemed important to have a comprehensive understanding of marine fish populations across space to ensure persistence throughout their geographic range (Berkeley et al. 2004).

The relationship between abundance in terms of the number of individuals and spatial distribution has been studied for several fish species, but not yet between spatial distribution and SSB; a primary indicator of the reproductive potential of fish populations (Jakobsen et al. 2009). Spawning biomass is generally considered a better indicator of the spawning potential than spawning number, because SSB is more closely related to larger, older fish, that are more successful at spawning, whereas spawning stock number is more closely related to the high number of younger age classes; considered less successful reproducers (Cotter et al. 2009a).

Here, the shapes of the relationships between spatial distribution indicators and SSB are examined and compared. The relationship is described between SSB and three key characteristics of spatial distribution that reflect different aspects of the distribution characteristics of fish populations: range, concentration, and density (Zwanenburg et al. 2002). Specifically, I examine: (i) Area occupied (AO) to measure changes in range (Ricard 2012); (ii) D90% or the proportion of total survey area, occupied by the top 90th percentage of the total population (Swain and Sinclair 1994); (iii) Gini Index or evenness of the spread of biomass across an area to measure changes in concentration (Myers and Cadigan 1995, Ricard 2012); and (iv) Density Area or the proportion of tows consisting of high, medium and low biomass across the surveyed area to measure changes in density (Hutchings 1996). This list is by no means exhaustive, and many other indicators are available describing similar and other aspects of spatial distribution (Woillez et al. 2009). This is intended as a first exploratory analysis, and AO, D90%, Gini Index and Density Area are selected, because they incorporate different pieces of information from the survey data regarding the spatial distribution of fish. The primary objective is to determine if any of these spatial distribution metrics (SDMs) can be considered a reliable indicator for rapid changes or turning points in SSB. For the SDMs that can be considered a reliable indicator for disproportionately large SSB changes, a time series analysis is applied to detect whether these SDMs can also be considered predictive indicators that precede rapid changes in SSB in time. These analyses are needed to explore the potential utility and development of fisheries management reference points based on spatial criteria.

2.2   Methods

We analyzed annual survey data of the fishery independent groundfish trawl survey of the Scotian Shelf and Bay of Fundy in Northwest Atlantic Fisheries Organization (NAFO) areas 4V, 4W, 4X, 5Y, 5Z (Figure 2.1).
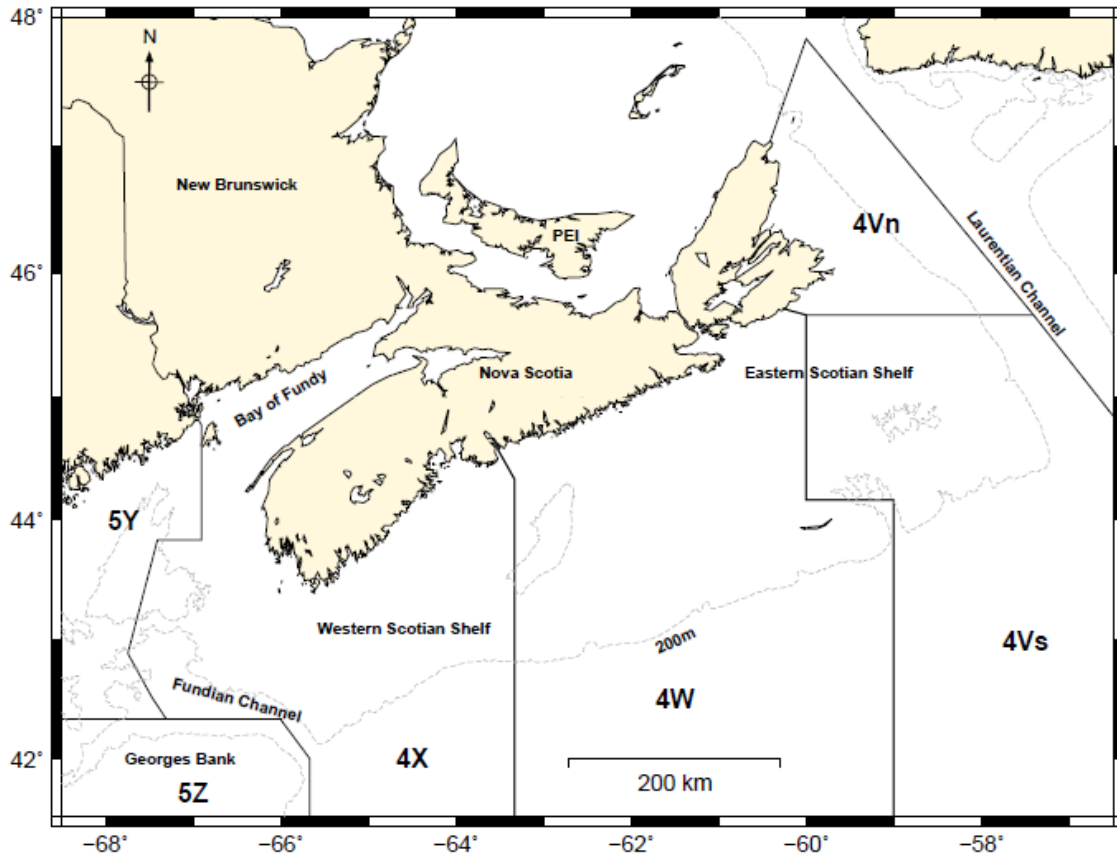
Figure 2.1 NAFO Subdivisions (Ricard and Reuchlin-Hugenholtz 2013).

The Department of Fisheries and Oceans (DFO) has conducted these annual surveys since 1970. The survey follows a standardized random sampling protocol and tows follow a random sampling design within areas stratified by depth. This design enables the collection of unbiased estimates of population abundance through time (Doubleday 1981). The number of sets or hauls that are taken every year (within one month), is in the hundreds and differences in the survey from one year to another are considered minimal, since spatial coverage is constant. It is assumed that the stock area associated with each stock encompasses a meta-population or a series of related populations and minimal immigration or emigration is assumed. The spatial distribution for each SDM is calculated within the same NAFO area for which the abundance metric, i.e. SSB from DFO stock assessments has been estimated, and SDMs are corrected for differences in stratum area.

The examined species include American plaice (*Hippoglossoides platessoides*), cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), halibut (*Hippoglossus hippoglossus*), pollock (*Pollachius virens*), redfish (*Sebastes spp.*), silver hake (*Merluccius bilinearis*), white hake (*Urophycis tenuis*) and winter flounder (*Pseudopleuronectes americanus*). These species have experienced large changes in SSB, increasing the likelihood that a relationship between SSB and the SDM will be detected. In table 2.1 the examined stocks are listed, along with their locations, years included in the analyses, and magnitude of SSB decline.

Table 2.1 Information regarding examined stocks. NAFO survey divisions on the Scotian Shelf, SSB and SDM years included in the analyses and maximum percentage of decline compared to maximum value of SSB recorded in the respective time series.

Species	Name used	NAFO division	Years included	Maximum decline SSB
Hippoglossoides platessoides	American plaice	4VWX	1970-2009	64.0%
Gadus morhua	WSS cod[i]	4X	1980-2008	88.0%
Gadus morhua	ESS cod[ii]	4VsW	1970-2011	97.2%
Melanogrammus aeglefinus	Haddock	4X5Y	1970-2008	69.0%
Hippoglossus hippoglossus	Halibut	4VWX	1970-2009	77.1%
Pollachius virens	Pollock	4Xopqrs+5Yb+5Zc	1982-2008	88.5%
Sebastes spp.	Redfish	4X+4Wdehkl (Unit 3)	1970-2012	93.0%
Merluccius bilinearis	Silver hake	4VWX	1993-2012	94.2%
Urophycis tenuis	White hake	4X	1970-2011	94.3%
Pseudopleuronectes americanus	Winter flounder	4X	1970-2011	99.4%

[i]WSS=Western Scotian Shelf, [ii]ESS=Eastern Scotian Shelf.

Given that SSB data are not available for winter flounder, Spawning Stock Number (SSN) is used, which can be considered proportional to SSB (Mark Fowler, Bedford Institute of Oceanography, Dept. Fisheries & Oceans, Mark.Fowler@dfo-mpo.gc.ca, personal communication).

The first SDM is AO, a measure of range. This is a presence and absence measure of the amount of area that is occupied. The proportion of area occupied in survey year k, by stock n, is calculated as the sum over all strata of the proportions of tows with catch c in each stratum s, and multiplied by the area A of the respective stratum. This, in turn, is divided over the total area to calculate the proportion of area occupied $AO_{k,n}$:

$$(1) \quad AO_{k,n} = \frac{\sum_{s=1}^{S_k} \frac{t^C_{k,n,s}}{t_{k,n,s}} A_{k,s}}{\sum A_s}$$

where $t^C_{k,n,s}$ is the number of tows with catch (in biomass) per year, per stock, per stratum; $t_{k,n,s}$ is the total number of tows per year, per stock, per stratum; $A_{k,s}$ is the surface area per year per stratum; $\sum A_s$ is the total area (Ricard 2012).

The second SDM is a metric of concentration. The minimum area containing 90% of the survey biomass (D90%) as a proportion of the total area, is calculated from information on the mean stratum-weighted biomass ($\overline{WB}$), which is calculated by taking the mean biomass ($\bar{B}$) in survey year (k), per stock (n), per stratum (s), weighted by the proportion of surface area (A) in survey year (k), per stratum (s) and dividing that by its sum:

$$(2) \quad \overline{WB}_{k,n,s} = \frac{\bar{B}_{k,n,s} * \frac{A_{k,s}}{\sum_{s=1}^{S_k} A_{k,s}}}{\sum \left(\bar{B}_{k,n,s} * \frac{A_{k,s}}{\sum_{s=1}^{S_k} A_{k,s}} \right)}$$

This yields $\overline{WB}_{k,n,s}$, the weighted proportion of mean biomass per stock, per year, per stratum. These $\overline{WB}_{k,n,s}$ values are ordered from the highest $\overline{WB}_{k,n,s}$ (highest biomass across area) to the lowest, until the cumulative sum of $\overline{WB}_{k,n,s}$ equals 0.9. Then, the cumulative sum of the associated proportion of surface area is identified, and this number represents the proportion of area needed to capture 90% of the population biomass, referred to as D90%.

The third SDM is the Gini index, also a metric of concentration, but one that measures how evenly biomass is spread across an area. The Gini index is bounded by 0 and 1 and captures the deviation from the equal distribution (Gini=0) of the cumulative sum of $\overline{WB}_{k,n,s}$ versus the cumulative sum of associated proportion of surface area. The greater the Gini index value, the less evenly the spatial distribution of biomass and the greater the degree to which that biomass is spatially concentrated. To calculate the Gini coefficient $\overline{WB}_{k,n,s}$ is ordered by increasing values and the cumulative proportion of the survey biomass is calculated. The Gini index per year (k), per species (n) is estimated by:

$$(3) \quad Gini_{k,n} = 1 - 2 \int_0^1 L_x dx \quad ,$$

or the area between the 1:1, or 45 degree-line (equal distribution of the biomass across area) and the Lorenz curve L_x, which is the curve of cumulative proportion of biomass versus the cumulative proportion of area multiplied by 2. Thus, the Gini index also incorporates zero biomass per stratum, which could indicate either a real absence or the wrongful inclusion of an area that does not belong to the species domain. Strata in the survey that never recorded an individual of the respective species in the respective stock area, across the full time series, are excluded (from all SDMs) to reduce the probability of wrongful inclusion.

The fourth SDM is a measure of density that follows a method that has been applied to northern Atlantic cod. Hutchings (1996) quantified temporal changes in cod densities by partitioning research survey data into low (0-100 kg), medium (100-500 kg), and high (>500 kg) biomass levels per tow, and subsequently calculated the proportion of tows falling within each category. Each tow samples approximately the same surface area of ocean bottom. The data on survey tow densities are partitioned into high, medium, and low density areas, based on quantiles of the overall biomass per tow across the entire time series for each stock, to allow for comparison among stocks. A large amount of survey tows contain no biomass, therefore the quantiles are calculated without zero density tows, and a fourth zero density area metric is added. Thus, the metric is comprised of four categories, with the proportion of tows falling in the following density area categories: $0 = Zero$, $0 < Low \leq 33.3\%$, $33.3\% < Medium \leq 66.7\%$ and $66.7\% < High \leq 100\%$.

Based on previous results for Newfoundland's northern cod (Hutchings 1996), I anticipate for the two cod stocks on the Scotian Shelf that as SSB declines, medium density areas (MDAs) might decrease, whereas low density areas (LDAs) and zero density areas (ZDAs) will increase. High density areas (HDAs) are expected to decline increasingly rapidly as SSB declines. Given this expectation that the relationship between SSB and HDAs will be sensitive to the level of tow density considered to be 'high', several HDA categories are explored, for which the quantile distribution of biomass per tow varies; taking the highest 33.3% of the biomass per tow quantile distribution (HDA 33), highest 15% (HDA 15), highest 10% (HDA 10), highest 5% (HDA 5), and highest 2.5% (HDA 2.5). When calculating D90%, Gini index, LDA, MDA and various

categories of HDA (HDA *x*), individual size limits to exclude pre-spawners are not applied, since information regarding size at maturity is not available for every species.

To determine whether changes in the SDM are related to SSB changes and whether these are proportional or not, the shape of the relationship between SSB and the SDM AO, D90%, Gini index, ZDA, LDA, MDA and HDA *x* is assessed, using a non-linear least squares regression model (Harley et al. 2001, Cotter et al. 2009b):

$$(4) \qquad SSB_{k,n} = b * SDM_{k,n}^{c} \qquad .$$

In case of a negative relationship between SSB and SDM, the SDM is inverted. This inversion allows the same model to be applied and allows for a comparison of the shape of the SDM-SSB relationship among stocks:

$$SSB_{k,n} = b * (1 - SDM_{k,n})^{c}.$$

Utilizing the model estimates, a t-test is applied to test whether parameter c is significantly different from 1. Exponent c determines the shape of the relationship: a type I (concave) relationship occurs when c < 1, a type II when c =1, and type III (convex) when c > 1 (Figure 2.2).
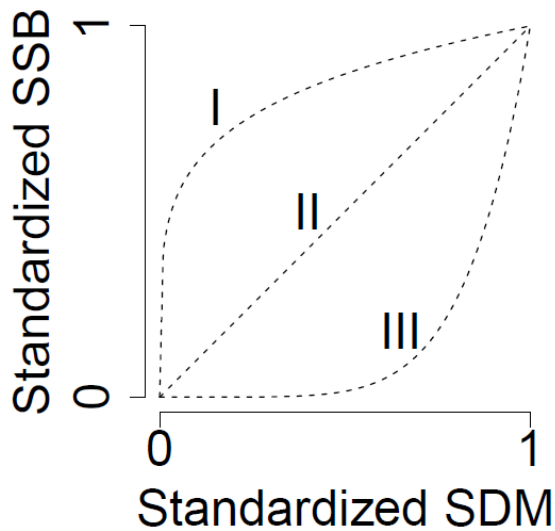

Figure 2.2   Hypothetical concave (type I), linear (type II) and convex (type III) SDM – SSB relationship. These relationships are generated from $SSB = b * SDM^{c}$. An exponent or c-value >1 will generate a convex relationship, whereas a c-value < 1 will generate a concave relationship. A c-value not significantly different will generate a linear relationship.

The SSB and the SDMs are standardized by scaling each metric by its maximum, to facilitate comparison of the regression analysis among SDMs and stocks:

$$(5) \quad Z_m = \frac{m}{m_{max}} \quad ,$$

where Z_m is the standardized value and m is SSB, AO, D90%, Gini index, ZDAs, LDAs, MDAs, HDA x, and where m_{max} is the maximum value of the respective metric. However, I will refer to standardized values such as Z_{AO}, Z_{SSB}, simply as AO and SSB in the text and figures. The same standardization model 5 is used for both the non-linear least squares regression model and the linear regression model 6.

$$(6) \quad SSB_{k,n} = a \pm b * SDM_{k,n}$$

In cases where both a significant linear and non-linear relationship is found, the model with the best fit based on Akaike's Information Criterion (AIC) is selected (Akaike 1974). Thus the linear model is selected, when c in the non-linear model (4) is not significantly different from 1 and/or when the linear model has the same or a lower AIC value, indicating a better fit.

It might be that in all three types of SDM-SSB relationships (concave or type I, linear or type II, convex or type III, see Figure 2.2), the SDM leads or lags linear or non-linear changes in SSB. If the SDM leads changes in SSB, this could be valuable information for fisheries management, because the SDM is then likely to reach a spatial value associated with a particular SSB (biomass) reference point, before SSB reaches that SSB reference point. However, a time series analysis will be limited to the non-linear relationships (type I and type III). Non-linear relationships are particularly of interest to assessing the added value of spatial reference points, because they might indicate that changes in the SDM precede accelerated changes in SSB. A cross-correlation function is therefore applied to the non-linear relationships (type I and type III) to test whether the SDM leads or lags SSB by lag h. The cross-covariance function $\gamma_{SDM,SSB}(h)$

$$(7) \quad \gamma_{SDM,SSB}(h) = cov\,(SDM_{t-h}, SSB_t) = E[(SDM_{t-h} - \mu_{SDM})(SSB_t - \mu_{SSB})],$$

is needed to apply the cross correlation function between the SDM and SSB, which yields $\varrho_{SDM,SSB}$; the cross correlation between the SDM and SSB time series.

$$(8) \quad \varrho_{SDM,SSB} = \frac{\gamma_{SDM,SSB}(h)}{\sqrt{\gamma_{SDM}(0)*\gamma_{SSB}(0)}}, \qquad \varepsilon \sim N(0,\sigma^2,I) \quad .$$

The peak in this cross correlation function defines the maximum correlation ϱ_{max} at lag h (Shumway and Stoffer 2006). A negative lag would indicate that the SDM leads changes in SSB, whereas a positive lag would indicate that SSB leads changes in the SDM. Before application of model 8, generalized least squares and linear regression models are used to transform and detrend the time series and to account for residuals that do not demonstrate approximate normal distributions, zero mean, constant variance, independence. The data analysis is performed in R (R Development Core Team, 2011).

2.3   Results

Many of the indices yielded significant associations between the SDM and SSB, as listed in Table 2.2. Populations showed considerable variability in terms of SSB sensitivity to different SDMs. For example, the SSB of haddock was spatially linked with only one index (AO). Alternatively, the SSB of WSS cod was significantly related to all four examined spatial distribution methods. There was a significant relationship between SSB and AO for four stocks. The relationship was linear for haddock but convex for winter flounder, ESS and WSS cod (Figure 2.3).

Table 2.2   Results of the SDM-SSB relationships for ten stocks on the Scotian Shelf. The relationships are defined as a linear model $SSB = a \pm b * SDM$ (listing NAs for c), or as a non-linear model $SSB = b * SDM^c$, where p(curve) represents the p-value for significant deviation of the exponent value from 1. * Symbolizes an inverted SDM, thus representing a negative relationship between the SDM and SSB.

| Species	SDM	b			c				Shape
		Value	S.E.	p-value	value	S.E.	p-value	p(curve)	
Cod (ESS)	AO	0.80	0.09	<0.001	2.49	0.53	<0.001	0.01	III
Cod (WSS)	AO	0.82	0.10	<0.001	2.62	0.64	<0.001	0.02	III
Haddock	AO	0.49	0.24	0.05	NA	NA	NA	NA	II
Winter flounder	AO	0.46	0.06	<0.001	1.81	0.40	<0.001	0.05	III
American plaice	D90%	1.00	0.33	<0.01	NA	NA	NA	NA	II*
Cod (WSS)	D90%	0.85	0.37	0.03	NA	NA	NA	NA	II
White hake	D90%	0.80	0.24	<0.01	NA	NA	NA	NA	II*
American plaice	Gini	0.92	0.37	0.02	NA	NA	NA	NA	II
Cod (WSS)	Gini	0.61	0.32	0.07	NA	NA	NA	NA	II*
Pollock	Gini	0.52	0.25	0.05	NA	NA	NA	NA	II
White hake	Gini	0.61	0.08	<0.001	2.06	0.57	<0.001	0.07	III
American plaice	HDA 33	0.78	0.13	<0.001	NA	NA	NA	NA	II
Cod (ESS)	HDA 33	0.84	0.09	<0.001	NA	NA	NA	NA	II
Cod (WSS)	HDA 33	0.82	0.10	<0.001	NA	NA	NA	NA	II
Halibut	HDA 33	0.35	0.14	0.02	NA	NA	NA	NA	II
Pollock	HDA 33	0.59	0.20	<0.01	NA	NA	NA	NA	II
Redfish	HDA 33	0.49	0.19	0.01	NA	NA	NA	NA	II
Silver hake	HDA 33	0.62	0.30	0.05	NA	NA	NA	NA	II
White hake	HDA 33	0.57	0.08	<0.001	0.64	0.21	<0.01	0.09	I
Winter flounder	HDA 33	0.47	0.06	<0.001	NA	NA	NA	NA	II
Cod (ESS)	MDA	0.91	0.24	<0.001	NA	NA	NA	NA	II
Cod (WSS)	MDA	0.71	0.29	0.02	NA	NA	NA	NA	II
Winter flounder	MDA	0.27	0.12	0.03	NA	NA	NA	NA	II
American plaice	LDA	0.98	0.18	<0.001	NA	NA	NA	NA	II*
Cod (ESS)	LDA	1.07	0.12	<0.001	7.31	1.18	<0.001	<0.001	III*
Cod (WSS)	LDA	0.79	0.08	<0.001	3.83	0.95	<0.001	0.01	III*
Halibut	LDA	3.86	1.64	0.02	NA	NA	NA	NA	II*
Pollock	LDA	0.81	0.11	<0.001	4.40	1.06	<0.001	<0.01	III*
White hake	LDA	0.96	0.41	0.02	NA	NA	NA	NA	II*
American plaice	ZDA	0.33	0.17	0.06	NA	NA	NA	NA	II
Cod (ESS)	ZDA	0.88	0.10	<0.001	3.46	0.68	<0.001	<0.001	III*
Cod (WSS)	ZDA	0.77	0.09	<0.001	2.81	0.76	0.001	0.02	III*
Winter flounder	ZDA	0.49	0.06	<0.001	2.08	0.45	<0.001	0.02	III*
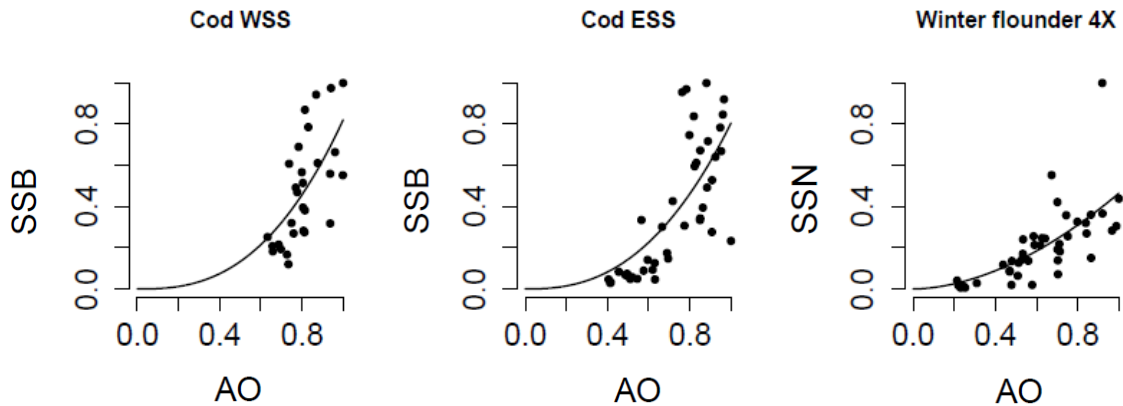
Figure 2.3 Significant convex relationships between AO and SSB for WSS cod, ESS cod and between AO and SSN for winter flounder 4X, according to $SSB = b * AO^c$.

The convex relationship, for example, for WSS cod means that a decline to 0.20 SSB (i.e. a loss of 80% of SSB relative to its maximum) is associated with a relatively much smaller reduction in maximum AO (0.58 AO, or a 42% loss of AO relative to its maximum).

WSS cod showed a positive linear relationship between D90% and SSB, meaning that an increase in SSB is associated with a constant expansion of area across which 90% of the biomass is found. For American plaice and white hake, D90% showed a negative linear relationship with SSB, meaning that with an increase in SSB, there is a decrease in area across which 90% of the biomass is concentrated. D90% was not significantly related to the SSB of any of the other assessed stocks.

The relationship between SSB and the Gini index was negative and linear for WSS cod, but positive and linear for American plaice and pollock, and positive and convex for white hake. According to these relationships, as WSS cod SSB increases, the population becomes more evenly distributed, whereas the American plaice, pollock and white hake populations become less evenly distributed as SSB increases. According to its convex shape, white hake experiences a relatively faster reduction of even spread than its SSB increases.

Relationships between the tow-density indices and SSB varied with the index examined and varied by stock. For nine out of ten populations, HDA 33 had a relationship with SSB, of which eight positive and linear and one positive and concave.

Three out of ten stocks exhibited a linear relationship between MDA and SSB, while six demonstrated a significant negative relationship between LDA and SSB, of which three linear and three convex, shown in Figure 2.4.
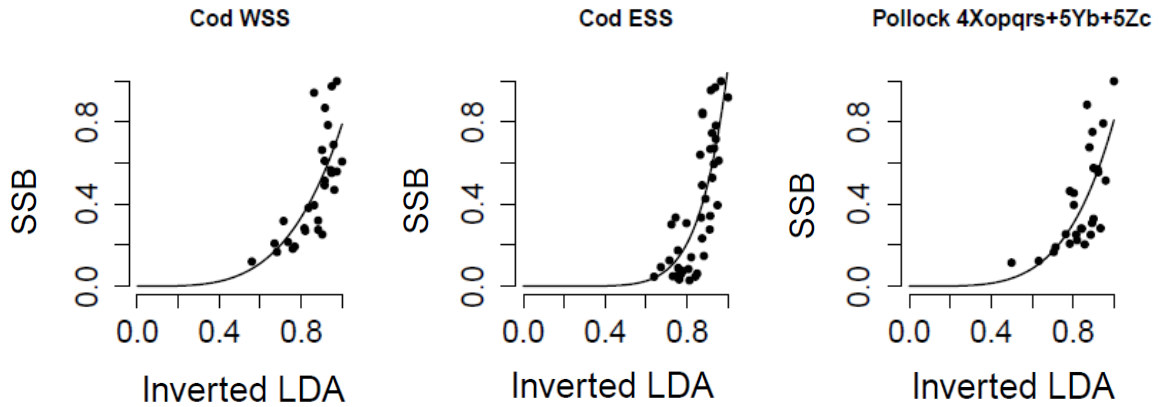
Figure 2.4   Significant convex LDA-SSB relationships for WSS and ESS cod and pollock 4Xopqrs+5Yb+5Zc according to $SSB = b * LDA^c$. The LDAs are inverted, i.e. an increase on the x-axis represents a decrease in the proportion of LDAs.

For 4 stocks, a significant relationship existed between ZDA and SSB, of which 3 are negative and convex and one (American plaice) positive and linear. This indicates that for American plaice, SSB increases with an increase in the frequency of encountering ZDAs, a result consistent with the patterns of increased concentration seen in the relationships of D90% and the Gini index with SSB for this species.

SSB was significantly related to several high-density area categories in 9 out of 10 stocks (Table 2.3).

Table 2.3 Results of the significant relationships between various levels of HDA and SSB. The relationship is defined as a linear model $SSB = a \pm b * SDM$ (listing NAs for c), or as a non-linear model $SSB = b * SDM^c$, where p(curve) represents the p-value for significant deviation of the exponent value from 1.

Species	SDM	b			c				Shape
		value	S.E.	p-value	value	S.E.	p-value	p(curve)	
American plaice	HDA 15	0.91	0.05	<0.001	0.52	0.08	<0.001	<0.001	I
Cod (ESS)	HDA 15	0.92	0.09	<0.001	0.64	0.11	<0.001	<0.01	I
Cod (WSS)	HDA 15	0.91	0.09	<0.001	0.70	0.13	<0.001	0.03	I
Halibut	HDA 15	0.34	0.11	<0.01	NA	NA	NA	NA	II
Pollock	HDA 15	0.49	0.19	0.01	NA	NA	NA	NA	II
Redfish	HDA 15	0.60	0.09	<0.001	0.59	0.19	<0.01	0.04	I
Silver hake	HDA 15	0.75	0.27	0.01	NA	NA	NA	NA	II
White hake	HDA 15	0.65	0.08	<0.001	0.66	0.15	<0.001	0.03	I
Winter flounder	HDA 15	0.83	0.08	<0.001	1.30	0.14	<0.001	0.04	III
American plaice	HDA 10	0.87	0.05	<0.001	0.43	0.06	<0.001	<0.001	I
Cod (ESS)	HDA 10	0.91	0.08	<0.001	0.60	0.10	<0.001	<0.001	I
Cod (WSS)	HDA 10	0.79	0.07	<0.001	0.58	0.13	<0.001	<0.01	I
Halibut	HDA 10	0.32	0.12	<0.01	NA	NA	NA	NA	II
Pollock	HDA 10	0.54	0.16	<0.01	NA	NA	NA	NA	II
Redfish	HDA 10	0.54	0.09	<0.001	0.41	0.18	0.02	<0.01	I
Silver hake	HDA 10	0.72	0.21	<0.01	NA	NA	NA	NA	II
White hake	HDA 10	0.65	0.08	<0.001	0.51	0.14	<0.001	<0.001	I
Winter flounder	HDA 10	0.57	0.07	<0.001	NA	NA	NA	NA	II
American plaice	HDA 5	0.86	0.04	<0.001	0.39	0.05	<0.001	<0.001	I
Cod (ESS)	HDA 5	0.90	0.12	<0.001	0.56	0.13	<0.001	<0.01	I
Cod (WSS)	HDA 5	0.51	0.18	0.01	NA	NA	NA	NA	II
Halibut	HDA 5	0.24	0.12	0.04	NA	NA	NA	NA	II
Pollock	HDA 5	0.49	0.14	<0.01	NA	NA	NA	NA	II
Redfish	HDA 5	0.62	0.11	<0.001	0.40	0.16	0.02	0.001	I
Silver hake	HDA 5	0.89	0.15	<0.001	0.63	0.19	<0.01	0.07	I
White hake	HDA 5	0.70	0.10	<0.001	NA	NA	NA	NA	II
Winter flounder	HDA 5	0.68	0.09	<0.001	NA	NA	NA	NA	II
American plaice	HDA 2.5	0.56	0.07	<0.001	NA	NA	NA	NA	II
Cod (ESS)	HDA 2.5	0.94	0.19	<0.001	0.50	0.16	<0.01	<0.01	I
Cod (WSS)	HDA 2.5	0.39	0.18	0.04	NA	NA	NA	NA	II
Redfish	HDA 2.5	0.45	0.13	<0.001	NA	NA	NA	NA	II
Silver hake	HDA 2.5	0.78	0.17	<0.001	0.41	0.22	0.08	0.02	I
White hake	HDA 2.5	0.78	0.09	<0.001	NA	NA	NA	NA	II
Winter flounder	HDA 2.5	0.73	0.09	<0.001	NA	NA	NA	NA	II

With the exception of a convex relationship between SSB and HDA 15 (the highest 15% of the biomass per tow quantile distribution) for winter flounder, all relationships are positive and either linear or concave. For various high density area categories, there is good evidence for a non-linear concave relationship with SSB, demonstrated by the exponent c values staying below 1 (Figure 2.5).
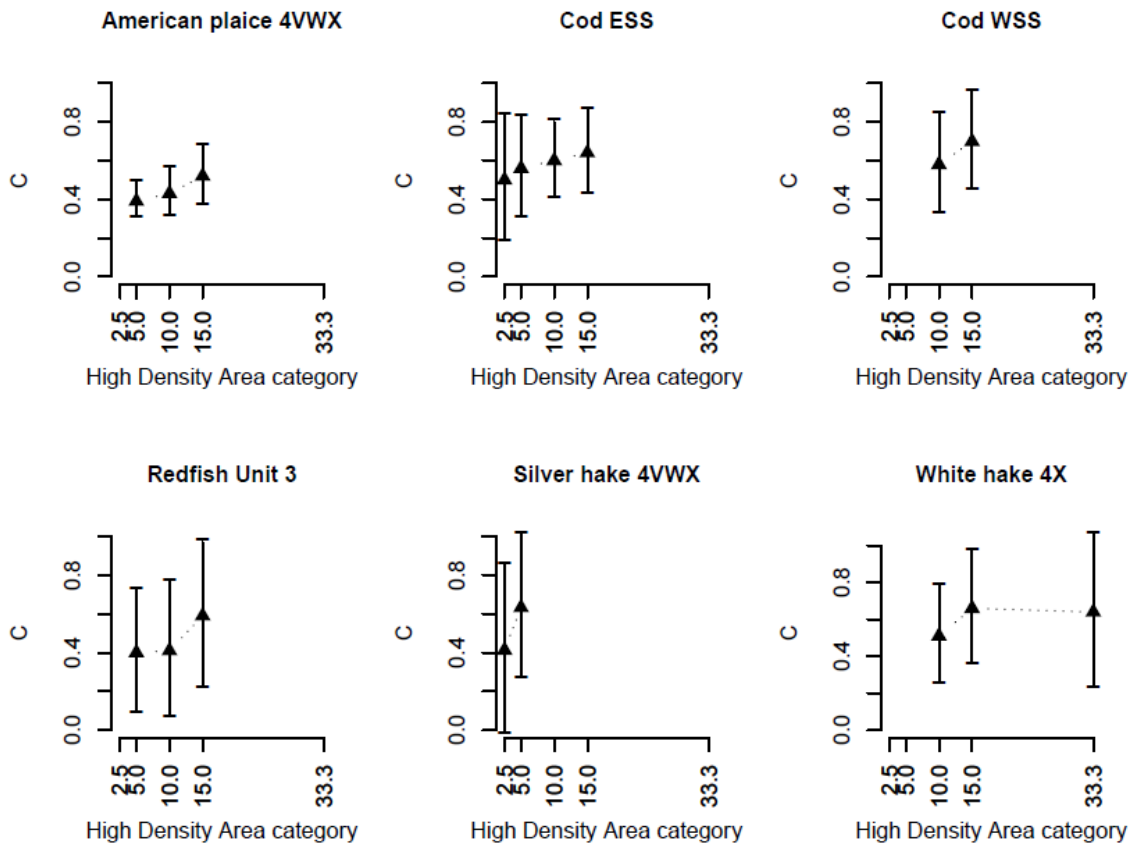
Figure 2.5   Exponent *c* values with 95% confidence interval for different categories of HDA for six stocks on the Scotian Shelf from significant concave relationships according to $SSB = b * HDA^c$.

The concave relationship appears robust for ESS cod, as HDA 15, 10, 5, 2.5 all demonstrate a significant, positive and concave relationship with SSB. The same significant concave relationship is found between white hake HDA 33, 15, 10 and SSB; redfish and American plaice HDA 15, 10, 5 and SSB; WSS cod HDA 15 and 10 and SSB; and silver hake HDA 5 and 2.5 and SSB (Figure 2.5). Pollock on the other hand, expressed non-significant concave relationships between HDA categories and SSB, with exponent values of 1 lying within its 95% confidence interval and with linear models proving a more appropriate fit. This is also the case for winter flounder, except where the exponent values for HDA 15 is significantly larger than 1, making the relationship between SSB and HDA 15 convex.

     For most stocks, the spatial distribution methods HDA 5 and HDA 2.5 contained a large number of zeros (see Appendix A to Appendix J for HDA *x* - SSB and all other

SDM-SSB plots). The HDA 15 and HDA 10 categories generally contained few zeros, and across stocks, SSB appears most sensitive to changes in HDA 15 and HDA 10, with a concave shape for five stocks (Figure 2.6).
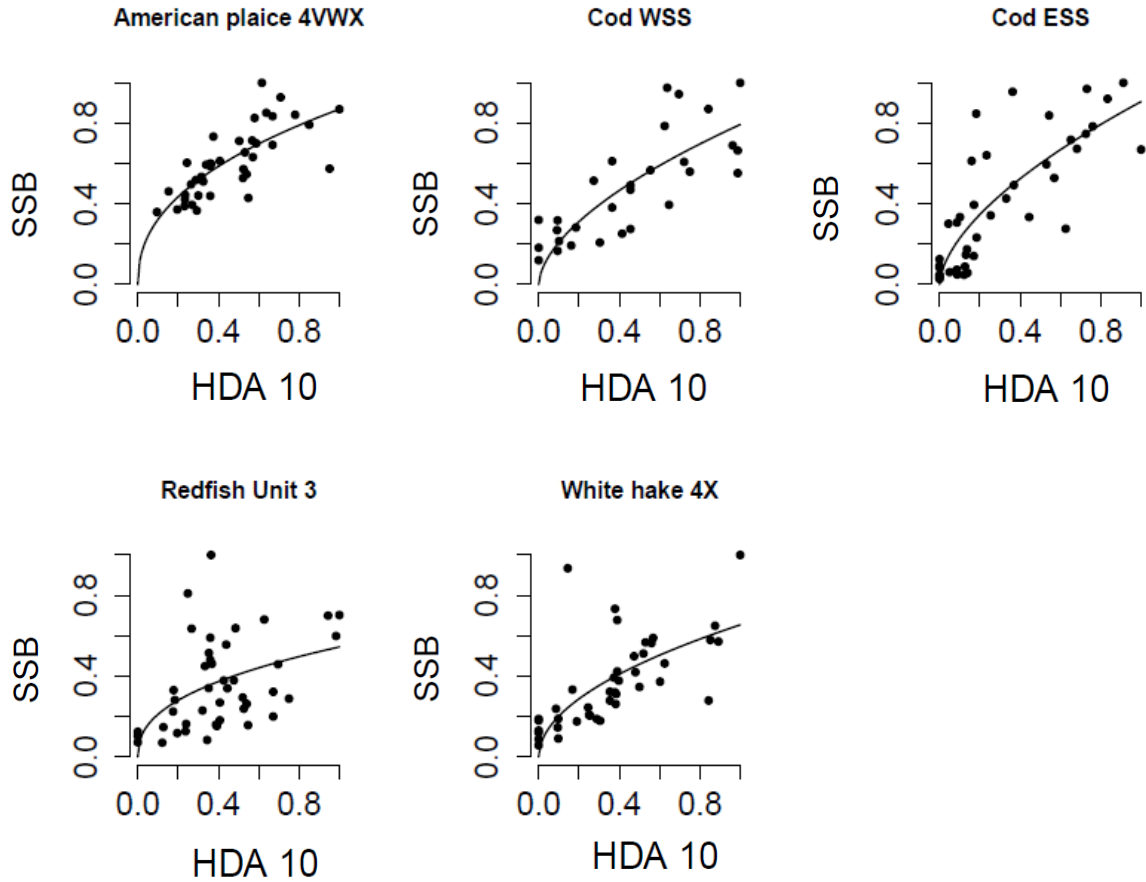

Figure 2.6 Significant positive and concave HDA 10-SSB relationships according to $SSB = b * (HDA\ 10)^c$.

Of the significant concave and convex relationships, there are a few in which the SDM precedes changes in SSB, indicated by the negative lag h in Table 2.4. All other stocks with a concave or convex SDM-SSB relationship not listed in Table 2.4, were found maximally correlated at a zero lag (see Appendix A to Appendix J for the plotted time series analyses and associated cross-correlation functions of all concave and convex SDM-SSB relationships).

Table 2.4   Results of the time series analyses of concave (type I) and convex (type III) SDM-SSB relationships wherein SDM precedes changes in SSB, indicated by negative lag h. The time series residuals were obtained using OLS: ordinary least squares regression, GLS-AR1: generalized least squares regression with an auto-correlation or auto-regressive process of order 1, GLS-ARMA (p,q): generalized least squares regression with a p order auto-regressive and q order moving average process, Log: indicates that the SSB time series was log-transformed before applying regression analysis. *Indicates the SDM is inverted. A negative $\varrho_{SDM,SSB}$ indicates a negative relationship between SDM and SSB.

Species	SDM	Maximum significant Cross Correlation (ϱ_{max})		Type SDM-SSB relation-ship	SDM time series residuals via	SSB time series residuals via
		$\varrho_{SDM,SSB}$	Lag (h) in year(s)			
Cod (ESS)	AO	0.671	-1	III	GLS-AR1	Log GLS-AR1
Cod (WSS)	AO	0.442	-1	III	OLS	Log GLS-AR1
Winter flounder	AO	0.378	-2	III	OLS	Log GLS-AR1
Cod (ESS)	LDA	0.520	-3	III*	GLS-AR1	Log GLS-AR1
Cod (ESS)	ZDA	0.640	-1	III*	GLS-AR1	Log GLS-AR1
Winter flounder	ZDA	0.313	-2	III*	OLS	Log GLS-AR1
American plaice	HDA 15	-0.412	-3	I	OLS	GLS-AR1
Cod (ESS)	HDA 15	0.719	-1	I	GLS-AR1	Log GLS-AR1
Cod (WSS)	HDA 15	0.521	-1	I	OLS	Log GLS-AR1
American plaice	HDA 10	0.404	-6	I	OLS	GLS-AR1
Cod (ESS)	HDA 10	0.690	-1	I	GLS-AR1	Log GLS-AR1
Cod (WSS)	HDA 10	0.469	-1	I	OLS	Log GLS-AR1
Cod (ESS)	HDA 5	0.585	-2	I	GLS-ARMA (2,1)	Log GLS-AR1
Cod (ESS)	HDA 2.5	0.515	-1	I	GLS-AR1	Log GLS-AR1

For cod, HDAs precede declines in SSB with a one year time lag, except ESS cod HDA 5, which leads SSB with a two year time lag. The time series and cross correlation between ESS and WSS cod HDA 10 and SSB are depicted in Figure 2.7. The cross correlation function demonstrates that maximum cross correlation occurs when ESS cod HDA 10 leads changes in SSB with a one year time lag. Cross correlation is also high (although lower than the maximum cross correlation at $h= -1$) at other time lags, including positive lags. The time series show that it is mainly the rapid declines (not increases) in SSB that are preceded by HDA 10 declines. For WSS cod, the large SSB increase leading up to 1990 and 1996 and decline afterwards were preceded by an increase and decrease in HDA 10. For American plaice the cross-correlation between HDA 10 and SSB is maximum at a lag of $h= -6$, although a cross correlation at a lag of $h=0$ is presumably more likely.

AO precedes changes in SSB for ESS and WSS cod and winter flounder (Table 2.4) and the time series and cross correlation functions are depicted in Figure 2.8. For ESS cod, AO increases before SSB, whereas the SSB decline appears to happen more simultaneously with AO declines. For WSS cod the 1990 and 1996 SSB peak of WSS cod are visibly preceded by an increase in AO. For winter flounder the AO peaks appear to approximately align with SSN peaks when AO leads by two years, but not very clearly across the entire time series and this is reflected by a relatively low $\varrho_{AO,SSB}$ value.
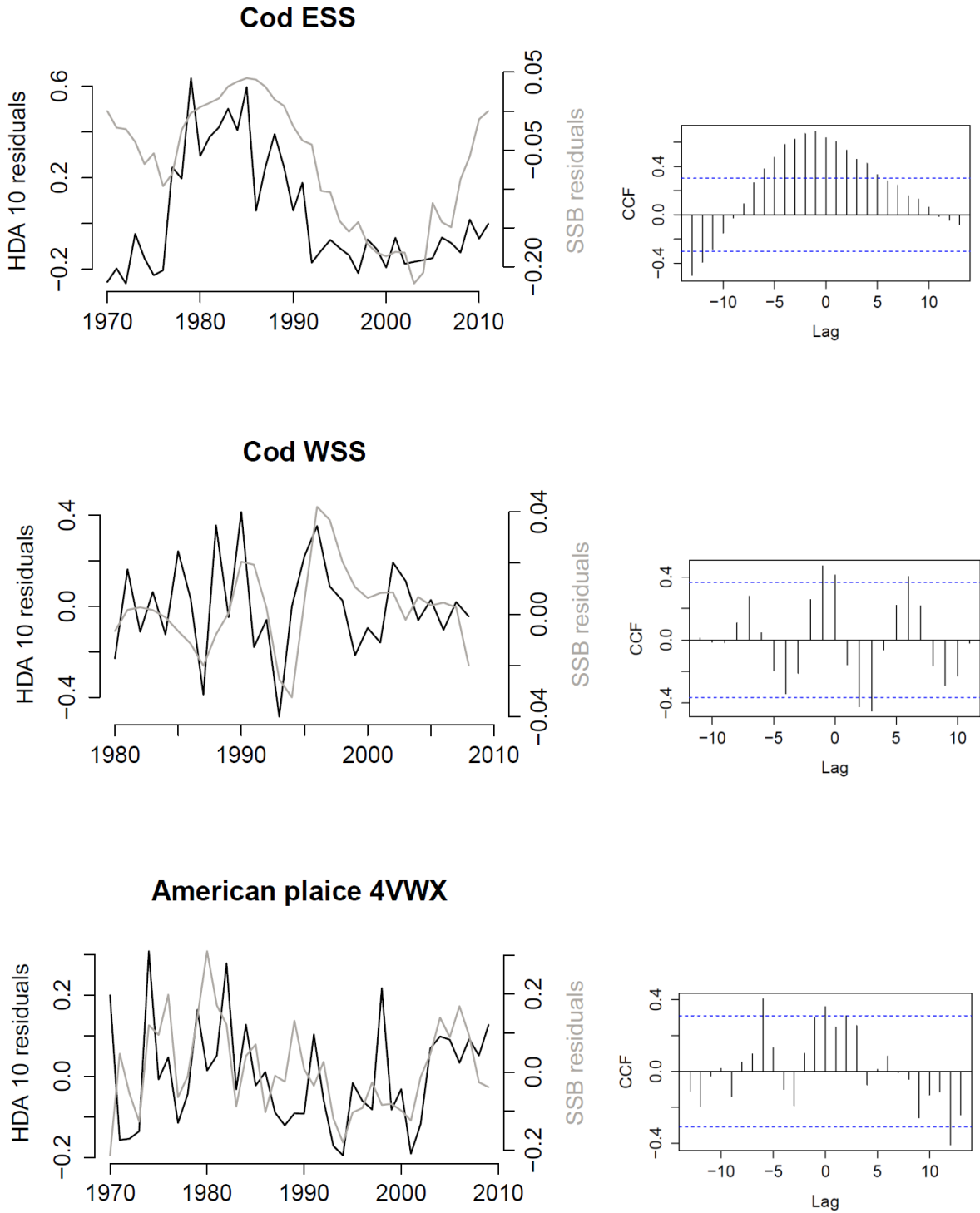
Figure 2.7 HDA 10 and SSB time series (left) and associated cross correlation functions (right) showing the maximum cross correlation between HDA 10 and SSB at a lag h=-1 for WSS cod and ESS cod and h= -6 for American plaice (See Table 2.4 for the models used to create the time series residuals).
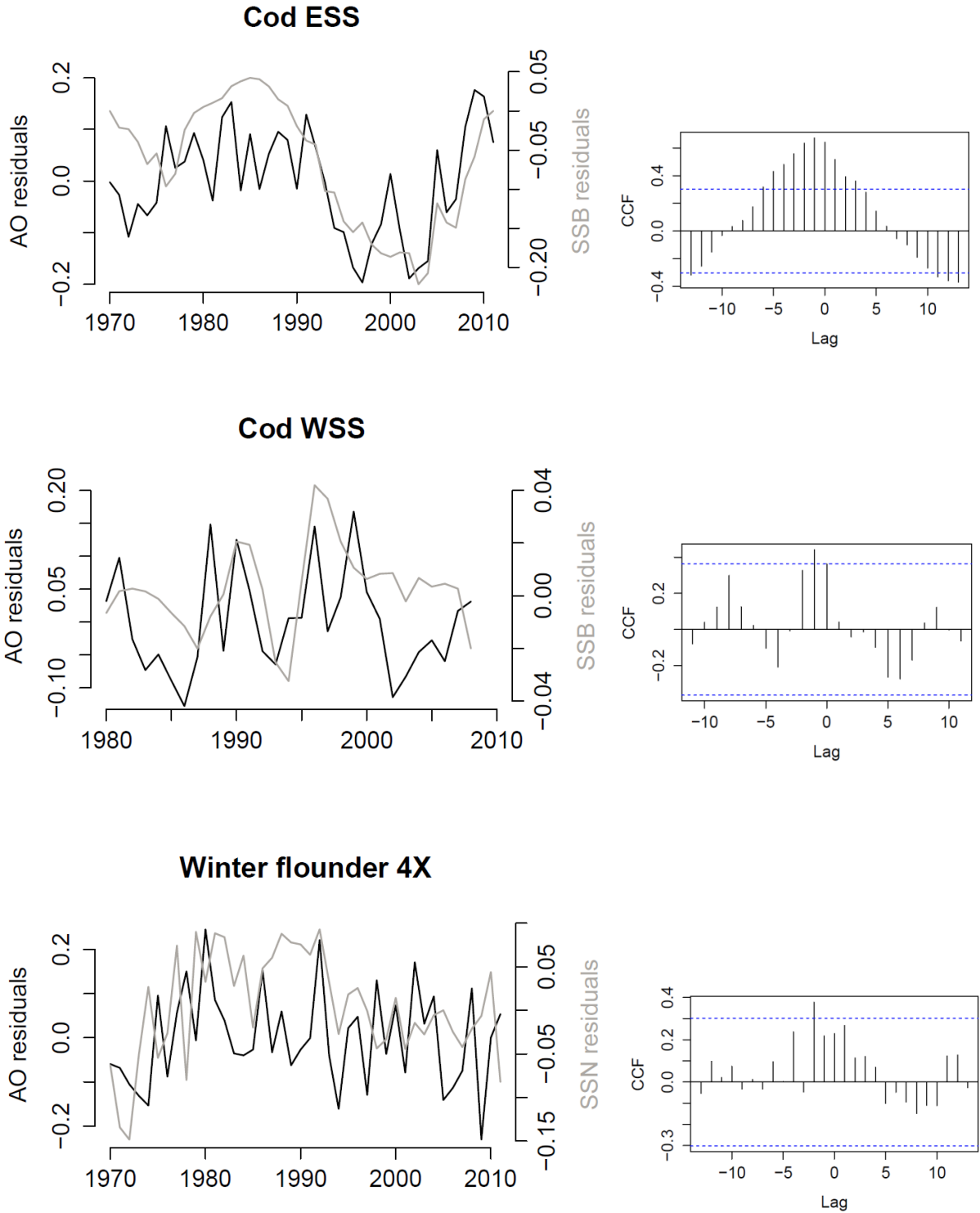
Cod ESS

Cod WSS

Winter flounder 4X

Figure 2.8   AO and SSB time series (left) and associated cross correlation functions (right), showing the maximum cross correlation between AO and SSB at a lag *h*=-1 for WSS cod and ESS cod and h=-2 for winter flounder (See Table 2.4 for the models used to create the time series residuals).

2.4　　　　　Discussion

The reproductive component of marine fish populations is related to their spatial distribution. Among the spatial indices that have been used for marine fishes in the past, some are more sensitive to changes in SSB and better predictors of rapid changes in SSB than others. It is these indices that are likely to be of greatest utility when identifying distributional targets for recovery and establishing spatially informative limit reference points to prevent population collapse.

Of the SDMs examined for 10 groundfish populations, the HDA metric was found to be the SDM most frequently (significantly) related to SSB. HDAs generate type I or concave relationships with SSB. In a type I relationship, SDMs decline faster than SSB, until HDAs have declined to a point where each additional HDA decline is associated with a relatively larger SSB decline. For cod, declines in HDA also appear to precede rapid declines in SSB in time. This makes HDAs a potential indicator for forecasting imminent SSB declines, and supports further development of HDAs as a primary correlate of SSB for fisheries management purposes.

The other SDMs have either a linear (type II) or convex relationship (type III) with SSB. For example, a type II relationship is evident between D90% and SSB for WSS cod, a pattern consistent with the results reported for cod abundance and D90% by Swain and Sinclair (1994) and for abundance and D95% by Blanchard et al. (2005). SDMs that reflect a type II or linear relationship with SSB indicate no differential loss of range, concentration or density. These SDMs might prove useful as a proxy for SSB when resources or data do not permit an annual assessment of SSB. In case the SDMs precede changes in SSB in time, they might also be useful as an indicator for forecasting SSB changes. However, the SSB changes would be proportional to SDM changes and for that reason, the SDM would not be able to signal accelerated declines or increases in SSB. When SSB data are available and when the SDM has no ability to predict changes in SSB, these SDMs that are linearly related with SSB will not provide additional information and are unlikely to be informative indicators of population collapse or (fast) recovery.

Type III relationships are mainly found between SSB and AO (positive relationship), and between SSB and LDAs and ZDAs (negative relationship). For

populations that follow a type III or convex relationship, the decline in SDM values occurs relatively slower than the decline in SSB values. This means that a stock can experience large SSB declines, while SDM values remain relatively high. For example, the convex relationship between WSS cod AO and SSB demonstrates that an AO reduction from maximum to slightly lower levels is associated with a relatively large drop in SSB. This relationship might emerge from SSB 'spreading thin', whereby a population's SSB drains while the population still manages to retain a relatively large range and numerous lower density areas. A decrease of ZDAs and LDAs in favour of higher density areas could potentially indicate an increased probability of migration among patches that are occupied.

Conversely, a relatively large SSB increase in a type III relationship does not occur until these SDMs reach relatively high levels. For example with a convex relationship between AO and SSB, it appears a minimum level of area needs to be occupied, before associated high values of SSB can be observed. This could indicate a need for recolonization of an area (Frisk et al. 2011). The type III relationship between AO and SSB (cod and winter flounder) is consistent with previous research reporting declines in abundance of greater magnitude than concomitant changes in area of occupancy (Crecco and Overholtz 1990, Frisk et al. 2011, Ricard 2012). Increases in AO also appear to precede rapid increases in SSB for cod and winter flounder. SDMs that generate type III relationships with SSB may prove useful as indicators, with regard to a spatial distribution level and perhaps a level of recolonization that a stock needs to reach before it might achieve recovery of SSB values to relatively high levels.

The ability of HDAs in type I relationships to indicate a level below which relatively large SSB declines occur – and in the case of cod the ability of HDAs to signal upcoming large SSB declines in time - could be the result of a number of ecological processes. According to DDHS, habitat preference will vary at different levels of abundance (Swain and Kramer 1995). If the theory of ideal free distribution holds and DDHS is at play, population density will map habitat suitability and accordingly HDAs will be indicative of productive habitat. A differential loss of HDAs, possibly a result of the overexploitation of HDAs that would have a higher catch-per-unit-effort (Hutchings and Myers 1994), may thus reflect a loss of density across highly productive areas.

Losing highly productive areas could negatively affect reproduction and survival and consequently reduce SSB. The perceived ability of HDAs to signal a decline in SSB is consistent with results for northern cod, for which HDAs were shown to be a leading indicator of the collapse (Hutchings 1996). These northern cod HDAs consisted of the highest 2-3% of the biomass per tow quantile distribution. In addition to Scotian Shelf cod, it was found that American plaice, redfish and white hake all demonstrate a relatively faster decline in both HDA 10 and HDA 15 than in SSB, until a threshold is reached below which each additional loss of a HDA is associated with relatively larger SSB declines.

Alternatively, with this type I relationship, I observe that recovery from a very low to a relatively high SSB level is associated with a relatively small increase in HDAs. The basin model - founded on DDHS - suggests that density is highest where habitat is most suitable, such that any particular location is thought to reflect a density dependent reduction of realized suitability (MacCall 1990). HDAs can thus be thought of as a reflection of areas of high resource value and high realized suitability, and this may be the reason high SSB levels with relatively few additional HDAs are observed. At a certain point, the suitability of these optimal HDA habitats will decline and the population will start to expand into other areas, which in turn may eventually create more HDAs. This process may be supported by recolonization of areas through increases in area of occupancy and reductions in ZDAs and LDAs, enabling an increase of MDAs and eventually HDAs; trends seen for example in ESS cod. In addition to the possibility that HDAs represent highly realized suitable habitat, they also reflect high density aggregations. The densities associated with a high SSB might reflect an aggregation behaviour that has maximized fitness, and losing these HDAs might reduce fitness advantages that come with having more individuals per unit area (Colwell and Rangel 2009). These advantages can include protection from predators, increased probability of locating prey (Pitcher and Parrish 1993), and an increased probability of eggs being fertilized (Rowe et al. 2004). Thus, when beneficial high density aggregations associated with high SSB are reduced, the decreased ability to spawn, feed and escape predators may lead to a reduction in individual fitness (Allee effect) and consequently SSB of that fish population.

Why, compared to the other SDMs, HDAs generate the highest number of significant relationships with SSB across the examined fish populations, might be because they contain information about actual biomass per tow per area, whereas presence and absence data (AO), or taking the mean biomass (D90% and Gini index), may not be always be sensitive enough to pick up changes in SSB. Also, considering that no size threshold could be applied and that consequently SDMs measured both spawners and pre-spawners, the SDMs may have been overestimated in years when biomass consisted mostly of pre-spawners. Since HDA measures the areas of the highest density and these areas are likely to contain actual spawners, this could lead to HDA being a better indicator of SSB compared to the other SDMs.

The models used to estimate Scotian Shelf SSB are based on different population models, each considering survey biomass per tow information to a varying degree. If a model to estimate SSB is highly influenced by biomass per tow data, it would likely be strongly related to the density area metrics, and it could be argued that a relationship might stem from a lack of independence between the two variables. Indeed, SSB from stock assessments is calculated based on extrapolation of number or biomass per tow information. However, SSB is likely to deviate from biomass per tow information, considering that stock assessments also include information (and uncertainty and error associated with) regarding total catches, maturity, sex-ratio and natural mortality (Quinn and Deriso 1999, Cotter et al. 2009b, Mesnil et al. 2009). The SSB models applied to the stocks examined in this analysis vary by both assessment year and species. For example, for American plaice, SSB is based on a stage based model and a numbers-to-tons equivalence of q-adjusted survey numbers at length (DFO 2012b). For cod on the Scotian Shelf, a VPA model is used to estimate SSB. This model uses survey and fishery catch at age, as well as an assumed natural mortality to reconstruct the numbers at age. The SSB is estimated from the total numbers at age, using mean weight and maturity ogive (proportion of the population that is mature) at age by year, as well as the fraction of mortality before spawning. (Bedford Institute of Oceanography, Dept. Fisheries & Oceans, Don.Clark@dfo-mpo.gc.ca, personal communication). Thus, per stock, biomass per tow is incorporated into the final SSB estimate to a varying degree. In addition, SSB is often based on an *average* biomass per tow, which could lead to important information

being lost (Hutchings 1996). For this reason, the average biomass per tow was not used, which can be expected to be linearly related to SSB. Rather, biomass was divided between low, medium and high density to find out whether these could be considered sensitive indicators of rapid SSB changes, i.e. which have non-linear relationships with SSB. Generally concave relationships between SSB and HDAs were found and linear relationships between SSB and MDAs. Thus, monitoring values closer to average biomass per tow and leaving out spatial information regarding important HDAs renders the indicator less sensitive to changes in SSB.

Similar to the relationship between abundance and the catchability coefficient (Wilberg et al. 2010), density dependent processes may underlie the relationship between SSB and HDA. Catchability or q is the proportion of the stock caught per unit effort, and it is affected by availability of the fish stock to the gear (how many fish are in the area at the time of the haul), and catching efficiency (how many fish can be retained in the net) (Jennings et al. 2009). When abundance declines, a larger proportion of total abundance may become available to the gear due to DDHS, which can increase catchability (Hutchings 1996). This can cause fishery catch-per-unit-effort (CPUE) to be hyperstable, i.e. CPUE stays high despite a decrease of abundance (Hilborn and Walters 1992, Harley et al. 2001, Wilberg et al. 2010). The concave relationships between HDA and SSB reflect that a larger proportional loss of total biomass occurs with each additional loss of HDA, arguably due to DDHS. In addition to DDHS, this process might also be explained by mathematics, since a higher proportion of the total biomass is likely located within the HDA as total biomass declines. Considering that a range of values of the biomass per tow distribution are incorporated into HDA x (see Table 3.3), this is however not a (mathematical) rule. The DDHS mechanism that could explain the shape of the relationships between catchability q and abundance and between SSB and HDA x may be the same, however q and HDA measure something different. When q is high, there is a higher mean proportion of total biomass caught per unit effort, but the division between areas of low, medium and high abundance is not taken into account and a pattern of disappearing HDAs may be left undetected. When HDA is high, there are relatively many areas containing a high biomass, since HDA measures the proportion of total tows that

contain only high densities. Therefore, HDA could arguably be considered a more direct and sensitive spatial measure of the aggregating behaviour of fish.

Reasons for not observing a relationship between SSB and a SDM could possibly be attributed to the magnitude of change being insufficient. When spatial distribution falls to sufficiently low levels a change in SSB will (eventually) emerge, justifying the forcing of model 5 through the origin; a conventional practice in fisheries science applied for example to stock-recruitment relationships (Quinn and Deriso 1999). However, populations may not show this until extremely low levels. Not seeing changes in range when SSB is increasing could also be attributed to e.g. concentration providing benefits, while preferred habitat is limited or unsaturated, or both (Shackell et al. 2005, Horsman and Shackell 2009). This might also provide an explanation for the negative relationship between D90% and SSB, and between ZDAs and SSB for American plaice, whereby an increase in SSB is associated with an increase in ZDAs and a decrease in the area across which 90% of the biomass is concentrated.

SDMs showing type I or type III relationships with SSB might be useful metrics of population collapse and recovery. Both yield information about quantities of range, concentration and density associated with productive levels of SSB and potential thresholds associated with collapse or recovery. Thus the spatial distribution of SSB can be utilized at low and at high levels and monitor stocks in their path towards recovery.

Of the SDMs that demonstrate a type I or type III relationship with SSB, HDAs could most often signal changes in SSB (six out of ten stocks). AO, LDAs and ZDAs each signal disproportional changes in SSB for three out of ten stocks. HDA appears to be a sensitive indicator, especially at lower SSB levels, whereas e.g. AO and LDAs and ZDAs display a range of values at lower SSB. SDMs that have a type III relationship with SSB would therefore not be appropriate for indicating disproportionately large SSB declines, but HDAs would be appropriate. Therefore the potential of HDAs to serve as a spatial distribution limit reference point will be further explored in Chapter 3.

The relationships between SSB and the various SDMs may not necessarily be causal relationships, nor do they necessarily indicate that DDHS is at play. It may be that SSB and the SDM co-vary with an un-parameterized, density-independent variable (Shepherd and Litvak 2004). Irrespective of the causal mechanism, it appears there may

be merit in further exploring how HDAs could serve as a spatial distribution indicator for SSB and how developing reference points based on spatial criteria could contribute to currently used biomass reference points in fisheries management.

CHAPTER 3   Spatial reference points for groundfish

3.1   Introduction

The recovery and persistence of species depends on the ability of populations to rebound from low abundance (Hutchings and Reynolds 2004, Keith and Hutchings 2012). Collapsed fish stocks contribute little to species richness or ecosystem functioning and have major social and economic implications for coastal communities (Branch et al. 2011). The longer that a depleted population continues to decline and the longer it takes for meaningful reductions in fishing mortality to be effected, the longer and more uncertain will be the recovery period (Neubauer et al. 2013). Effective control of fishing mortality at different levels of stock abundance is greatly enhanced by the establishment of reference points for management purposes (Hilborn and Stokes 2010). These reference points fall into two categories: limit reference points (LRPs) that identify levels of abundance below which populations are considered to be subjected to serious harm, and target reference points (TRPs) that identify levels at which the population or the fishery is expected to attain an optimal level of productivity (Caddy and Mahon 1995).

Current LRPs and TRPs are often based on the amount of adult biomass or SSB needed to support a maximum sustainable yield (MSY), i.e. the maximum yield that can presumably be taken from a stock without adversely affecting future reproduction and recruitment. Given that it is the fishing effort causing fishing mortality (F), not SSB that can be controlled by fisheries management, LRPs and TRPs are also set for levels of exploitation or fishing pressure (F_{MSY}) at which the population is allowed and expected to reach and maintain SSB_{MSY}.

There are a number of problems associated with using the concept of MSY, including its estimation (given data and model uncertainty), problems with the appropriateness of MSY as a management goal (given other objectives for management), and problems with our ability to implement a harvest strategy based on MSY effectively (Punt and Smith 2001). Due to the uncertainty in accurately estimating the MSY and the risks associated with overshooting the unknown and dynamic level of MSY, management bodies are increasingly using F_{MSY} as an upper boundary instead of a target (Gabriel and Mace 1999).

Despite its limitations (Finley 2011), the notion remains that MSY provides a useful reference against which exploitation can be measured (Punt and Smith 2001), which is why several jurisdictions use SSB_{MSY} as a basis for reference points. Australia (Australian Government 2007) and the United States (U.S. Department of Commerce 1998) have adopted a LRP of 0.5 SSB_{MSY}, the level of biomass they try to avoid reaching and below which a stock is considered overexploited (Hilborn 2010, Hilborn and Stokes 2010). Canada has set a lower LRP, with stocks generally considered to be in a 'critical zone' if the SSB is less than or equal to 0.4 SSB_{MSY} (DFO 2009). Rebuilding is aimed at achieving a TRP consistent with biomass levels capable of producing a maximum sustainable yield, or 1.0 SSB_{MSY} (Hilborn and Stokes 2010).

Fisheries management is often based solely on managing fishing pressure to maintain a certain level of population biomass, even though fish populations are not homogeneously distributed throughout their habitat. Rather, they have spatial structures and are aggregated to a greater or lesser extent (Myers and Stokes 1989, MacCall 1990, Fisher and Frank 2004, Shackell et al. 2005, Link et al. 2011b). Fisheries management generally ignores the effects of fishing on spatial distribution and the spatial structures present in fish populations (Cadrin and Secor 2009), even though these are arguably as important as maintaining a certain level of population biomass to ensure long-term sustainable fish populations (Berkeley et al. 2004; Hsieh et al. 2010)[1]. As mentioned in Chapter 2, changes in spatial structure might impact the ability of a fish population to successfully spawn (Rowe et al. 2004), migrate, find mates or prey, fend off predators and competitors (Pitcher and Parrish 1993) and therefore may affect recruitment at low population levels (Frank and Brickman 2000).

Bearing in mind the uncertainty associated with estimating and applying reference points based solely on SSB_{MSY} and F_{MSY}, there might be utility in developing spatial reference points that are concordant with biomass reference points, especially when information on spatial structure can be successfully employed to detect trends in population abundance (Ciannelli et al. 2013).

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[1] There are of course exceptions to this general statement, such as the haddock juvenile closed are on the Scotian Shelf aimed at protecting incoming recruits from being caught (Frank 2000) and the EU FISBOAT project that identifies ways to incorporate information about populations' spatial structures into stock assessments (Petitgas et al. 2009).

In Chapter 2, different spatial distribution indices reflective of the spatial distribution characteristics of fish populations were studied in relation to their abundance. Comparing the spatial indices AO, D90%, Gini index, ZDA, LDA, MDA and HDA x, HDA x are found most often related to SSB. For six stocks, HDAs decline faster than SSB declines, and for cod stocks HDA declines also appear able to signal rapid SSB declines.

Considering that HDAs indicate -and in case of cod precede- rapid declines in SSB, reference points based on these HDAs might help identify population thresholds that could be used to prevent a future collapse. Fisheries managers could set limits for fishing pressure, once the frequency of encountering HDAs has declined to levels approaching a threshold of rapid SSB decline. Spatial target reference points could help to minimize fishing pressure and maintain HDAs at levels corresponding to e.g. a productive (1.0 SSB_{MSY}) or healthy SSB (1.3 SSB_{MSY}) (National Oceanic and Atmospheric Administration 2012). An expansion of HDAs might be preceded by recolonization of empty areas to more densely populated areas and therefore, an increase in occupied area and a shift from lower to higher density areas could potentially be monitored during recovery. In addition, targets for AO above which SSB is likely to experience a disproportionately large increase, could serve population recovery. However, the scope of this chapter will be limited to exploring the utility of spatial reference points based on HDAs.

The objective of this chapter is to use fishery independent survey data in conjunction with biomass reference points to identify potential spatial reference points using the spatial indicator HDA. This is intended to be a qualitative analysis to determine the utility of spatially based reference point in different scenarios and to explore how a spatial reference point could be developed. In addition to incorporating spatial distribution or spatial differences in density in fisheries management, such indices or reference points might be of broader value since they take advantage of using survey data, for which no assumptions about the natural mortality or the fishing mortality are required. In addition, survey-based indices allow more rapid updates on the status of stocks compared to more complex stock assessments that incorporate numerous variables (Mesnil et al. 2009).

3.2 Methods

HDA measures the amount of areas that contain the highest x % of the biomass (kg) per tow quantile distribution HDA x. It was found that the highest 10% and highest 15% of the biomass per tow quantile distribution (HDA 10 and HDA 15) are sensitive indicators of changes in SSB for American plaice, ESS and WSS cod, redfish and white hake on the Scotian Shelf (Table 2.3). However, all levels of HDA previously found to be sensitive indicators of change in SSB are examined in this chapter. For example, for silver hake, it is not HDA 10, but the highest 2.5% and 5% of the biomass per tow quantile distribution (HDA 2.5 and HDA 5) that are sensitive indicators of changes in SSB.

We calculate levels of HDA x by taking the highest x% of the biomass per tow quantile distribution across the time series and base the upper quantile (e.g. 90%-100% quantile for HDA 10) on the biomass per tow distribution using only tows that contain > 0 kg/tow. The relationship between HDA and SSB is assessed according to model 4 and 5 in Chapter 2.2.

HDA x is then assessed relative to various biomass reference points, i.e. different levels of SSB$_{MSY}$. For American plaice, cod, redfish and silver hake populations on the Scotian Shelf, SSB$_{MSY}$ has been previously estimated. Even though the methods of estimating MSY vary among stocks, they are all meant to reflect SSB$_{MSY}$. For white hake, the SSB$_{MSY}$ level has not previously been assessed. To estimate the SSB$_{MSY}$ for white hake, a single-species surplus production model was applied (Worm et al. 2009). Surplus production P in year t is estimated by

$$1. \quad P_t = SSB_{t+1} - SSB_t + C_t \,,$$

where SSB_t is spawning stock biomass at time t, and C_t is catch at time t. The surplus production model is fitted to the catch and biomass data using a Schaefer model, which is based on a logistic population growth model (Quinn and Deriso 1999). The predicted surplus production in each year in the Schaefer model is given by:

$$2. \quad \hat{P}_t = \frac{4mSSB_t}{K} - 4m \left(\frac{SSB_t}{K} \right)^2,$$

where m is the maximum sustainable yield and K is the carrying capacity or equilibrium biomass in the absence of fishing (Worm et al. 2009, modified from Quinn and Deriso 1999). The parameters m and K are estimated using maximum likelihood, whereby

$$3. \quad SSB_{MSY} = 0.5K \; .$$

Different levels of SSB relative to the estimated MSY have been identified as biomass reference points. Two important points of reference are used:

1) 1.0 SSB_{MSY}: the level of spawning biomass at which the stock is expected to produce MSY; i.e. optimal production is thought to occur when SSB= 1.0 SSB_{MSY}. Generally fisheries of stocks with a biomass >1.0 SSB_{MSY}, are expected to be economically more profitable (Grafton et al. 2007) and have lower ecological impact (Worm et al. 2009 in Hilborn and Stokes 2010).

2) 0.5 SSB_{MSY}: this is 50% of the level of biomass associated with MSY, and when biomass falls below this point, stocks are generally considered overexploited (Branch et al. 2011). The governments of Australia and the United States have adopted this as a limit reference point (Hilborn and Stokes 2010). In this analysis 0.5 SSB_{MSY} will serve as the level at and below which the stock is considered overexploited.

These two levels of SSB_{MSY} are assessed relative to the spatial threshold. The relationship between HDA and SSB for the six stocks examined herein is a positive, concave one, in which a threshold or deflection point can be identified, below which relatively larger SSB declines occur with each additional reduction in HDA (Figure 2.6). This deflection point can be identified by calculating the maximum distance or D_{MAX}, a method developed in medical science aimed at determining the ventilatory and lactate threshold (Cheng et al. 1992). D_{MAX} would be the point on the SSB-HDA curve that yields the maximum, perpendicular distance from the secant (linear) line, that is formed between the end points of the predicted relationship, and the predicted relationship (i.e. the HDA-SSB curve) itself (see Figure 3.1). Cheng (et al. 1992) used an undisclosed computational model that selected the maximum distance from all the distances between data points on the predicted relationship and the secant line. Hence, no model was given to calculate D_{MAX} and therefore I formulated a model with which D_{MAX} can be obtained, hereafter referred to as HDA_T for HDA threshold. HDA_T is the point at which the derivative of the SSB-HDA curve (model 4) and the derivative of the secant line (model 5) are equal, which is their point of intersection and which yields HDA_T (model 6). Subsequently entering the HDA_T value in model $SSB = b * HDA^c$ will produce its associated SSB value.

4. $f'_{curve}(SSB) = bc * (HDA\ x)^{c-1}$

5. $f'_{secant}(SSB) = b$

6. $HDA_T = \left(\dfrac{b}{bc}\right)^{\frac{1}{c-1}}$
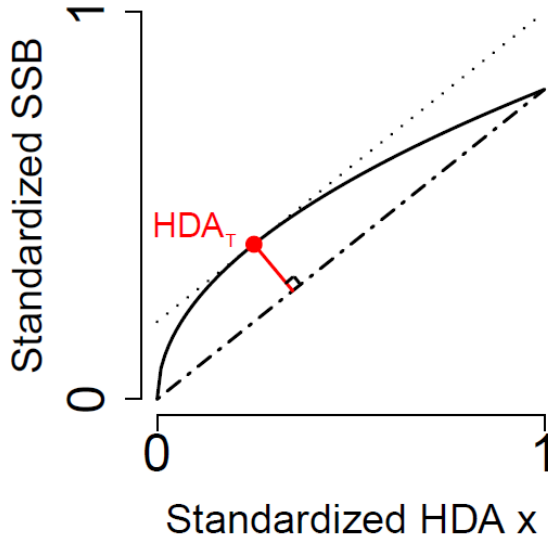
Figure 3.1 Predicted HDA x − SSB relationship, secant line and HDA$_T$. The predicted HDA x − SSB relationship according to $SSB = b * HDA^c$ is depicted with a black curve. Its secant line connecting the lowest and highest point of the predicted relationship is depicted as a line with dots and dashes. The red HDA_T dot is where the derivative of the predicted HDA x − SSB curve and the derivative of the secant line (small grey dots) would intersect and where a maximum perpendicular distance is observed between the curve and its secant line (modified from Cheng et al. 1992).

Considering that non-linear models are fitted (Chapter 2 analyses show parameter c demonstrates a significant departure from 1) to data with non-parametric distributions, the prediction limits for each stock's threshold are calculated using bootstrap (Cury et al. 2011). A semi-parametric bootstrap is applied with a beta-distribution that approximates the distribution of the original data. The dataset is sampled 1000 times to estimate the 95% prediction interval for HDA_T for each population, for each HDA x category that has a significant, non-linear concave relationship with SSB. By analyzing and comparing HDA_T for each HDA x value that was found previously to have a significant, non-linear and concave relationship with SSB, note can be taken of the potential sensitivity of HDA_T to a varying HDA x category.

3.3   Results

The SSB_{MSY} for all six stocks is given in Table 3.1, including the model that SSB_{MSY} is derived from and the information source. In addition to the five assessment-produced estimates of SSB_{MSY}, the Schaefer surplus production model for white hake yields a predicted surplus production with a MSY of 3610 tonnes and an estimated SSB_{MSY} of 26491.5 tonnes (Table 3.1 and Figure 3.2).

Table 3.1 SSB_{MSY} information regarding the six examined stocks, including the NAFO area, the SSB_{MSY} values and the model used to estimate SSB_{MSY}.

Stock	NAFO area	SSB_{MSY} in tonnes	Model	Source
American Plaice	4VWX	32381	Stage-based population model using time series: 1970-2009.	(DFO 2012)
Cod	4X5Y	60000	Beverton-Holt stock recruitment model using time series: 1980-2007	(Clark et al. 2011, DFO 2012)
Cod	4VsW	125000	Sissenwine-Shepherd Production Model using the productive period 1958-1990	(DFO 2012)
Redfish	Unit 3 / 4X4Wdehkl	72500	Limit reference point is determined as 40% of the mean mature (>22cm) biomass index from 1970-2011; the mean biomass of that series is taken as a proxy for B_{MSY}. I assume $B_{MSY} \sim SSB_{MSY}$	(DFO 2012)
Silver hake	4VWX	20189	Discrete logistic biomass dynamic model (Schaefer) incorporating process uncertainty through a state space approach, using time series: 1993-2011. B_{MSY} estimated $\sim$ 59000t, multiplied by 0.34 (median of annual ratio of SSB/B) yields 20189t. I assume $B_{MSY} \sim SSB_{MSY}$	(DFO 2013)
White hake	4X5Y	26491	Schaefer Surplus Production model using time series 1970-2011	Data: jim.simon@dfo-mpo.gc.ca, personal communication. Model: Schaefer (1954) and Worm et al. (2009)
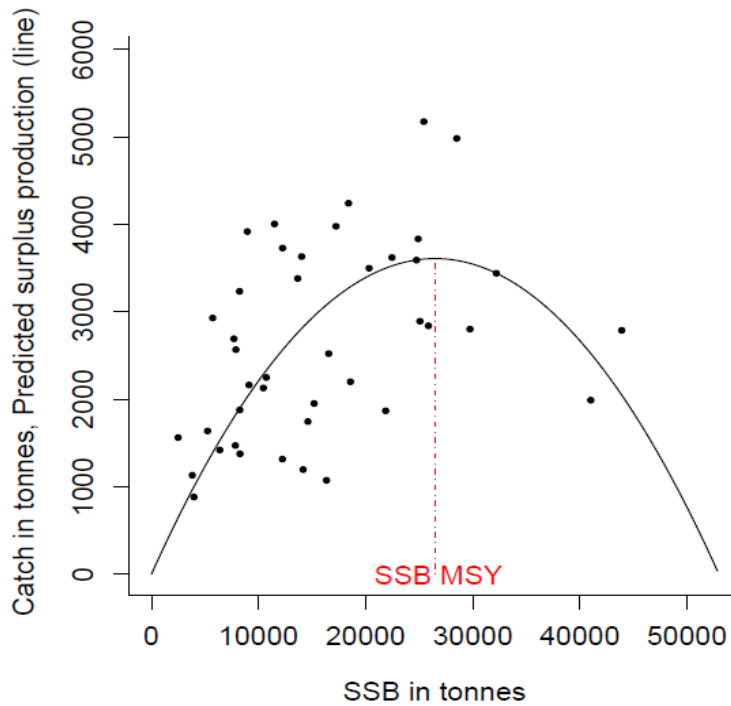
Figure 3.2   White hake SSB_{MSY} Schaefer surplus production model. This plot shows the white hake catch versus SSB in tonnes and predicted surplus production, according to the Schaefer surplus production model, with an estimated SSB_{MSY} of 26491.5 tonnes.

The SSB_{MSY} values from Table 3.1 are used to mark the (1.0) SSB_{MSY} and 0.5 SSB_{MSY} reference points in the HDA-SSB relationships, which are listed in Table 3.2. This table also lists the maximum recorded values of HDA and SSB for each stock, as well as the values of the indicators relative to their maximum recorded values when they are at SSB_{MSY} and 0.5 SSB_{MSY}.

Table 3.2 Values of SSB and HDA associated with HDA$_T$. The table shows percentages of SSB and HDA at the SSB$_{MSY}$ and 0.5 SSB$_{MSY}$ reference point, relative to their maximum recorded values and what this means in terms of actual amounts of SSB in tonnes, and actual proportion of tows falling within the HDA x category.

	Variable	Maximum recorded		At SSB$_{MSY}$	At 0.5 SSB$_{MSY}$
American Plaice	SSB	43012 t	Actual tonnes	32381	16191
			Standardized SSB	0.753	0.376
	HDA 5	8.16%	Actual%	5.79%	0.95%
			Standardized HDA 5	0.710	0.117
	HDA 10	15.7%	Actual %	11.3%	2.2%
			Standardized HDA 10	0.717	0.143
	HDA 15	22.2%	Actual %	15.5%	4.11%
			Standardized HDA 15	0.699	0.185
WSS Cod	SSB	88370 t	Actual tonnes	60000	30000
			Standardized SSB	0.679	0.339
	HDA 10	15.7%	Actual %	12.0%	3.6%
			Standardized HDA 10	0.765	0.231
	HDA 15	25.5%	Actual %	16.7%	6.18%
			Standardized HDA 15	0.655	0.242
ESS Cod	SSB	155525 t	Actual tonnes	125000	62500
			Standardized SSB	0.804	0.402
	HDA 2.5	8.3%	Actual %	6.06%	1.50%
			Standardized HDA 2.5	0.727	0.180
	HDA 5	12.2%	Actual %	9.98%	2.86%
			Standardized HDA 5	0.817	0.234
	HDA 10	21.4%	Actual %	17.5%	5.5%
			Standardized HDA 10	0.817	0.256
	HDA 15	31.0%	Actual %	25.0%	8.4%
			Standardized HDA 15	0.808	0.271
Redfish	SSB	209000 t	Actual tonnes	72500	36250
			Standardized SSB	0.347	0.173
	HDA 5	6.3%	Actual %	1.47%	0.14%
			Standardized HDA 5	0.236	0.023
	HDA 10	9.4%	Actual %	3.1	0.6%
			Standardized HDA 10	0.337	0.063
	HDA 15	13.3%	Actual %	5.2%	1.6%
			Standardized HDA 15	0.394	0.122
Silver hake	SSB	62850	Actual tonnes	20189	10094.5
			Standardized SSB	0.321	0.161
	HDA 2.5	3.7%	Actual %	0.43%	0.08%
			Standardized HDA 2.5	0.116	0.022
	HDA 5	5.7%	Actual %	1.14%	0.38%
			Standardized HDA 5	0.200	0.067
White hake	SSB	43908 t	Actual tonnes	26492	13246
			Standardized SSB	0.603	0.302
	HDA 10	15.1%	Actual %	12.9%	3.3%
			Standardized HDA 10	0.854	0.220
	HDA 15	18.6%	Actual %	16.5%	5.8%
			Standardized HDA 15	0.890	0.310

For example, Table 3.2 shows that the maximum value of HDA 10 (HDA 10_{max}) for ESS cod was reached in a year when 21.4% of all tows containing cod fell within that category. At the biomass level supporting a maximum sustainable yield, SSB_{MSY}, it can be observed that the HDA 10 tows make up 17.5% of all the tows that contain cod. That is equivalent to 0.817 HDA 10, considering that 17.5% of HDA 10_{max} (21.4%) is equal to a proportion of 0.817. At the level of overfishing (0.5 SSB_{MSY}), only 5.5% of all tows fall within the HDA 10 category (HDA 10 = 0.256) for ESS cod. This example is illustrated graphically by Figure 3.3.
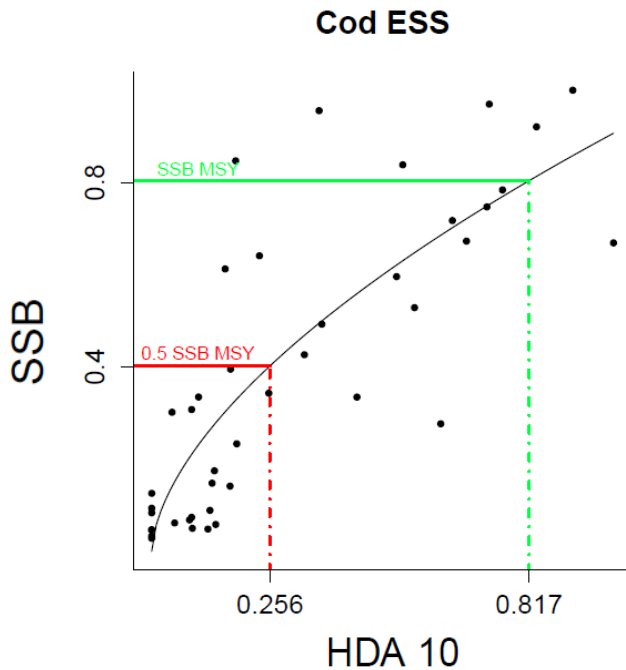
Figure 3.3   Position of SSB reference points in the ESS cod HDA 10-SSB relationship. The HDA and SSB values associated with 1.0 SSB_{MSY} (green) and with 0.5 SSB_{MSY} (red) indicate the proportions of the maximum recorded SSB and HDA 10 values (see Table 3.2).

Data for all six stocks exhibit a relationship that is significantly concave, meaning that the c-value or exponent value in the $SSB = b * HDA\ 10^{c}$ relationship deviates significantly from a value of 1 (linear relationship) for each stock. These concave HDA-SSB relationships reveal that stocks are most productive or at SSB_{MSY}, when HDA levels drop by no more than 30%, relative to the recorded maximum amount of HDA, i.e. they

are at approximately 70% or 0.7 HDA or higher (Table 3.2). Once HDA levels drop by 70% or more, relative to their recorded maxima (they are at 0.3 HDA or lower), SSB reaches a level at which it is considered overexploited (0.5 SSB_{MSY}), as depicted in Figure 3.4.
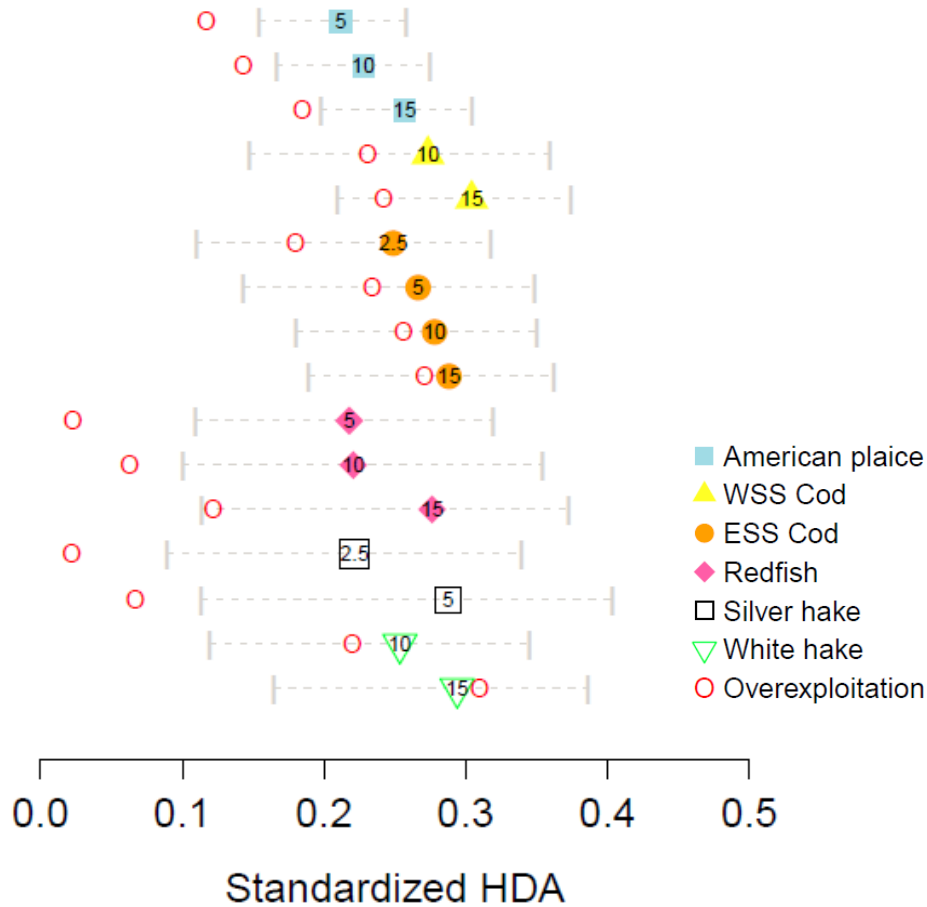
Figure 3.4 HDA_T values per stock per HDA x category. The x category is indicated by the number in the symbol. The HDA_T 95% prediction interval is based on semi-parametric bootstrap and the value of HDA associated with the overexploitation level (0.5 SSB_{MSY}) is indicated by the open red circle.

Redfish and silver hake however appear able to sustain a larger drop in HDAs than 70%, while still maintaining an elevated SSB. For example, redfish experiences a 66.3% decline of HDA 10 (0.337 HDA 10) before reaching SSB_{MSY}, while the level of overfishing is not reached until HDA has dropped by approximately 93.7% (0.063 HDA 10). Silver hake endures an 80% decline in HDA 5 before reaching SSB_{MSY} and a decline of more than 93.3% before reaching the overexploitation level.

SSB is expected to decline at an accelerating rate at low levels of HDA for all stocks: American plaice, WSS Cod, ESS Cod, redfish, silver hake and white hake. Table 3.3 lists the HDA_T values that indicate the point in the HDA x − SSB relationship, below which SSB declines occur that are relatively larger with each additional HDA x loss. The thresholds are situated between 0.2 and 0.3 HDA x (0.1 and 0.4 HDA x; 95% prediction interval) for all six stocks, the level at which 70% to 80% (60 to 90%; 95% prediction interval) of HDA x is lost relative to the maximum recorded amount of HDA x. Therefore, according to the fitted relationships, when a stock loses 70% to 80% (60 to 90%; 95% prediction interval) of its high density areas, disproportionately large SSB declines might occur. Table 3.3 also shows what part of the kg per tow distribution each HDA x category is comprised of. For example, ESS cod HDA 10 records 29.7 kg per tow at the 90th percentile of the biomass per tow distribution, and 6731.7 kg per tow at the maximum recorded catch within the survey; the 100th percentile. Thus, when the amount of tows that fall into the 29.7-6731.7 kg category decline by more than 72.2% (i.e. more than 0.278 Standardized HDA 10), a threshold is reached below which the decline in SSB per unit HDA 10 accelerates.

Table 3.3   Values of HDA x and SSB associated with HDA$_T$.
This table lists the values of the biomass (kg) per tow distribution associated with each HDA x category and the (standardized) SSB and HDA x values that correspond to HDA_T.

Stock	HDA x Category	Kg/tow distribution	Standardized SSB	Standardized HDA	Standardized HDA bootstrap 95% prediction interval
American plaice	HDA 5	36.1 - 674.2	0.473	0.212	0.154-0.258
American plaice	HDA 10	19.8 - 674.2	0.460	0.228	0.166-0.275
American plaice	HDA 15	13.4 - 674.2	0.446	0.257	0.198-0.305
WSS cod	HDA 10	50.6 - 927.5	0.374	0.273	0.147-0.359
WSS cod	HDA 15	40.9-927.5	0.397	0.304	0.209-0.374
ESS cod	HDA 2.5	136.2 - 6731.7	0.472	0.249	0.110-0.318
ESS cod	HDA 5	64.2 - 6731.7	0.432	0.266	0.143-0.348
ESS cod	HDA 10	29.7 - 6731.7	0.422	0.278	0.180-0.350
ESS cod	HDA 15	36.0 - 6731.7	0.418	0.288	0.189-0.362
Redfish	HDA 5	400.0 - 3686.2	0.336	0.218	0.109-0.319
Redfish	HDA 10	176.8 - 3686.2	0.293	0.221	0.100-0.354
Redfish	HDA 15	89.7 - 3686.2	0.281	0.276	0.114-0.372
Silver hake	HDA 2.5	112.1 - 2510.5	0.419	0.222	0.098-0.339
Silver hake	HDA 5	63.8 - 2510.5	0.404	0.288	0.113-0.403
White hake	HDA 10	31 - 378.4	0.324	0.254	0.119-0.345
White hake	HDA 15	20.8 - 378.4	0.291	0.294	0.165-0.386

The selection of a particular HDA x category that yields a concave relationship with SSB does not appear to significantly affect the position of the HDA_T: for each stock the HDA_T resulting from the relationship between SSB and a particular HDA x category, falls within the 95% prediction intervals of the HDA_T in other HDA x categories (of that same stock).

When thresholds are compared to the level of overexploitation, the thresholds and their 95% prediction intervals either intersect with the level of overexploitation or the thresholds are situated above the HDA x level corresponding to the level of overexploitation (see Figure 3.4 and Appendix A, B, C, G, H, I). For example, in the case of ESS cod (Figure 3.5) WSS cod, and white hake, HDA_T is situated above 0.5 SSB$_{MSY}$, but 0.5 SSB$_{MSY}$ falls within the 95% prediction intervals of the HDA_T. For American plaice, redfish and silver hake HDA_T is located at significantly higher levels than the HDA x values associated with 0.5 SSB$_{MSY}$ (apart from redfish HDA 15, where HDA 15 levels associated with 0.5 SSB$_{MSY}$ fall within the lower prediction interval of HDA_T).

Redfish and silver hake HDA_T and 95% prediction intervals are actually positioned closer to HDA x levels associated with SSB_{MSY}, than to 0.5 SSB_{MSY} (see Appendix G and H).

Cod ESS
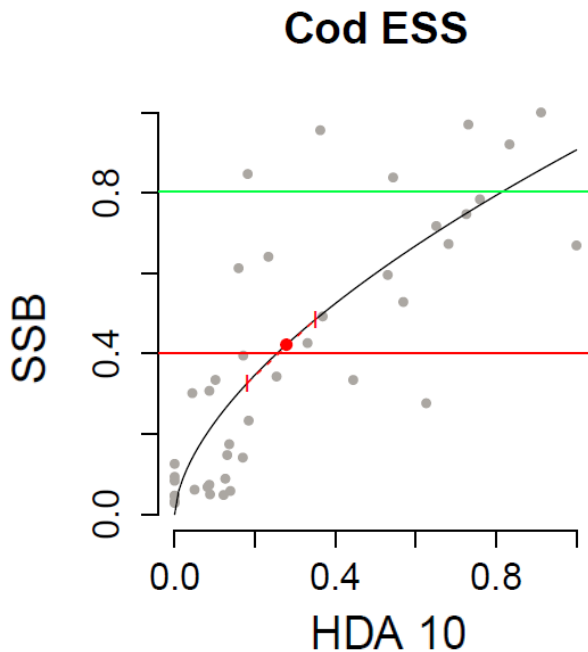
Figure 3.5 ESS cod HDA10-SSB and spatial threshold HDA_T. This example for ESS cod HDA 10 and SSB shows the spatial threshold (red dot) and its 95% prediction interval based on a semi-parametric bootstrap, compared to the level of optimal production (SSB_{MSY}; upper horizontal line in green) and the level of overexploitation (0.5 SSB_{MSY}; lower horizontal line in red). Appendix A, B, C, G, H, I contain plots of HDA_T compared to SSB reference points for ESS cod other stocks

3.4   Discussion

Reduced abundance and diminished spatial distribution each contribute to an increase in species extinction risk. As abundance and range are also related, populations can face a situation of double-jeopardy (Lawton 1993). Conversely, an increase in both spatial distribution and abundance might have a synergistic effect on populations, which can only be appreciated if the link between species spatial distribution and abundance is understood (Gaston et al. 1999, Overholtz 2002, Fisher and Frank 2004).

There is a clear relationship between spatial distribution in the form of HDAs and abundance in the form of SSB for six demersal marine fish stocks (five species). Moreover, HDA has the potential to serve as a spatial indicator for large SSB declines because of the concave, non-linear relationship that exists between HDA and SSB. This

allows for the identification of a spatial threshold that marks the point in the relationship below which the decline in SSB per unit HDA accelerates. For two out of the six stocks demonstrating this concave relationship (ESS cod, WSS cod) declines in HDAs also precede rapid SSB declines (Table 2.4, Figure 2.7). For these stocks the spatial indicator HDA might therefore have potential to serve as an early indicator for rapid SSB declines.

The spatial thresholds fall roughly between 0.2 and 0.3 HDA (0.1-0.4 HDA; 95% prediction interval; see Figure 2.5). This indicates that a 70%-80% loss (60%-90% loss; 95% prediction interval) of high density areas is associated with potentially very large SSB declines and -in case of cod- potentially very rapid SSB declines. Ideally, a stock's HDAs would remain at levels above the spatial threshold, given that below this threshold additional declines in HDA are associated with disproportionately large decreases in the biomass of spawning adults.

For WSS cod, ESS cod, and white hake the level at which the stock is overexploited (0.5 SSB_{MSY}) coincides with the stock's spatial threshold HDA_T and its 95% prediction interval. The spatial thresholds of American plaice, silver hake and redfish occur at levels significantly higher than 0.5 SSB_{MSY}. Spatial reference points can complement the use of biomass reference points when the HDA_T is situated above the level that triggers management action. In case management action is not triggered until a stock falls below 0.5 SSB_{MSY}, it appears that for American plaice, silver hake and redfish, a limit reference point of 0.5 SSB_{MSY} may not be safe to avoid surpassing the spatial threshold that marks a point of accelerated SSB decline with each additional loss of HDA. Accepting a limit reference point of 0.4 SSB_{MSY} (Canada) would mean accepting an even higher risk that such a spatial threshold is surpassed. Another scenario where a spatial reference point brings added value to existing biomass reference points is when HDA x declines precede rapid SSB declines and when HDA levels drop below the overexploitation level before SSB does. In that case, a spatial reference point is relevant regardless of whether HDA_T is situated significantly higher than the overexploitation level or within the 95% prediction interval of HDA_T.

We suggest that the spatial indicator HDA could serve a role in fisheries management to avoid a collapse and promote recovery of stocks, by ensuring stocks reach or stay at levels above the limit spatial threshold and reach spatial distribution

levels that are associated with a productive SSB or higher (>1.0 SSB_{MSY}). Staying above the HDA_T and its 95% prediction intervals would translate into a LRP of 0.3-0.4 Standardized HDA (depending on the stock; see Figure 3.4), i.e. 60%-70% loss of high density areas compared to the maximum observed amount. TRPs could be set to ensure that HDA stays within levels associated with a productive SSB; > 0.7 HDA or less than 30% HDA decline relative to its recorded maximum appears to be a relatively safe zone for all examined stocks (see HDA values at SSB_{MSY} in Table 3.2), although according to this analysis a target > 0.4 would suffice for redfish HDA 5, 10, 15 and for silver hake HDA 2.5, 5.

Based on the analysis, it appears that HDA, as an expression of spatial structure, and its often non-linear relationship with SSB yields an opportunity for the extraction of spatial thresholds and development of spatial reference points. As long as a concave relationship is detected between HDA and SSB, the choice for what part of the biomass per tow distribution within the top 15% constitutes 'high' in HDA does not appear to significantly affect the SSB-HDA relationship and associated thresholds. The utility of HDA is arguably further enhanced by its foundation on fisheries independent survey data. Considering that SSB estimated from stock assessment methods is typically known with much less certainty than estimates from fisheries-independent survey trawls (Mesnil et al. 2009), HDA could be of added value to fisheries management.

Certainty and reliability of assessment methods decline especially when stocks are depleted, and alternate, independent stock indicators that can detect changes in productivity, environment and spatial distribution are therefore desirable (Caddy and Agnew 2004). The development of more empirically based reference points, such as HDA_T, can help to decrease the risks associated with exclusively applying model based reference points and provide more information regarding the health of a stock (Hilborn and Stokes 2010).

As with all reference points, there is error and uncertainty associated with the use of HDA_T as a spatial reference point. Error might stem from a misspecification of the modeled relationship between SSB and HDA. The finding that HDA_T is situated between 0.2 and 0.3 HDA (0.1-0.4 HDA; 95% prediction interval), may simply be a function of the fitted relationships, where the curve is forced through the origin; HDA_T would

understandably be situated in the lower values of HDA. However, the applied model is supported by both a better fit of the power function (model 1) versus a linear model and is supported by the range of data for the examined stocks. When looking at the data points between HDA 10 and SSB (Figure 2.6), it is clear that the higher HDA values are associated with mostly high SSB values, whereas at ~ 0.4 HDA and below (i.e. losing more than 60% of HDAs), SSB values drop to low levels. For American plaice however, data below 0.36 SSB is not available. Error in the analysis may also stem from survey results not accurately reflecting the reality of the stock's biomass distribution across space, which could affect both the assessed relationships and the lagged cross correlation between HDA x and SSB. Uncertainty may come with the choice for a specific HDA category, although the HDA-SSB relationship and associated thresholds appear robust when the HDA category is within the top 15% of the biomass per tow distribution. However, selecting an HDA x category that is too high may result in recording a lot of zero values and leaving the HDA indicator too insensitive. Due to its inherent uncertainty, HDA is considered of value as a spatial reference point to be used in conjunction with other stock health indicators and reference points.

The utility of using high values of survey kg per tow has been previously recognized and proposed as a reference point in fisheries management (Hutchings 1996). For example, an average of 55 kg per tow currently demarks the limit reference point for northern cod (DFO 2011). This 55 kg/tow estimate would fall within the HDA 10 and HDA 15 category for both ESS and WSS cod stocks, so from the analysis it appears that, for cod, the estimate of 55 kg/tow as a reference point would indeed be useful from a spatial perspective. Average weight per tow has been used as an indicator of stock health (Link et al. 2011a) and as a biological reference point, for example as SSB_{MSY} proxy, by the U.S. National Oceanic and Atmospheric Administration (NEFSC 2008). However, unlike the average weight per tow, HDA x measures the number of tows (as a percentage of tows) that fall within the HDA x category and therefore reflect the number of areas that contain high densities across a stock's total area. Compared to using the average weight per tow, HDA x is arguably a more sensitive spatial indicator in terms of indicating changes in high density across area, and in terms of its ability to prelude SSB declines.

In fisheries management, the value of applying spatial reference points has been identified in particular for sedentary and semi-sessile species; spatial structures and effects of local densities on growth rate, natural mortality (by predation or disease) and spawning success have been documented (Shackell et al. 2013). Hence, the use of indicators that reflect, for example, the production per habitat area have been accepted for these species (Caddy 2004). Spatial structures are also increasingly detected in finfish populations, and the importance of spatial structures in terms of preceding changes in abundance of populations has been recognized (Ciannelli et al. 2013).

Current developments in fisheries policy and management provide an opportunity for the integration of spatial reference points. For example, the European Commission, in its Common Fisheries Policy, has determined that fish stocks are to be maintained within 'safe biological limits' (EC 2002) and current policy states that the aim is to achieve MSY goals for depleted stocks on an urgent basis, but no later than 2015 (EC 2006)[2]. From this analysis, it appears that spatial distribution is relevant to reproductive capacity and for maintaining stocks within 'safe biological limits' and there appears to be merit in assessing the potential of spatial reference points to maintain healthy and resilient fish stocks. Expanding this research to include more stocks across other management zones could help test the generality of HDA as a spatial indicator. The development of empirically derived spatial distribution indicators such as HDA would serve a precautionary management approach and would fit within global policy changes towards an MSY and a more ecosystem-based approach to fisheries management (Cotter et al. 2009b).

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[2] With regard to the MSY approach, the European Union's scientific advisory body defines 'safe biological limits' as having full reproductive capacity, whereby SSB is larger than MSY $B_{trigger}$ (the parameter which triggers advice on a reduced fishing mortality relative to F_{MSY}, where MSY $B_{trigger}$ is considered the lower bound of fluctuation around B_{MSY}) and $F < F_{MSY}$.

CHAPTER 4   Conclusion

4.1   Summary of Findings

With this thesis, I explore whether the creation of spatial reference points could add value to fisheries management in addition to currently used biomass reference points. In Chapters 2 and 3, a number of scenarios are described wherein spatial indices and reference points might contribute value. These scenarios are summarized below for the three types of SDM-SSB relationships:

I.   Non-linear, concave SDM-SSB relationship:

   A.   In situations for which resources or data do not allow for annual SSB assessments, a SDM that is significantly correlated with SSB could serve as a proxy for SSB. This means that a spatial reference point associated with biomass reference points, such as the level of SSB that is considered productive for fisheries (~1.0 SSB_{MSY}), would have to be set. Historic data are needed to determine the relationship between the SSB and SDM. For data-poor fisheries, spatial reference points could potentially be derived from a comparable stock.

   B.   When the current SSB limit reference point dictating management measures is situated at lower levels than the spatial threshold (indicating the point below which the decline in SSB per unit SDM accelerates and thus indicating that additional declines in the SDM are associated with disproportionately large decreases in the biomass of spawning adults), a spatial limit reference point could be implemented to increase the probability that the stock remains above that spatial threshold. Even though in this scenario the SDM is not predictive, the fact that an additional loss of the SDM is associated with disproportionately large declines in SSB can signal caution to fisheries managers.

   C.   In situations where changes in SDM precede changes in SSB, SDMs can be especially relevant to fisheries management, considering that the SDM will reach certain limits and targets before these are reached by SSB. For example, if the SDM decreases to the spatial threshold corresponding to a higher SSB than the SSB overexploitation level that would normally trigger meaningful fisheries management action, the spatial limit reference point set at the spatial threshold

would trigger management action at an earlier and more precautionary level. This could help prevent the SSB from collapsing to (and beyond) overexploited levels of abundance.

II. Linear SDM-SSB relationship:

A. The SDM and spatial reference points that are associated with existing SSB reference points could serve as a proxy for SSB when resources or data do not permit annual SSB assessments.

B. A limit and/or target reference point could be set, based on the SDM values associated with the SSB reference points, in cases where the SDM changes precede (proportional) changes in SSB. That is because the SDM might reach the SSB limit or target reference point before the SSB would reach these reference points, which would be informative for fisheries management.

III. Non-linear, convex SDM-SSB relationships:

A. A spatial reference point could contribute as a target reference point to achieve a level of spatial distribution associated with a level of SSB that is considered productive for fisheries (1.0 SSB_{MSY}) or healthy for the population and ecosystem (e.g. $\sim 1.3 \text{ SSB}_{MSY}$).This would add value to the existing SSB target reference point in case resources or data do not allow for an annual SSB assessment.

B. For a type III SDM-SSB relationship, a target SSB is achieved only after the SDM has attained relatively high SDM levels. A spatial threshold can be estimated to indicate the point above which the increase in SSB per unit SDM accelerates and beyond which healthy SSB levels are likely to occur. When the spatial threshold is situated at higher levels than the existing SSB limit reference point dictating management measures, a spatial limit reference point could add value. A spatial reference point would not be of additional value when the spatial threshold is situated at or below the SSB limit reference point because management measures would already have been triggered.

C. A spatial limit and/or target reference point is of added value to SSB reference points when the SDM precedes rapid changes in SSB. That is because the SDM might reach the SSB limit or target reference point before the SSB reaches that reference point, and this could be informative for fisheries management.

For each stock, the SDM-SSB relationships differ. However, some general patterns emerge from this study. In Chapter 2, the shape of the relationship between various SDMs and SSB in several fish stocks on the Scotian Shelf is assessed. In general, D90%, Gini index and medium density areas for several stocks were found to be linearly (type II) related with SSB (Table 2.2 and 2.3). These SDMs could thus serve as a proxy as described in scenario II-A. Scenario II-B was not examined.

AO, ZDAs and LDAs generally follow a type III or convex relationship with SSB (Table 2.2), whereby large fluctuations in SSB are associated with relatively small fluctuations of the SDM (at a relatively high level of the SDM). At relatively low levels of SSB, there are large fluctuations in the associated SDM values. SSB appears sensitive to changes at higher levels of these SDMs and large SSB values only occur when a certain level of e.g. range is occupied. Thus, a spatial limit reference point could be set at a minimum level of range associated with higher SSB values or at a spatial threshold in case Scenario III-B applies. Considering the type III shape of these SDM-SSB relationships, the spatial target reference point is probably situated relatively close to the spatial limit reference point; to assess the added value of reference points in scenarios III-A and III-B, additional analyses would be required. The increase in AO precedes a rapid increase in SSB for winter flounder, and for ESS and WSS Atlantic cod. The same III-C scenario applies to ZDA and LDA for ESS cod and ZDA for winter flounder.

HDAs were most often related to SSB and they generally follow a concave relationship with SSB, in which HDAs decline faster per unit SSB until a threshold is reached, below which each additional decline in HDAs is associated with a disproportionately larger SSB decline. Thus, according to the relationship, below the threshold the stock enters a "zone of potentially serious harm" where each additional loss of a HDA coincides with an accelerated decrease in SSB. For the stocks that have a significantly concave relationship between HDA and SSB (American plaice, ESS cod, WSS cod, redfish, silver hake, white hake), I assessed the levels of HDA relative to existing biomass reference points SSB_{MSY} in Chapter 3. This information could serve as described in scenario I-A. Generally speaking across stocks, if HDAs do not decline to more than 30% relative to their maximum recorded level, SSB will still be productive

(1.0 SSB_{MSY}). If HDAs decrease more than 70%, stock SSB will be at a level at which it is deemed overexploited (0.5 SSB_{MSY}). The HDA threshold for American plaice, silver hake and redfish is associated with a higher SSB level than 0.5 SSB_{MSY}. This indicates that the limit reference point of 0.5 SSB_{MSY} would not be safe to avoid erosion of HDAs down to a spatial threshold marking the point below which SSB declines become disproportionately larger with each additional HDA decline (scenario I-B). For ESS cod, WSS cod and white hake the HDA threshold that marks the point below which SSB per unit HDA declines accelerate, approximately coincides with the level of overexploitation. A spatial reference point would not add value in this situation where the spatial threshold is situated at or below the biomass limit reference point. That is because measures would already be triggered by the biomass reference point, unless there is no SSB assessment and HDA can be used as a proxy (scenario I-A). However, for ESS cod and WSS cod, a spatial reference point would add value, considering that for these stocks HDA precedes changes in SSB (scenario I-C).

There are a number of issues that must be taken into account when using HDA as a spatial indicator. First of all, a scientific survey might not reflect the real spatial distribution and changes in the real distribution might go undetected. Therefore, it is best that HDA be used in addition to SSB and in conjunction with other indicators to assess the state of a population. Secondly, for one stock (American plaice), SSB data at very low levels were not available. An increasingly larger SSB per unit HDA decline below the spatial distribution threshold may, therefore, not be more than a function of forcing the relationship through the origin (even though the data in other stocks support the assumption that the function passes through the origin). In the case of American plaice, it would be more precautionary to assume a forcing of the HDA-SSB relationship through the origin, rather than to assume that SSB remains high when there are no more HDAs.

That HDAs are important to SSB is supported by mathematics, because a higher proportion of the total biomass is likely located within the HDA as total biomass declines, but - considering the range of values incorporated into HDA (Table 3.3) - this is not necessarily the rule. Furthermore, the importance of HDAs is supported by the time series analysis, as well as by ecological theory. According to density dependent habitat selection, HDAs may be indicative of highly productive areas. Furthermore, high density

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aggregations are considered important for fish to locate prey, successfully spawn and evade predators.

4.2   Implications and originality of research

When comparing different SDMs in their relationship with SSB among various stocks, HDAs are relatively more often significantly and concavely related to SSB and have potential as a spatial indicator to add value to currently existing SSB reference points. Firstly, when compared to other spatial indices, it is a sensitive measure able to indicate occurrence of disproportionately large declines in SSB for various stocks. In cod stocks it appears able to signal rapid SSB declines even before a decline in SSB is observed. Secondly, HDA is derived from a scientific survey and incorporates less uncertainty and error than stock assessment models that incorporate numerous variables associated with error and uncertainty, especially catch data. In addition, by using survey data, fisheries managers have access to more rapid updates on the state of the stocks. HDAs could also serve well as a spatial indicator in data-poor fisheries and would arguably be more sensitive than average biomass per tow or average catch per unit effort.

Even though the relationship between spatial distribution and abundance has been established for a number of fish species, it has not previously been assessed between spatial distribution and the reproductive component of the population (SSB) or translated into spatial reference points. Also novel is the assessment of the threshold in the concave relationship between SSB and HDA, with which I introduce a method from medical science to fisheries science. With this method I am able to assess the position of the threshold, which then permits an assessment of the added value of spatial limit reference points to existing SSB limit reference points.

One potential implication of this research is that it could create a possibility to monitor simple, survey-based spatial indicators that are meaningful in their ability to indicate spatial distribution levels associated with productive and overexploited SSB levels. Another implication could be incorporation of the HDA indicator into cod fisheries management on the Scotian Shelf, given that HDA constitutes a simple, survey-based spatial indicator that can serve as an early warning for SSB declines. The identified spatial thresholds can help to define spatial limit reference points. The method that I

applied to assess the added value of spatial indices to currently used biomass reference points is easy to replicate for other indices that have non-linear relationships with SSB.

For future research, it would be interesting to test the generality of HDA as an (early) indicator for SSB declines by incorporating other species and similar species in other areas. For example, HDAs were already shown to be an important indicator for northern cod abundance (Hutchings 1996) and now also for ESS and WSS cod. Would the SSB of other cod stocks in other parts of the Atlantic Ocean show similar responses to changes in HDA? It would also be interesting to obtain relative values of the SDM and SSB by scaling these to 1.0 SSB_{MSY}, instead of the historically maximum observed values. By so doing, the patterns and trends would be informative when considering a spatial reference point in fisheries management of a stock for which historical data are lacking. If HDAs are to be incorporated into fisheries management, it would also be valuable to analyse what management measures could contribute to the persistence of high density areas, e.g. marine protected areas, seasonal and real time closures, overall effort control etc.

The present research contributes to our understanding of the relationship between spatial dynamics and spawning biomass for different fish stocks. It supports the notion that heterogeneous spatial distributions are important to consider in fisheries management. It contributes to fisheries management in terms of assessing spatial distributions needed to enable the recovery and to help prevent the (future) collapse of selected fish stocks on the Scotian Shelf. More generally, it contributes in terms of demonstrating how to locate a spatial threshold, which indicates (potentially imminent) changes in the SSB rate of increase or decrease per unit SDM. Furthermore, this research discusses the scenarios wherein such a spatial threshold would contribute to existing SSB reference points.

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APPENDIX A   American plaice 4VWX SDM-SSB plots

Significant SDM-SSB relationships are marked with a I, II or III for a significant type I, type II or type III relationship.
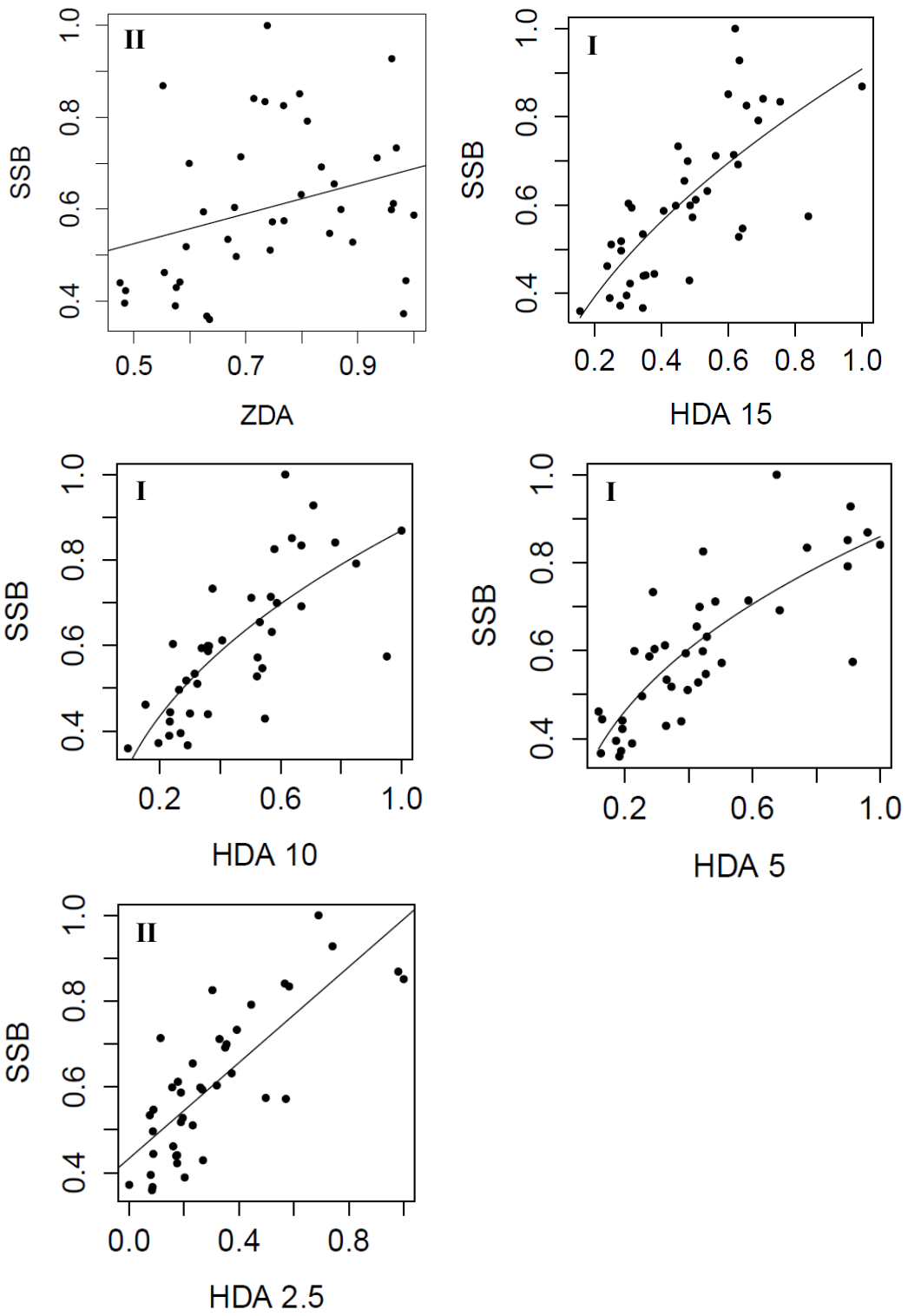
American plaice 4VWX time series analysis

SDM and SSB residuals over time (left), with associated cross-correlation function (right)
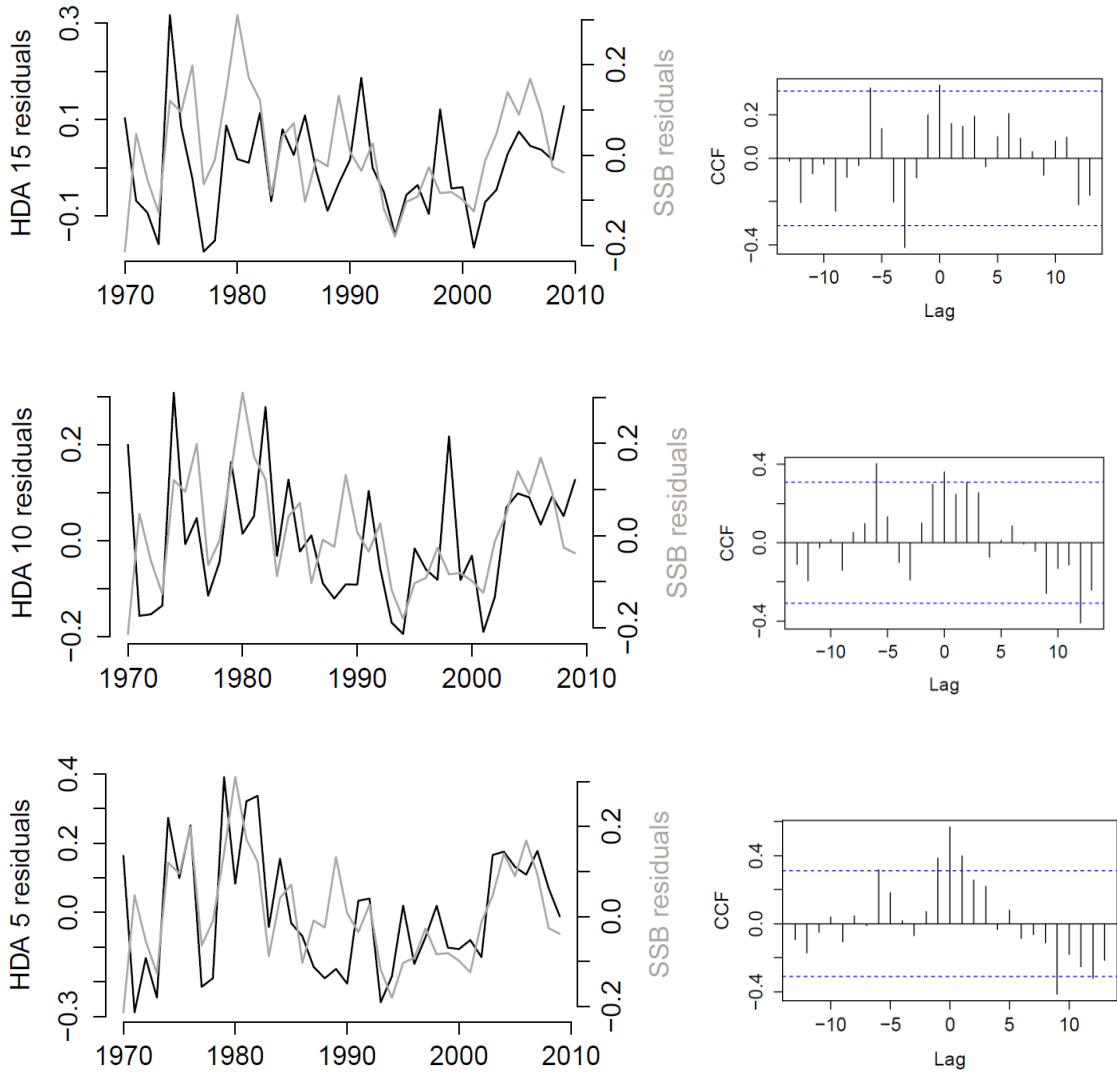
American plaice 4VWX HDA threshold
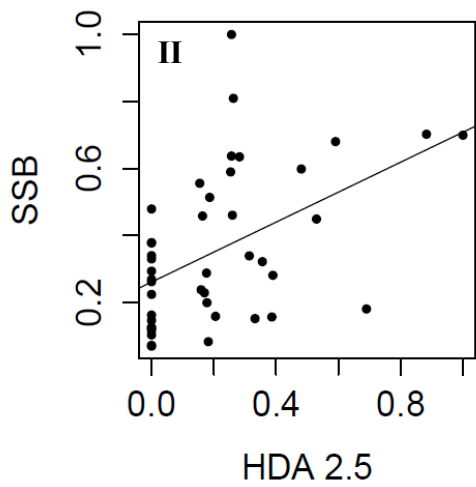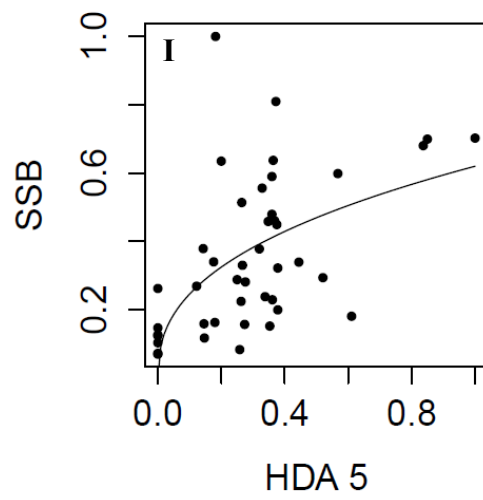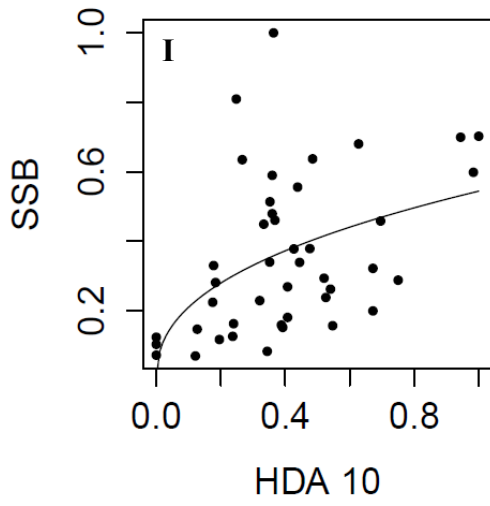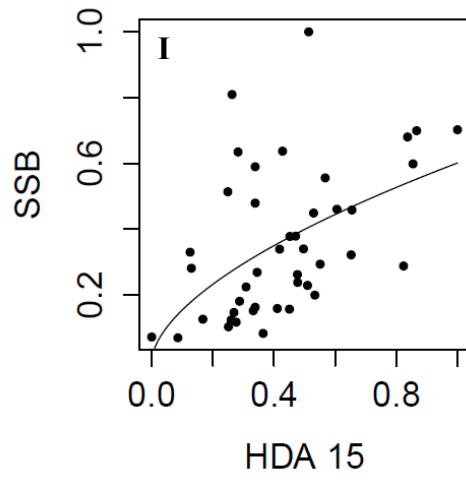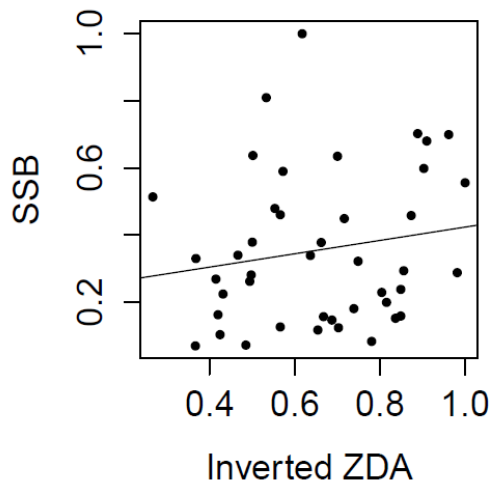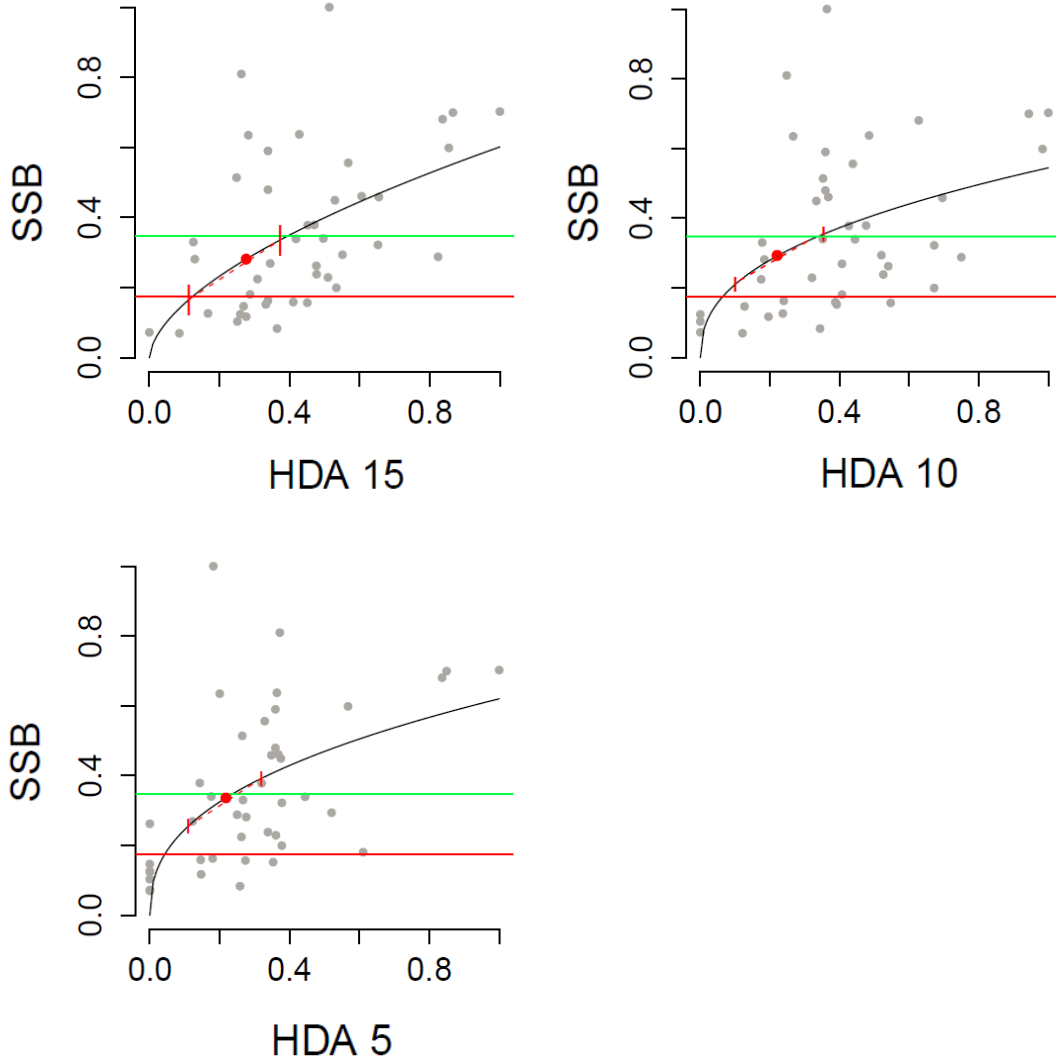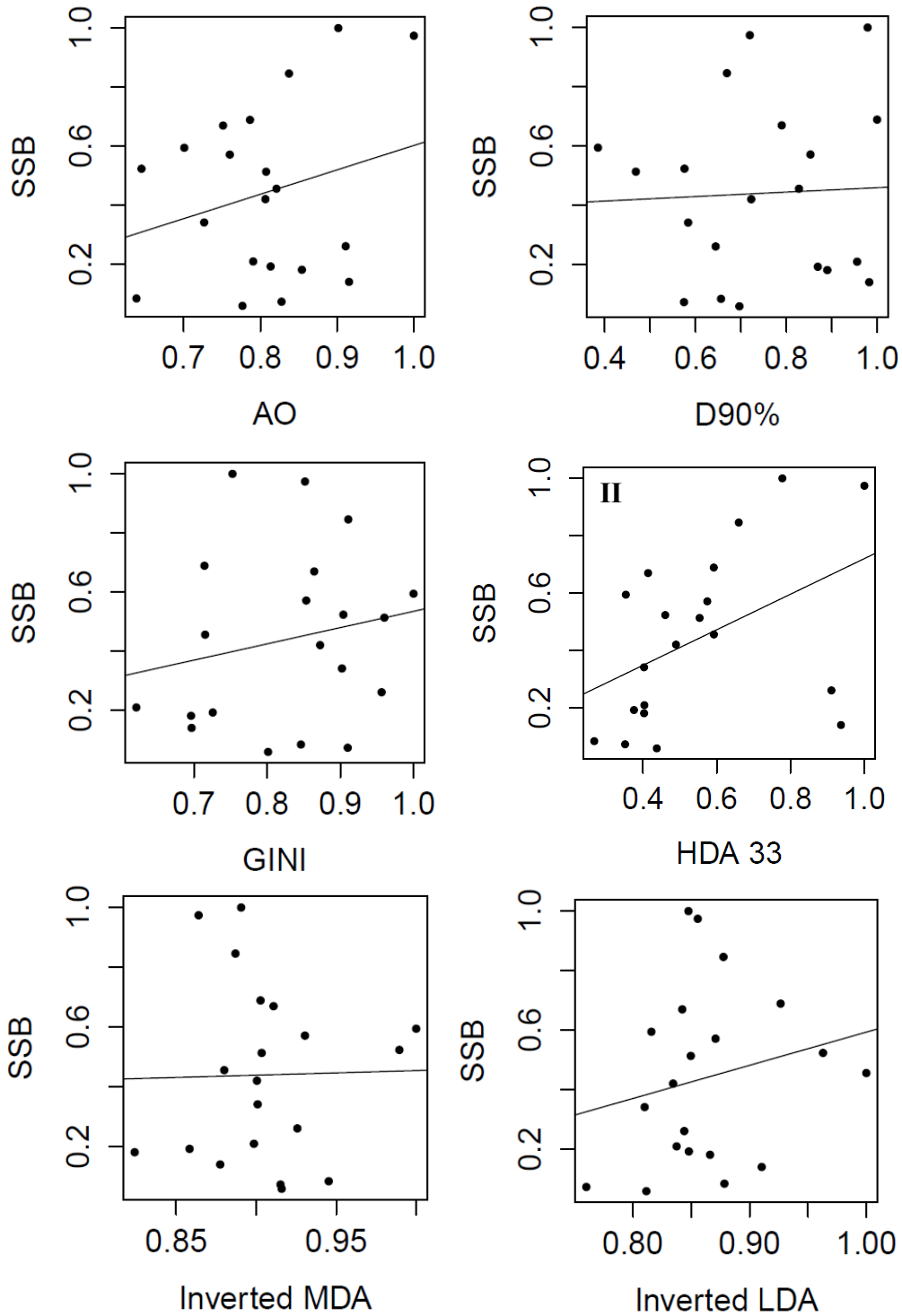
HDA_T indicated by red dot, including 95% prediction interval. Upper, horizontal green line indicates 1.0 SSB_{MSY} level; lower, horizontal red line indicates 0.5 SSB_{MSY} level.
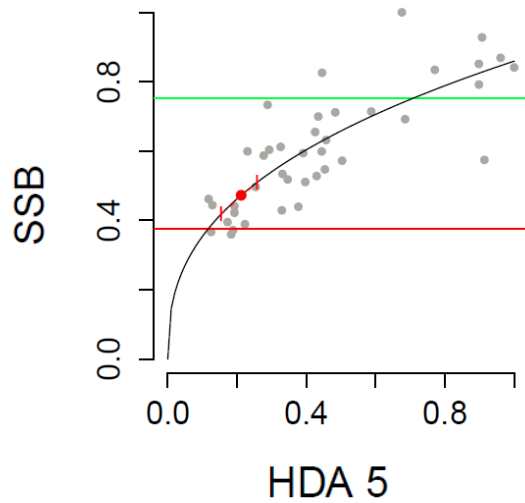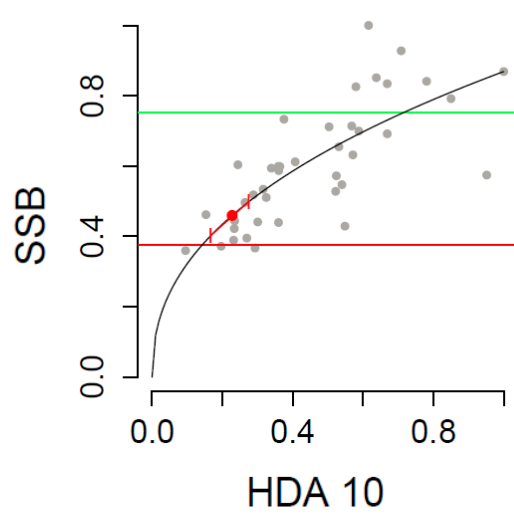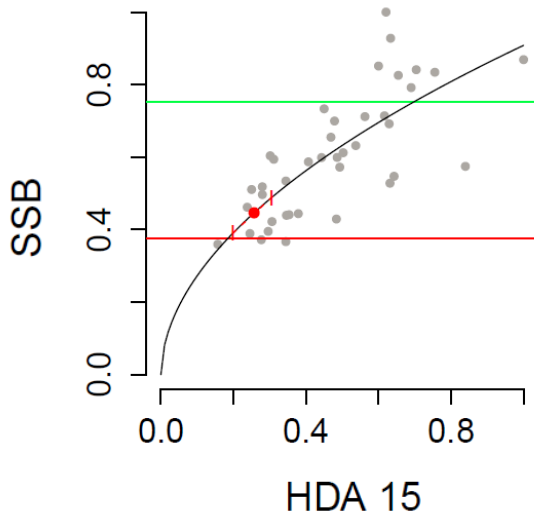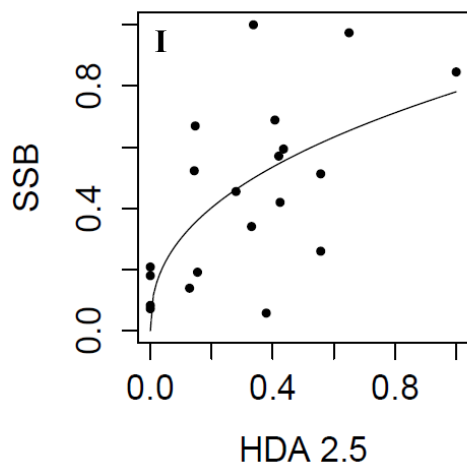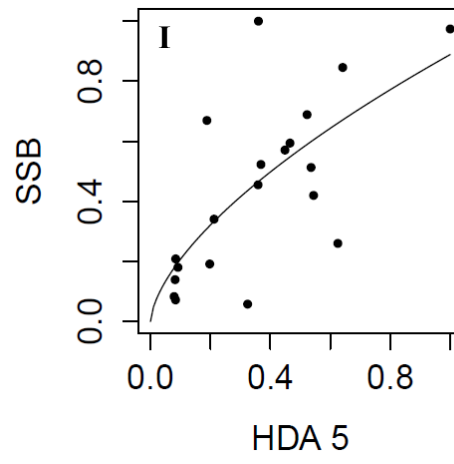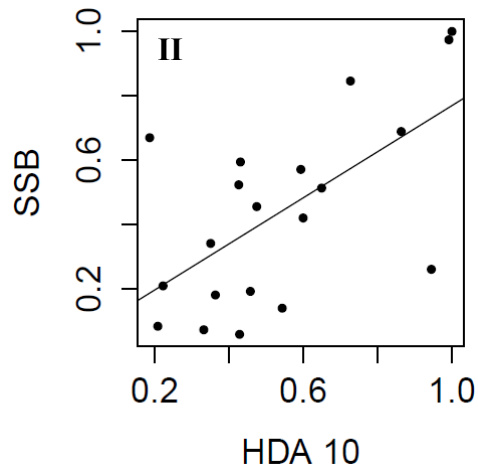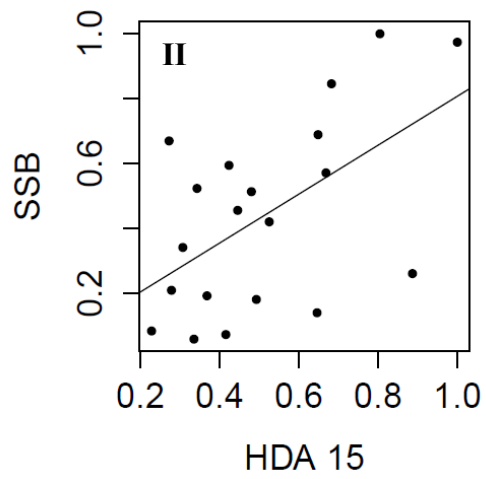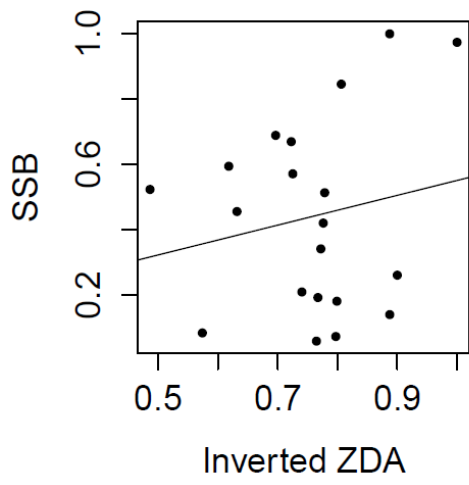
APPENDIX B   Cod ESS (4VsW) SDM-SSB plots

Significant SDM-SSB relationships are marked with a I, II or III for a significant type I, type II or type III relationship.
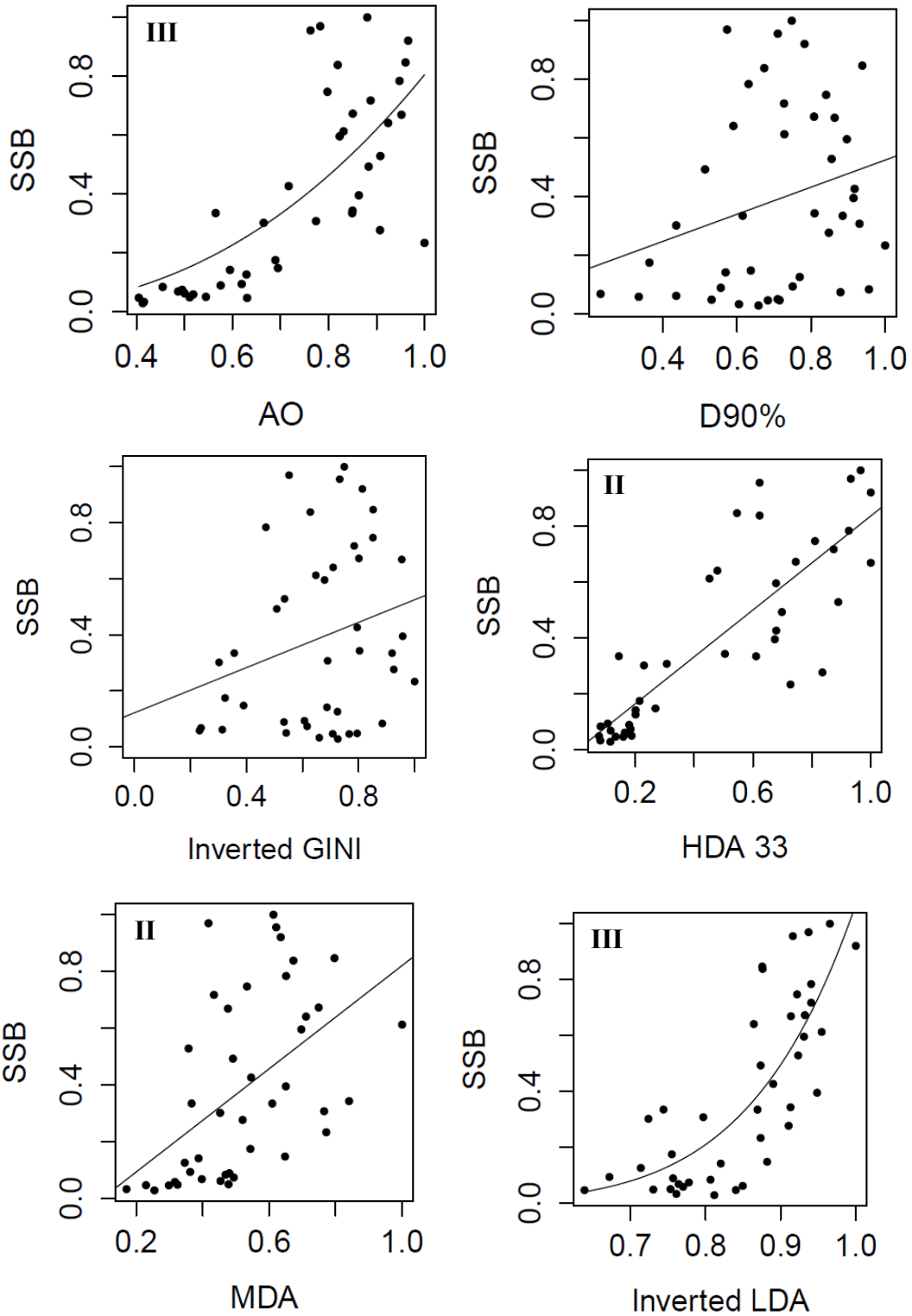
APPENDIX C   Cod ESS (4VsW) SDM-SSB plots (continued)
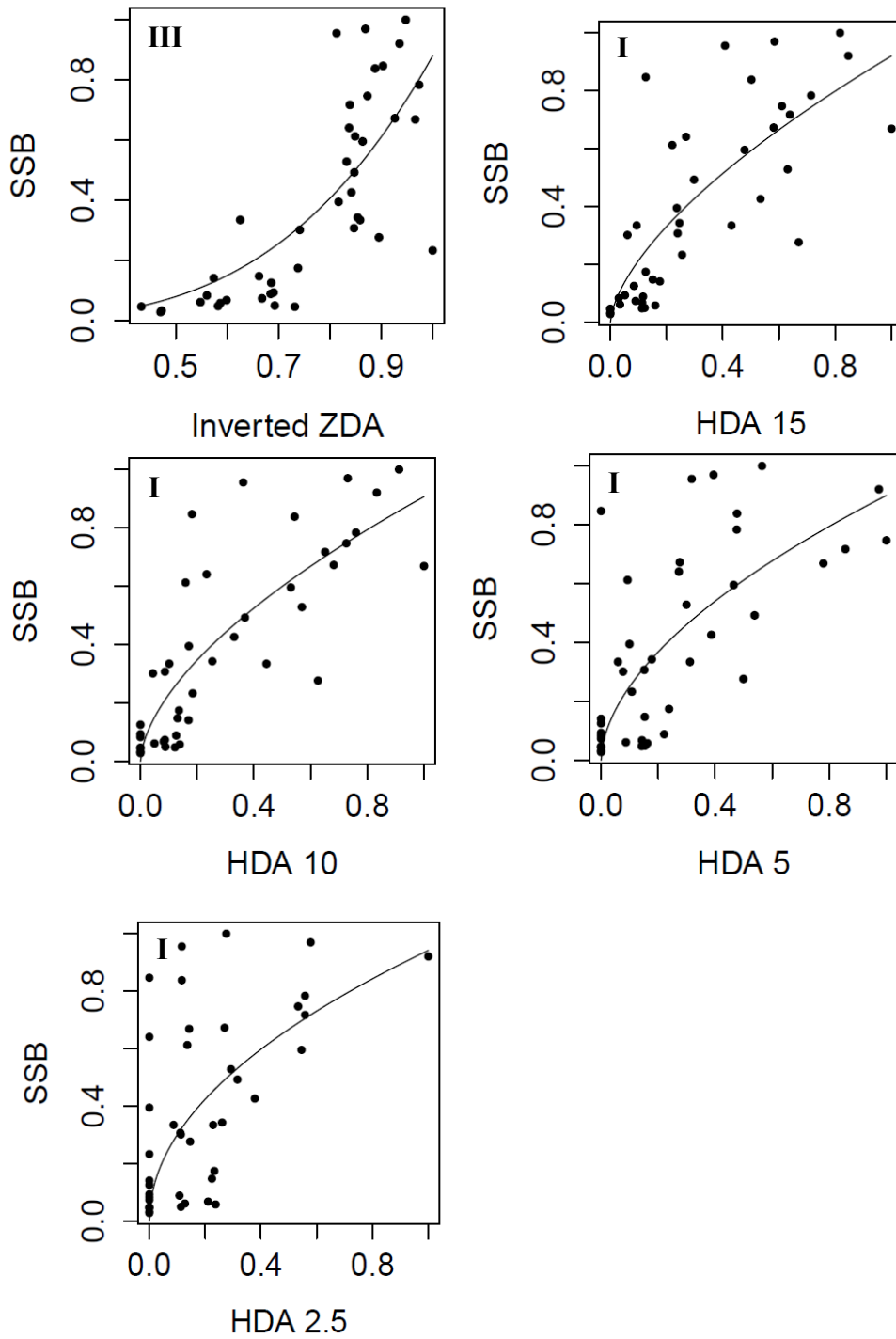
Cod ESS (4VsW) time series analysis

SDM and SSB residuals over time (left), with associated cross-correlation function (right)
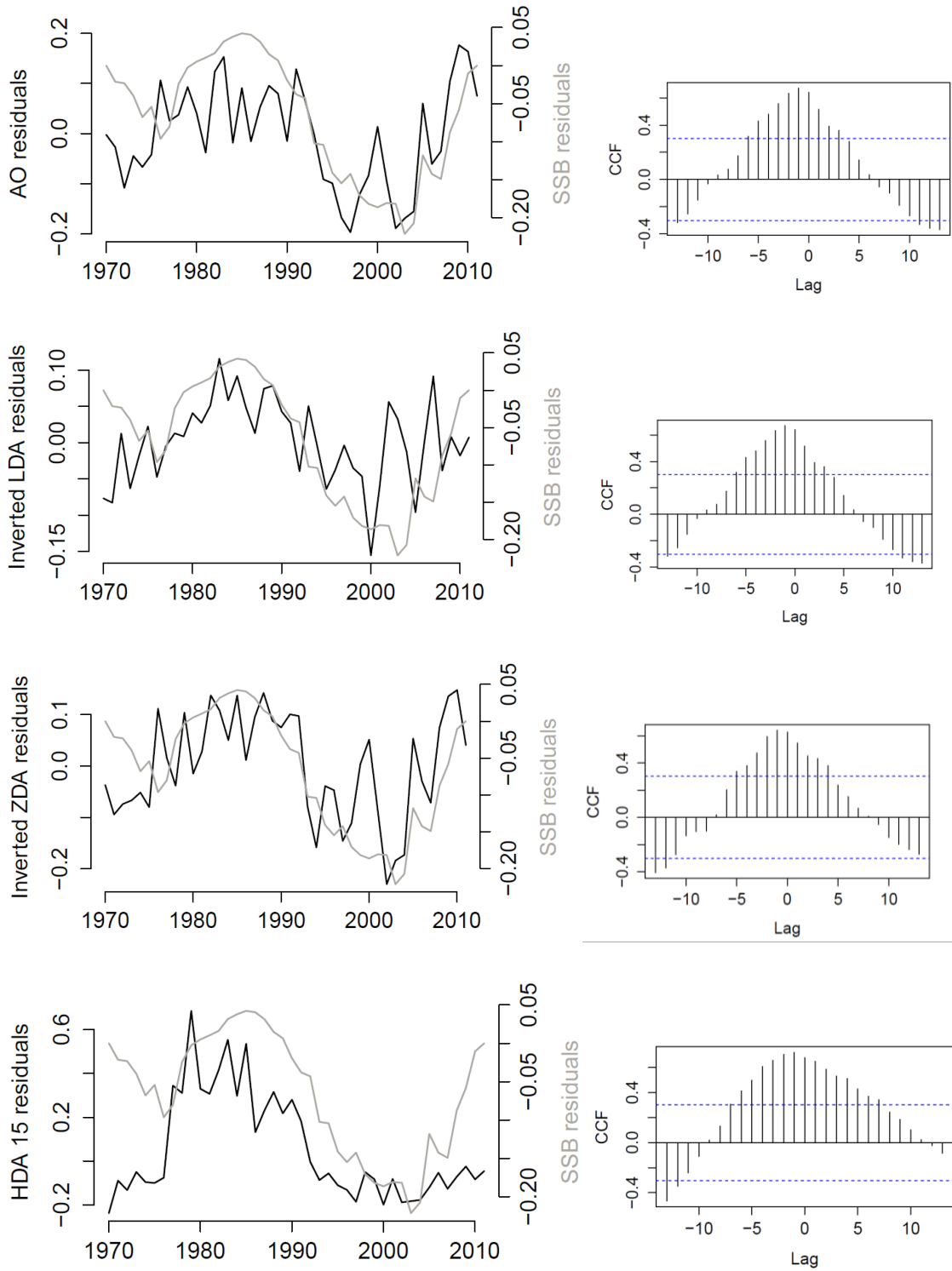
Cod ESS (4VsW) time series analysis (continued)
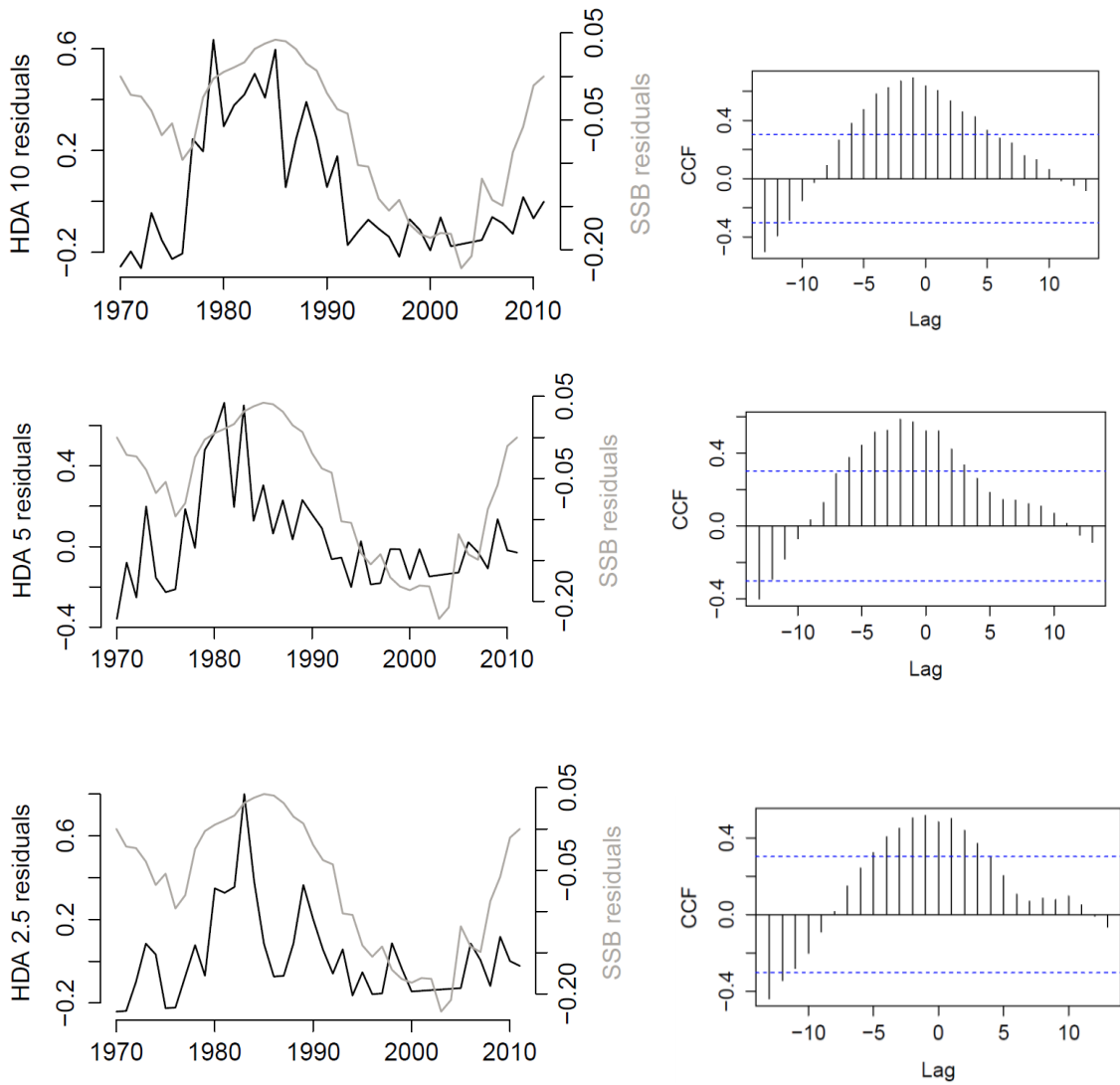
Cod ESS (4VsW) HDA threshold

HDA_T indicated by red dot, including 95% prediction interval. Upper, horizontal green line indicates 1.0 SSB_{MSY} level; lower, horizontal red line indicates 0.5 SSB_{MSY} level.
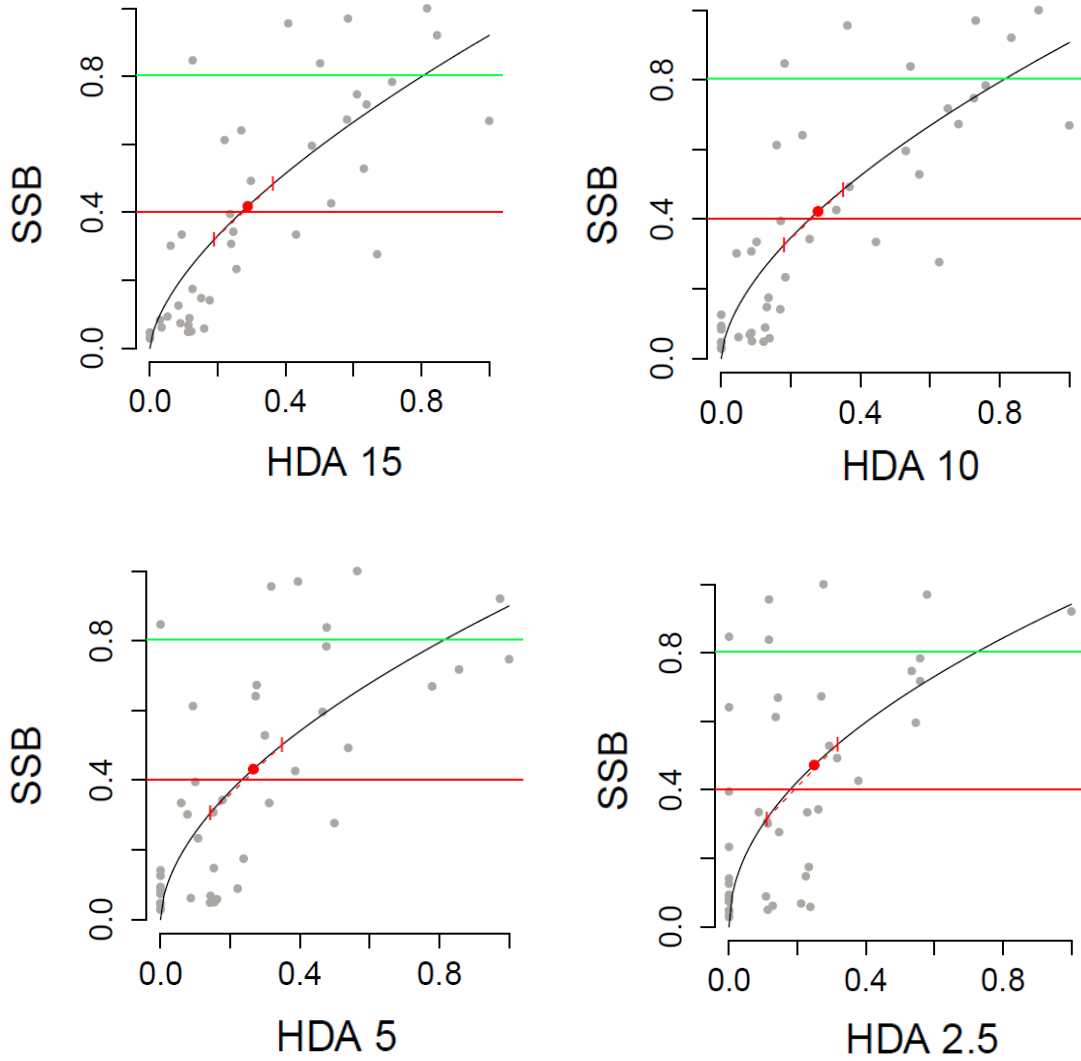
APPENDIX C   Cod WSS (4X) SDM-SSB plots

Significant SDM-SSB relationships are marked with a I, II or III for a significant type I,
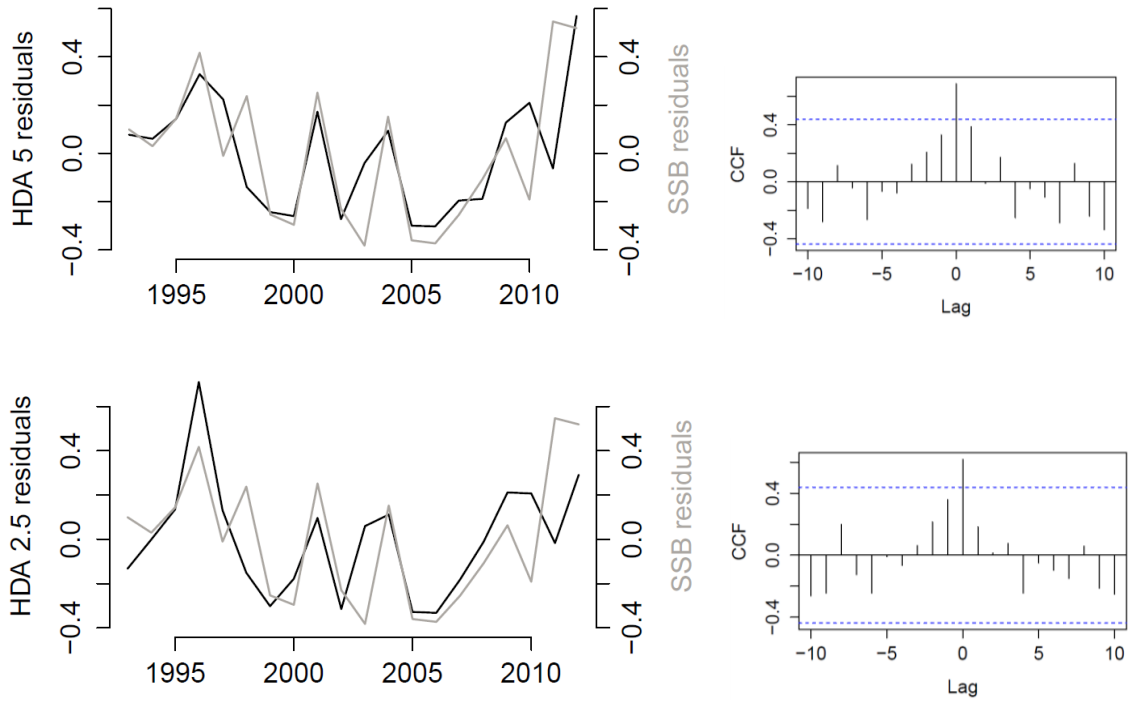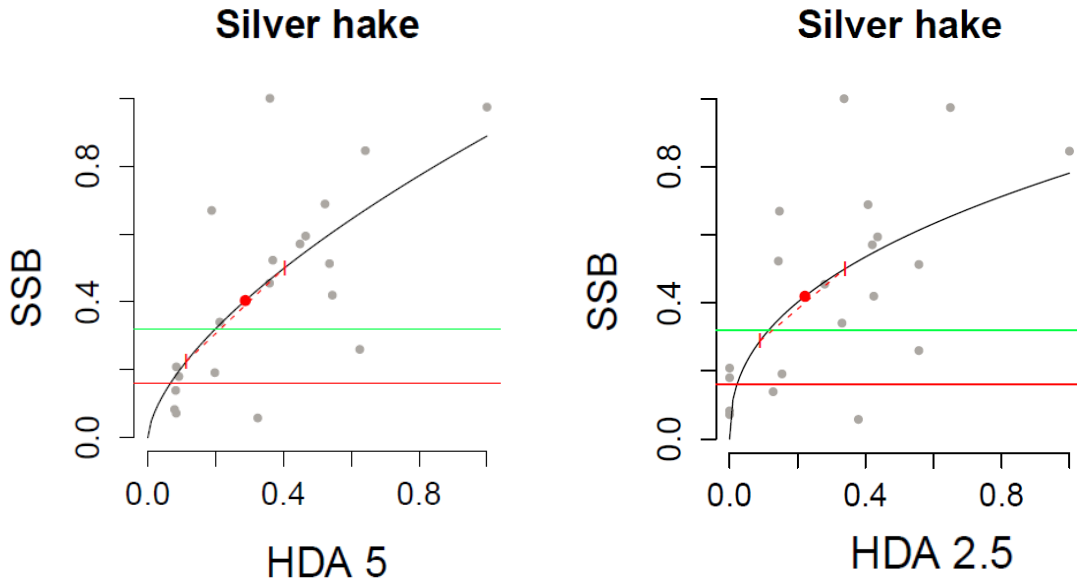type II or type III relationship.
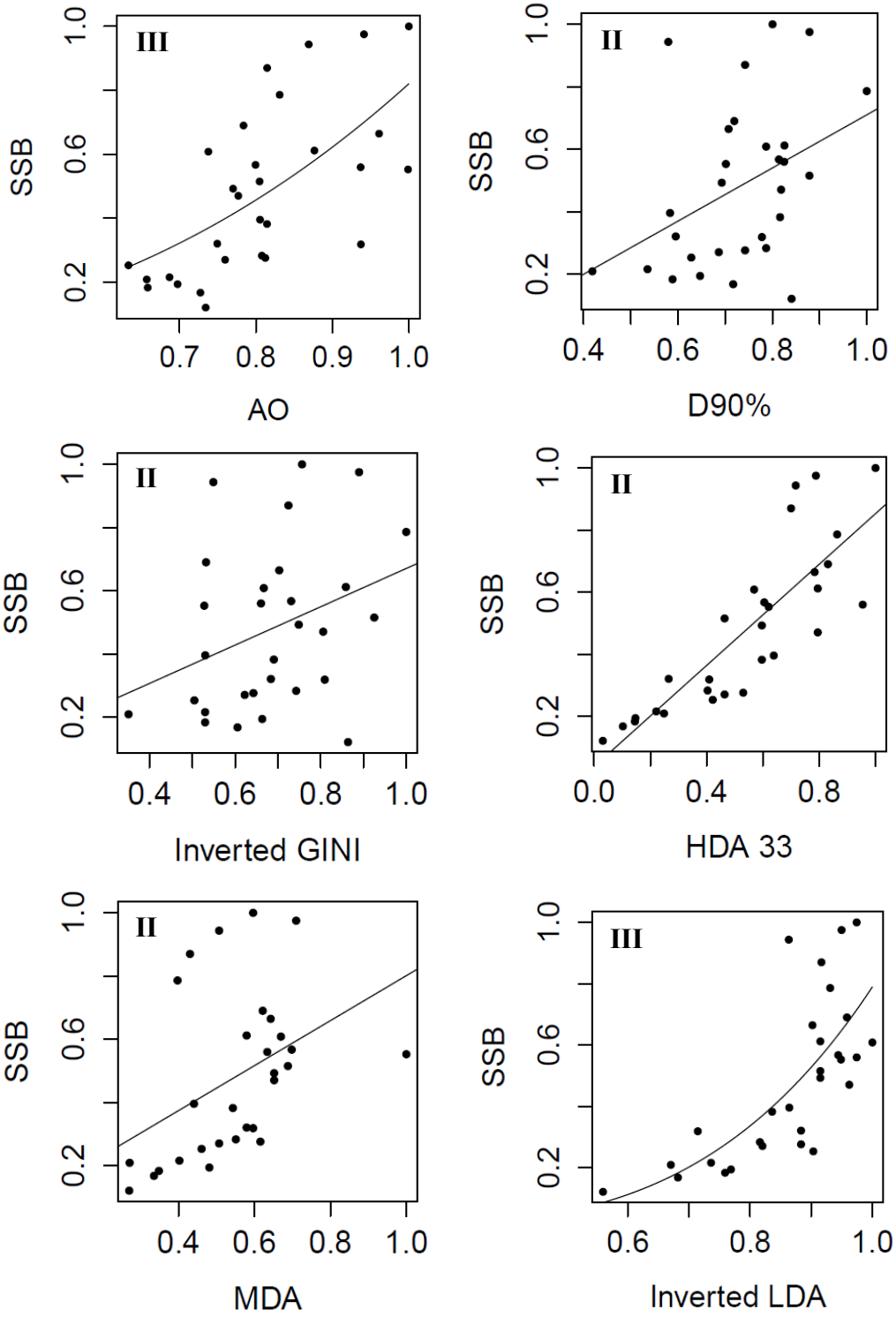
Cod WSS (4X) SDM-SSB plots (continued)
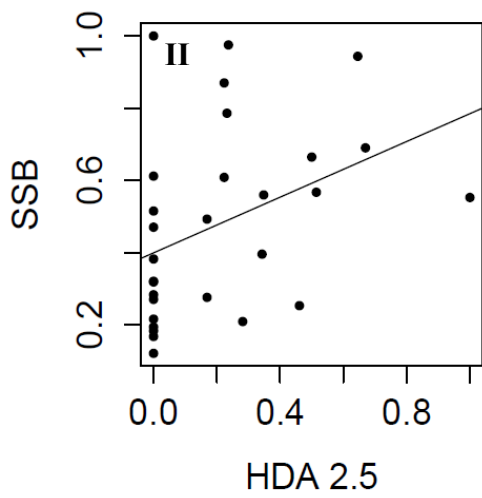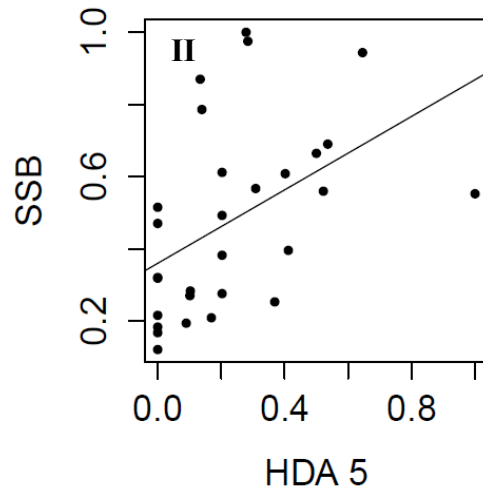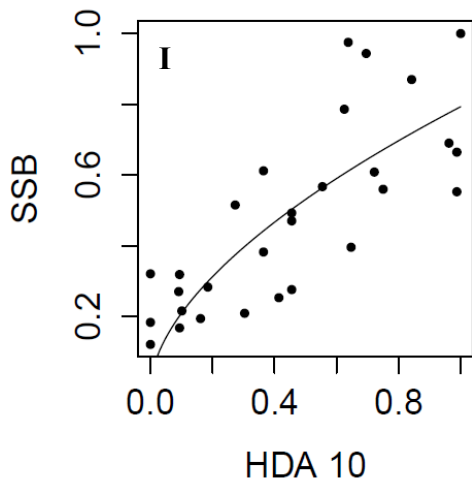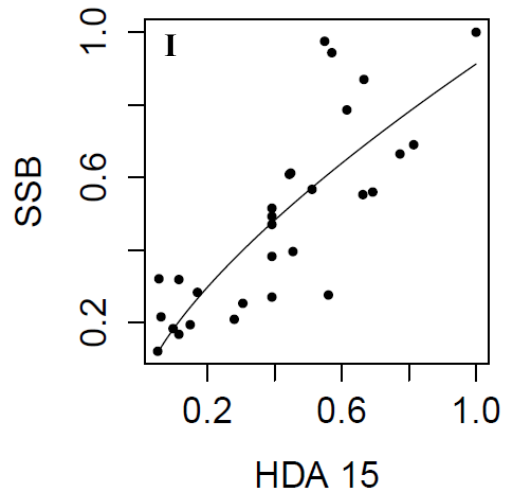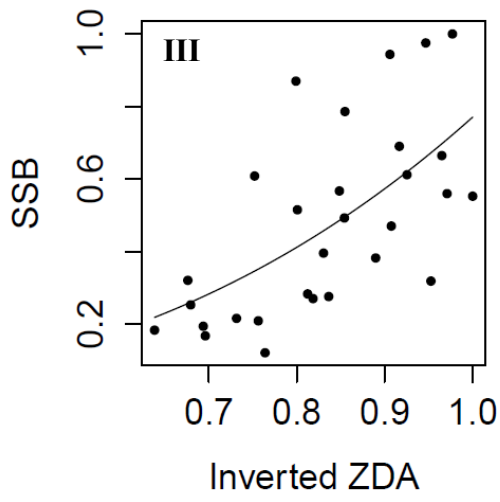
Cod WSS (4X) time series analysis

SDM and SSB residuals over time (left), with associated cross-correlation function (right)
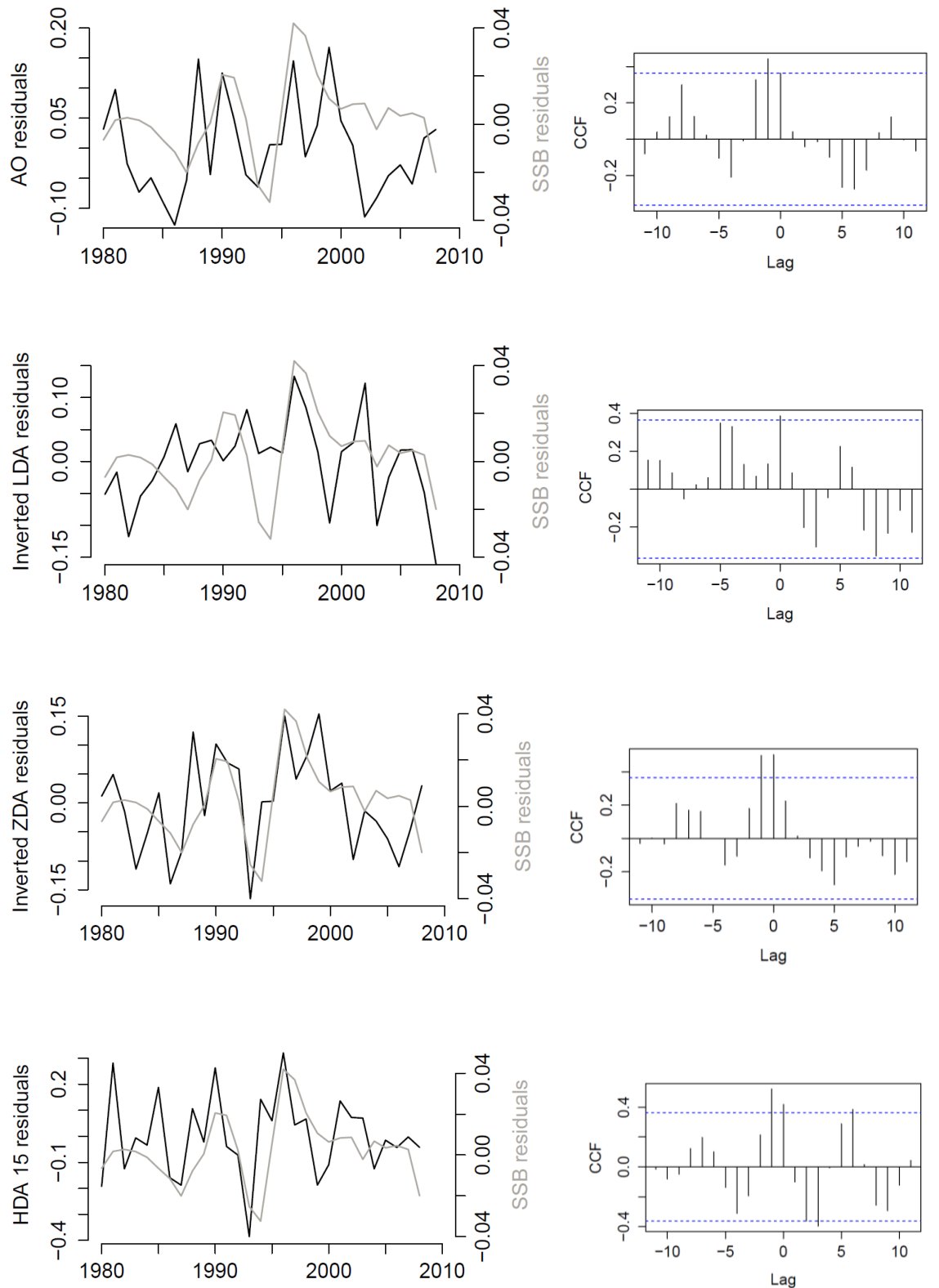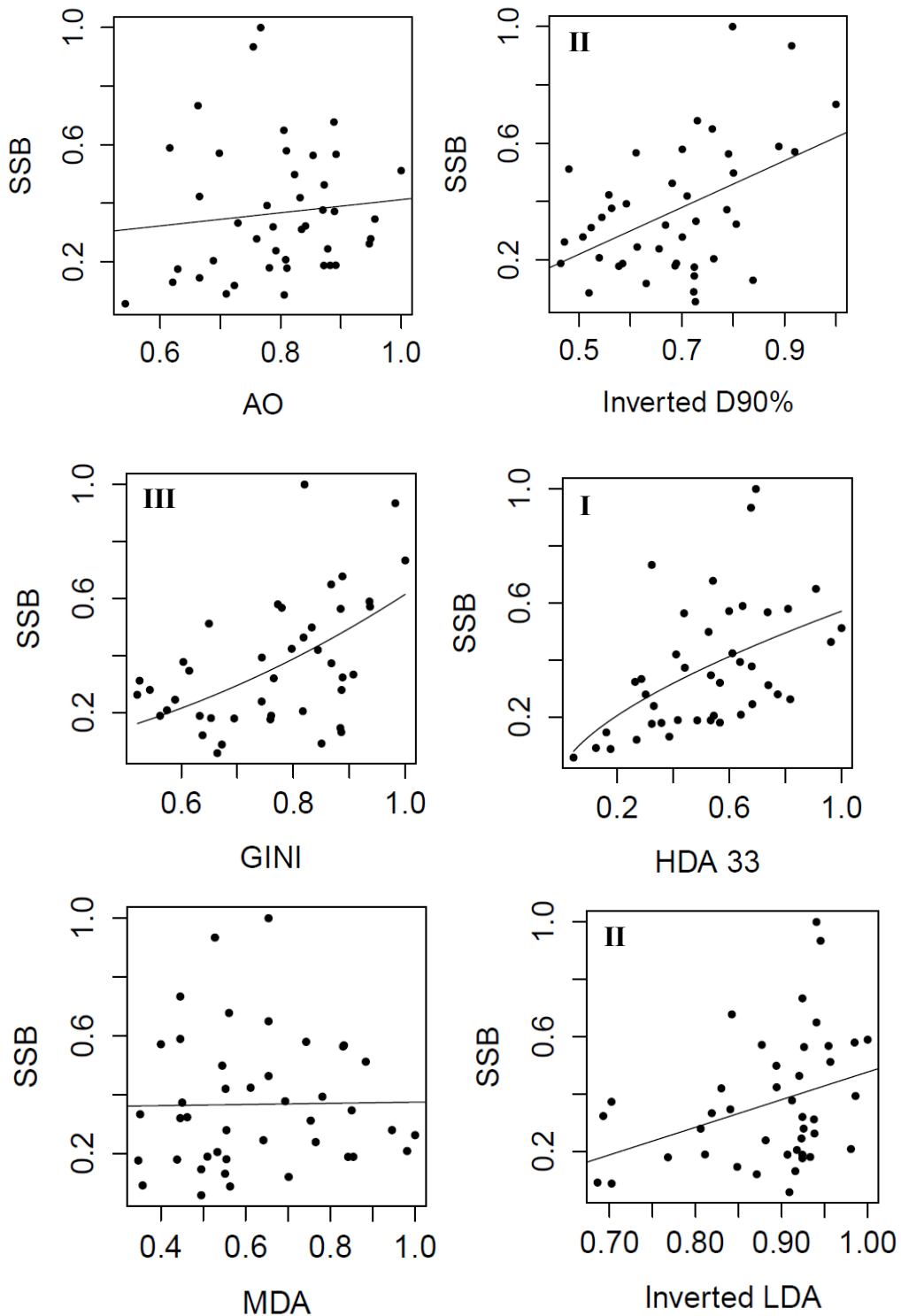
Cod WSS (4X) time series analysis (continued)
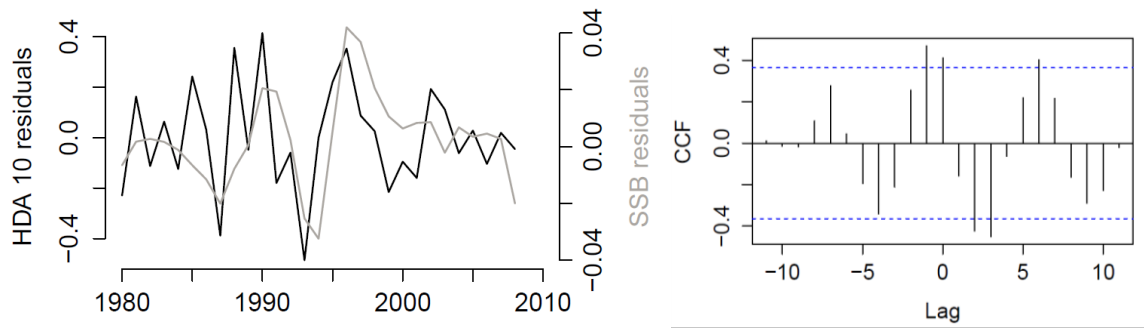
Cod WSS (4X) HDA threshold

HDA_T indicated by red dot, including 95% prediction interval. Upper, horizontal green line indicates 1.0 SSB_{MSY} level; lower, horizontal red line indicates 0.5 SSB_{MSY} level.
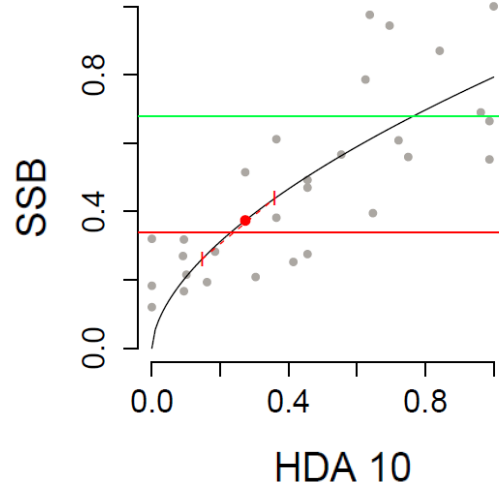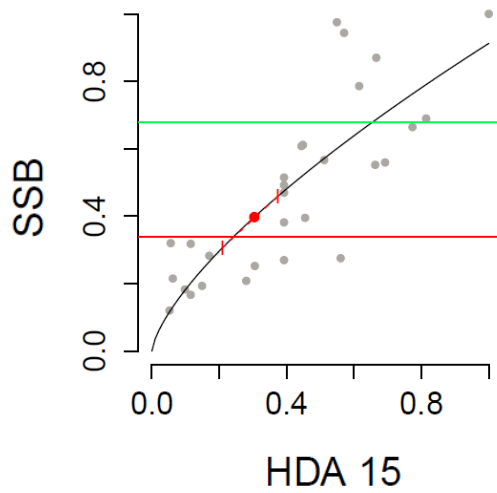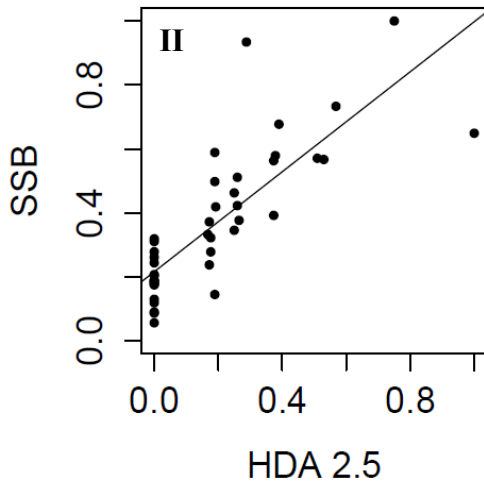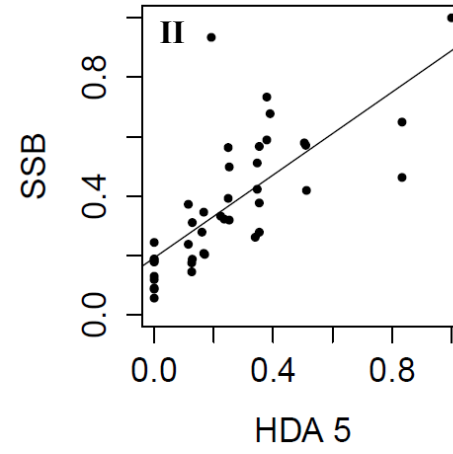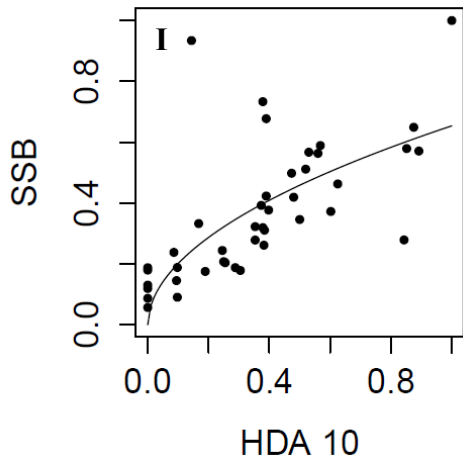
APPENDIX D   Haddock 4X5Y SDM-SSB plots

Significant SDM-SSB relationships are marked with a I, II or III for a significant type I, type II or type III relationship.
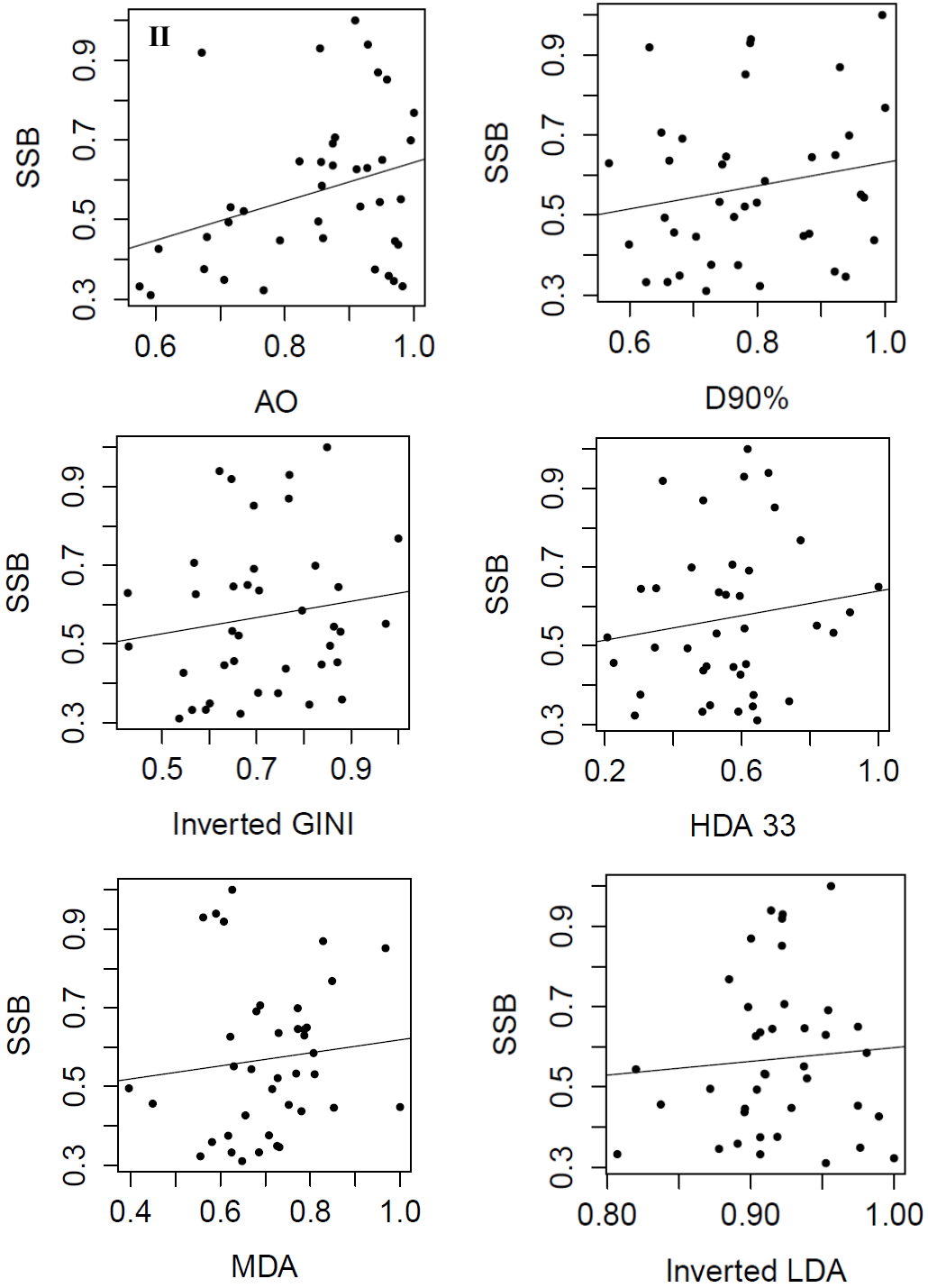
Haddock 4X5Y SDM-SSB plots (continued)
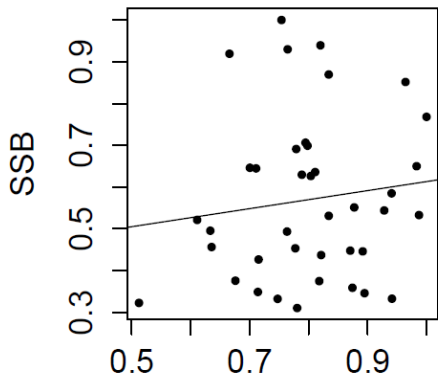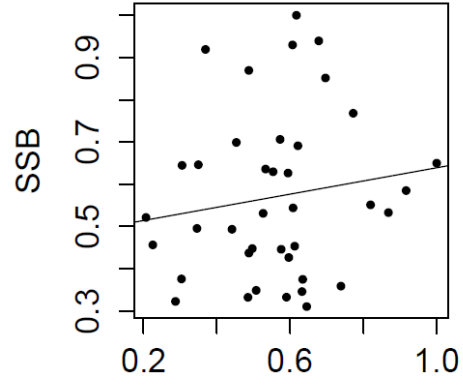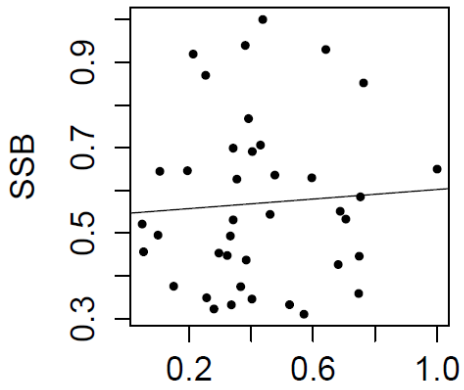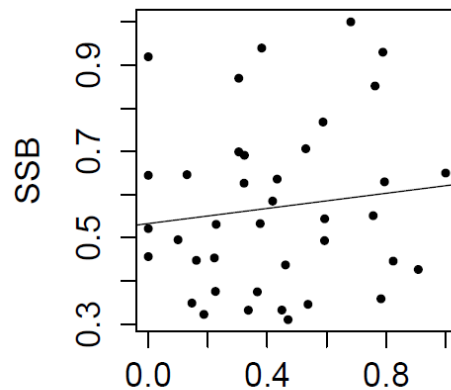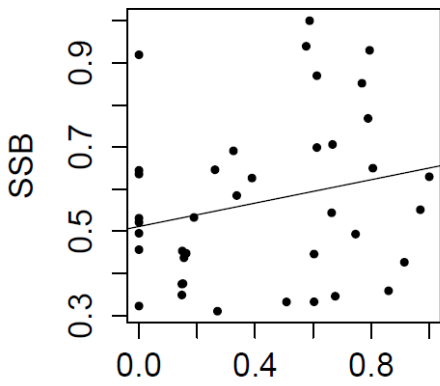
APPENDIX E   Halibut 4VWX SDM-SSB plots

Significant SDM-SSB relationships are marked with a I, II or III for a significant type I, type II or type III relationship. Absence of a mark indicates a non-significant relationship.
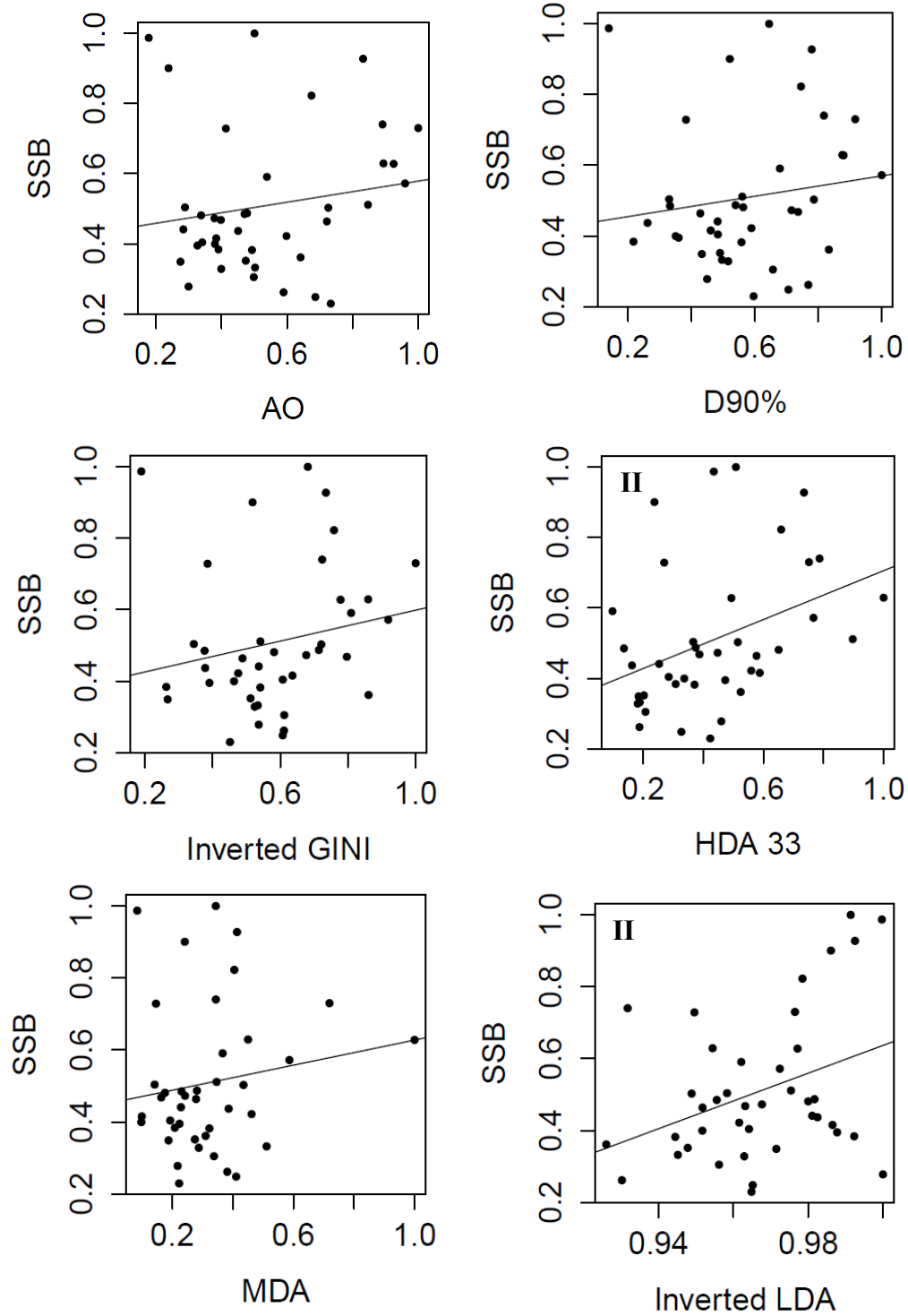
Halibut 4VWX SDM-SSB plots (continued)
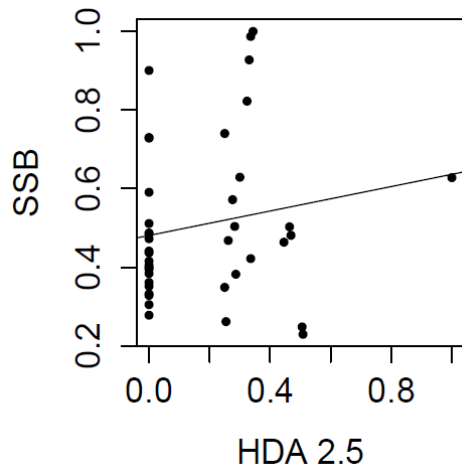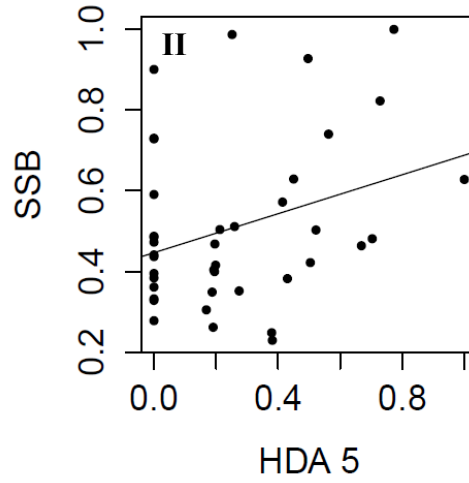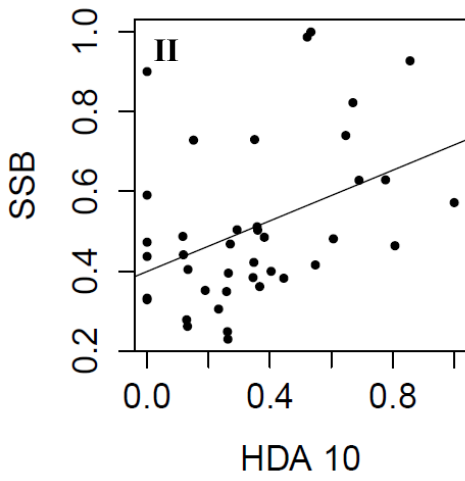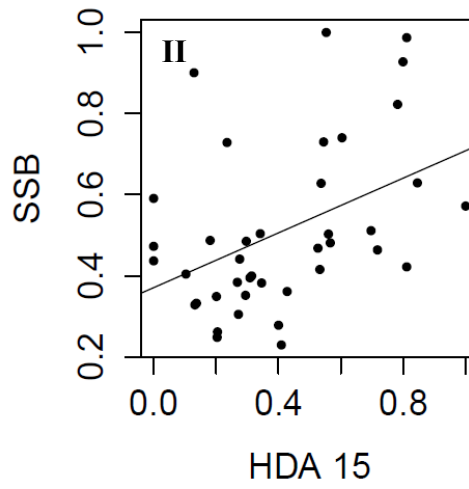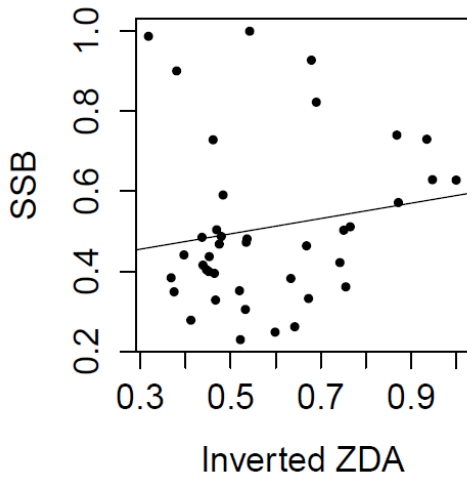
APPENDIX F   Pollock 4Xopqrs+5Yb+5Zc SDM-SSB plots

Significant SDM-SSB relationships are marked with a I, II or III for a significant type I, type II or type III relationship.
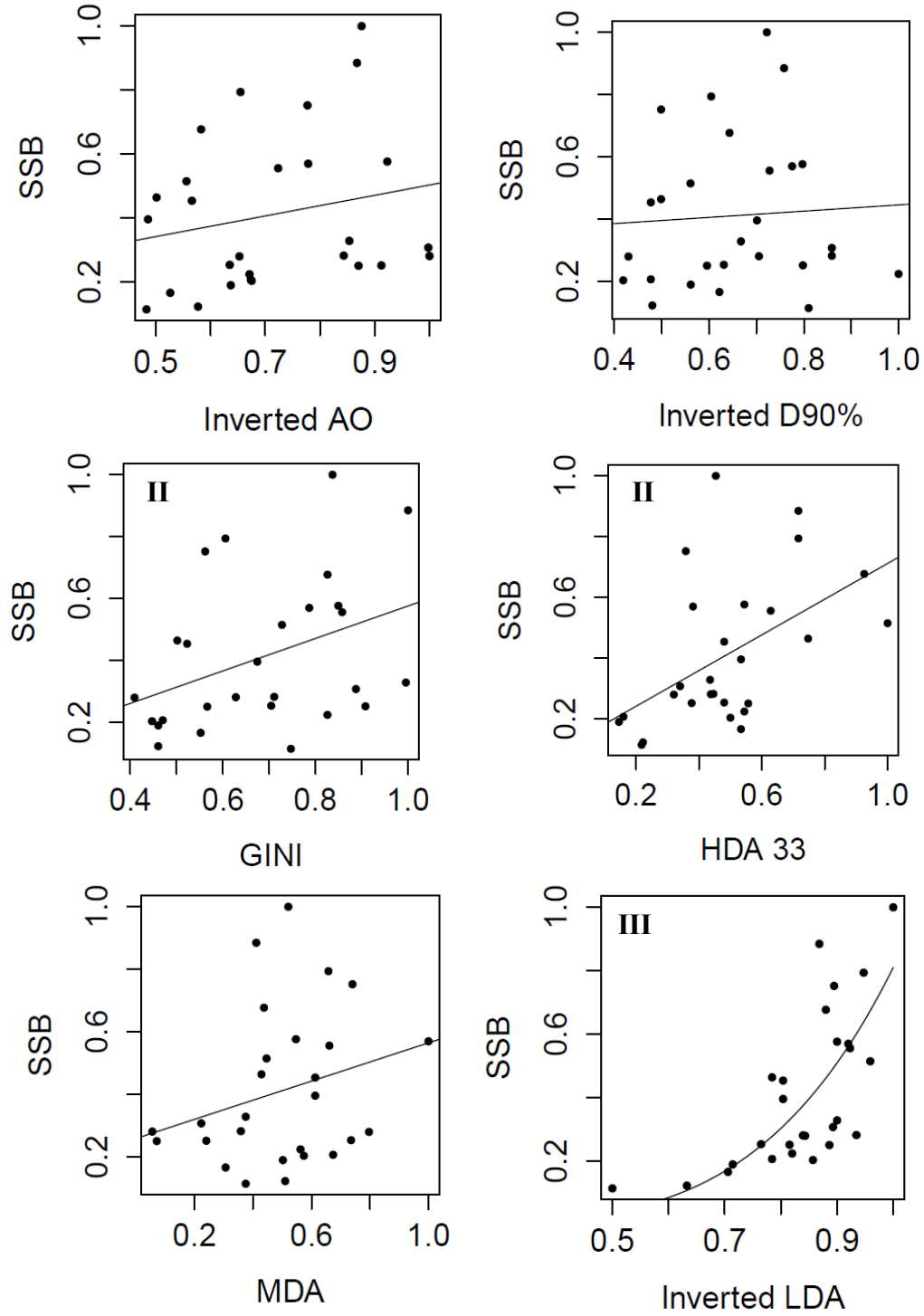
Pollock 4Xopqrs+5Yb+5Zc SDM-SSB plots (continued)
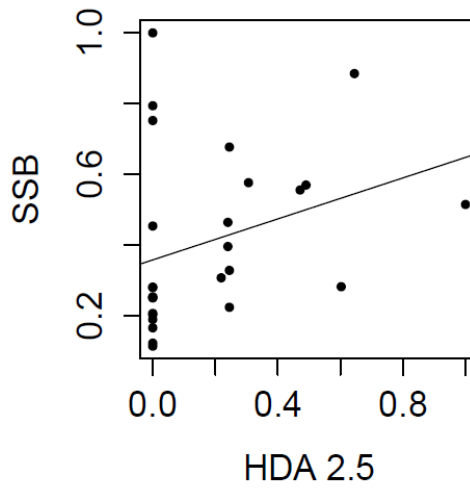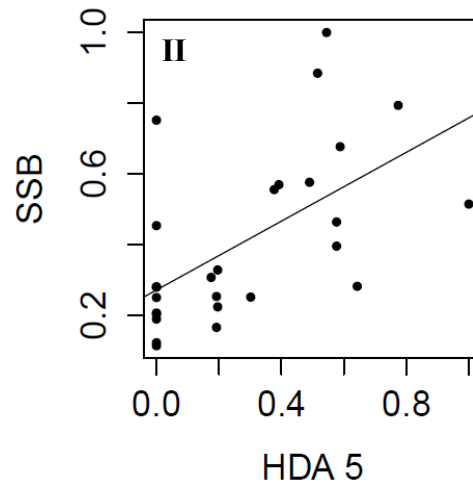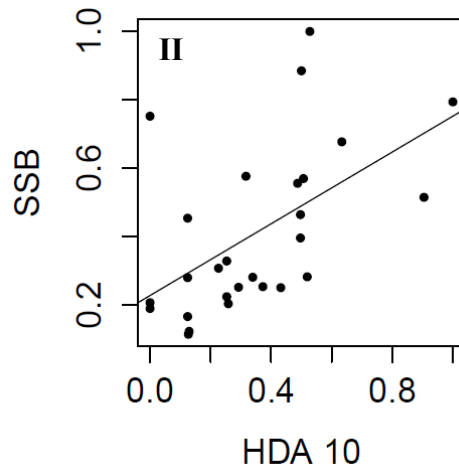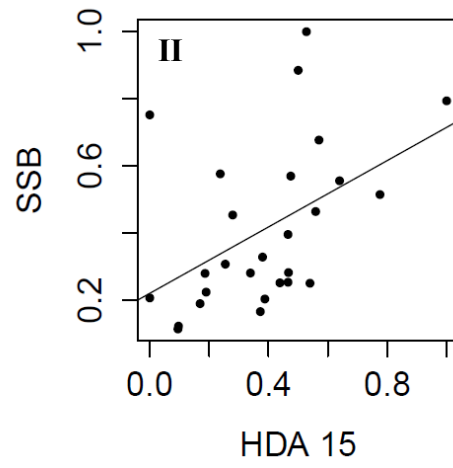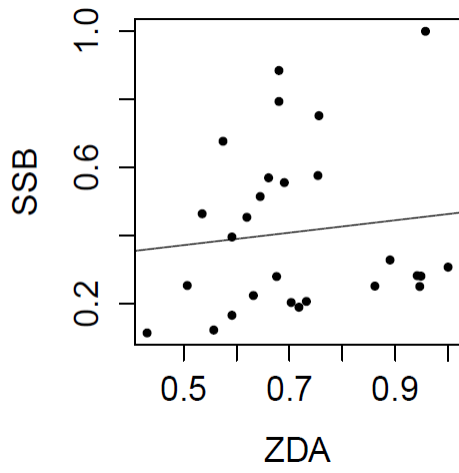
Pollock 4Xopqrs+5Yb+5Zc time series analysis

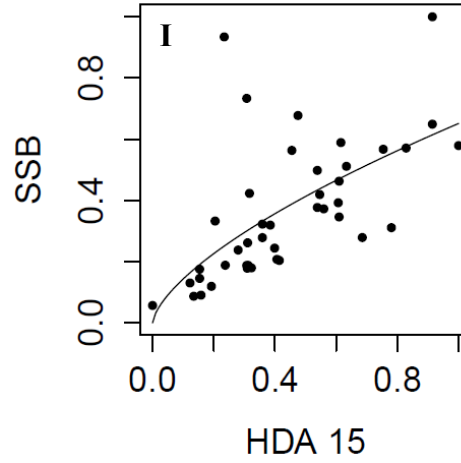SDM and SSB residuals over time (left), with associated cross-correlation function (right)
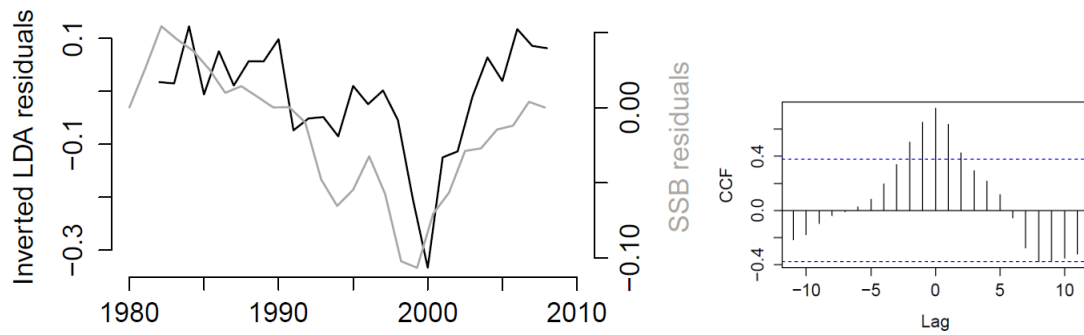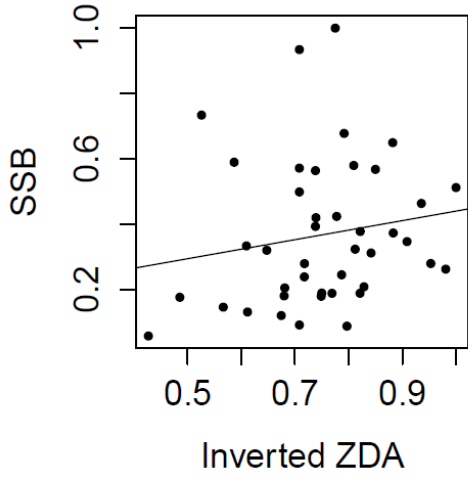
APPENDIX G   Redfish Unit 3 SDM-SSB plots

Significant SDM-SSB relationships are marked with a I, II or III for a significant type I, type II or type III relationship. Absence of a mark indicates a non-significant relationship.
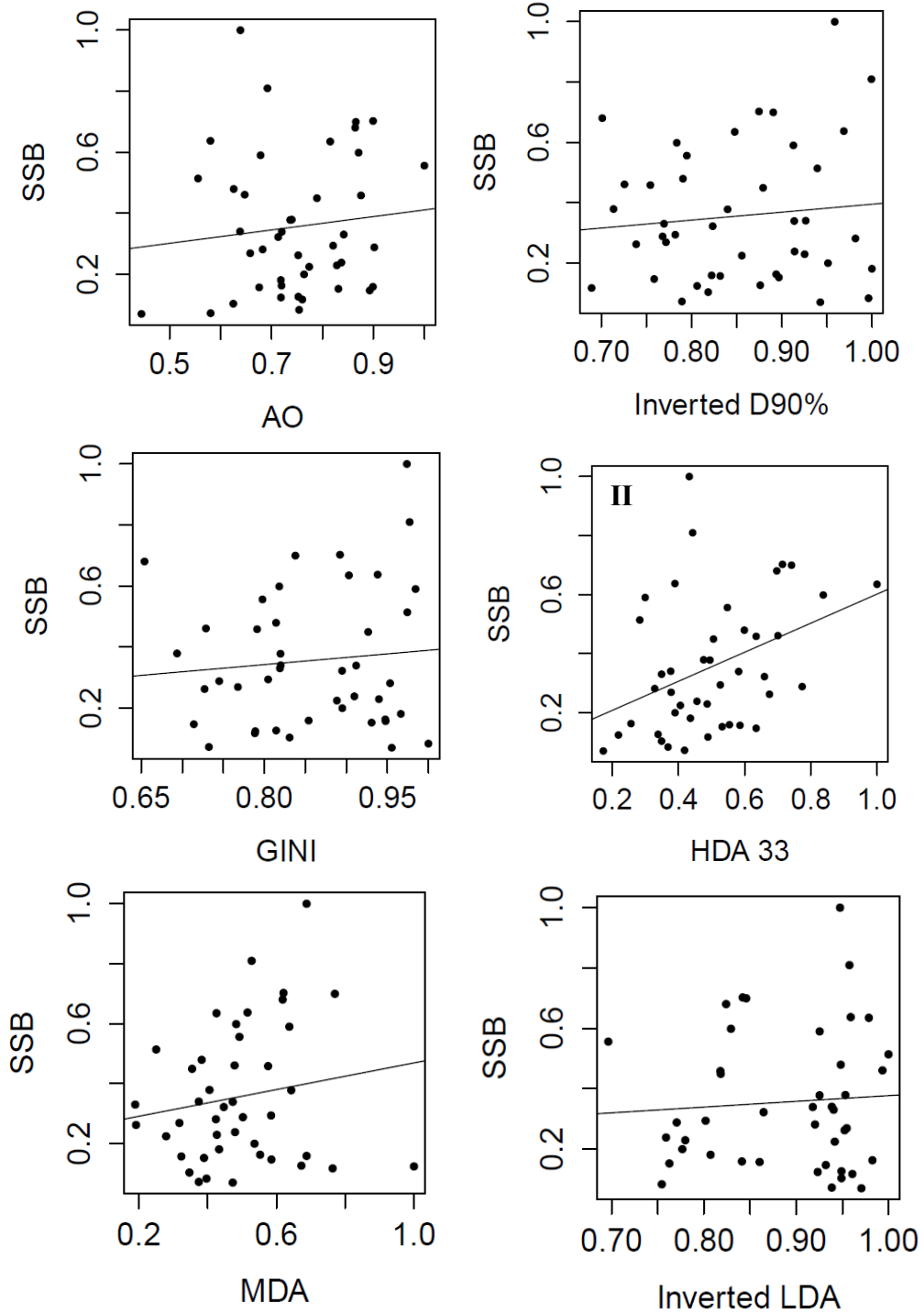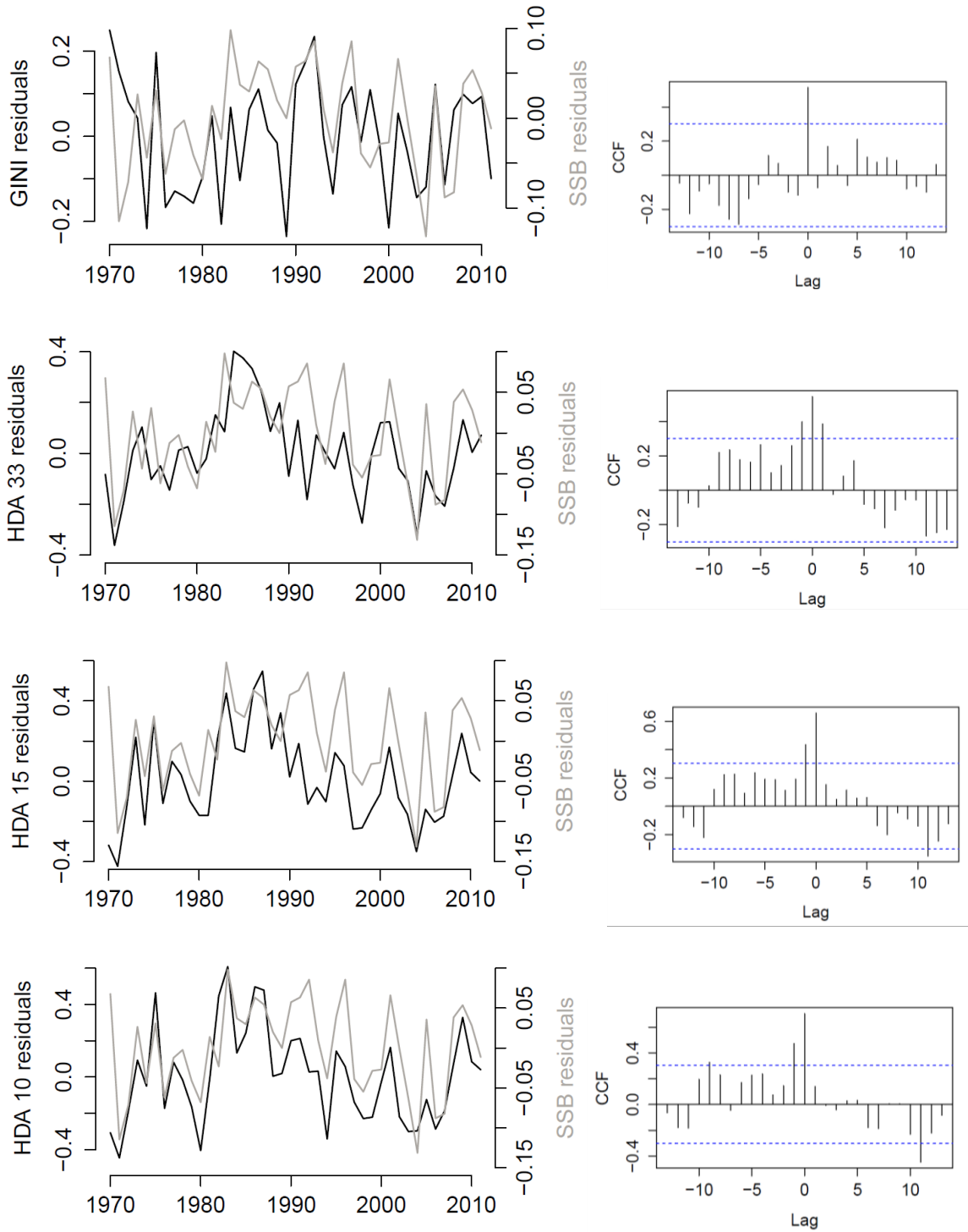
Redfish Unit 3 SDM-SSB plots (continued)

Redfish Unit 3 time series analysis

SDM and SSB residuals over time (left), with associated cross-correlation function (right)
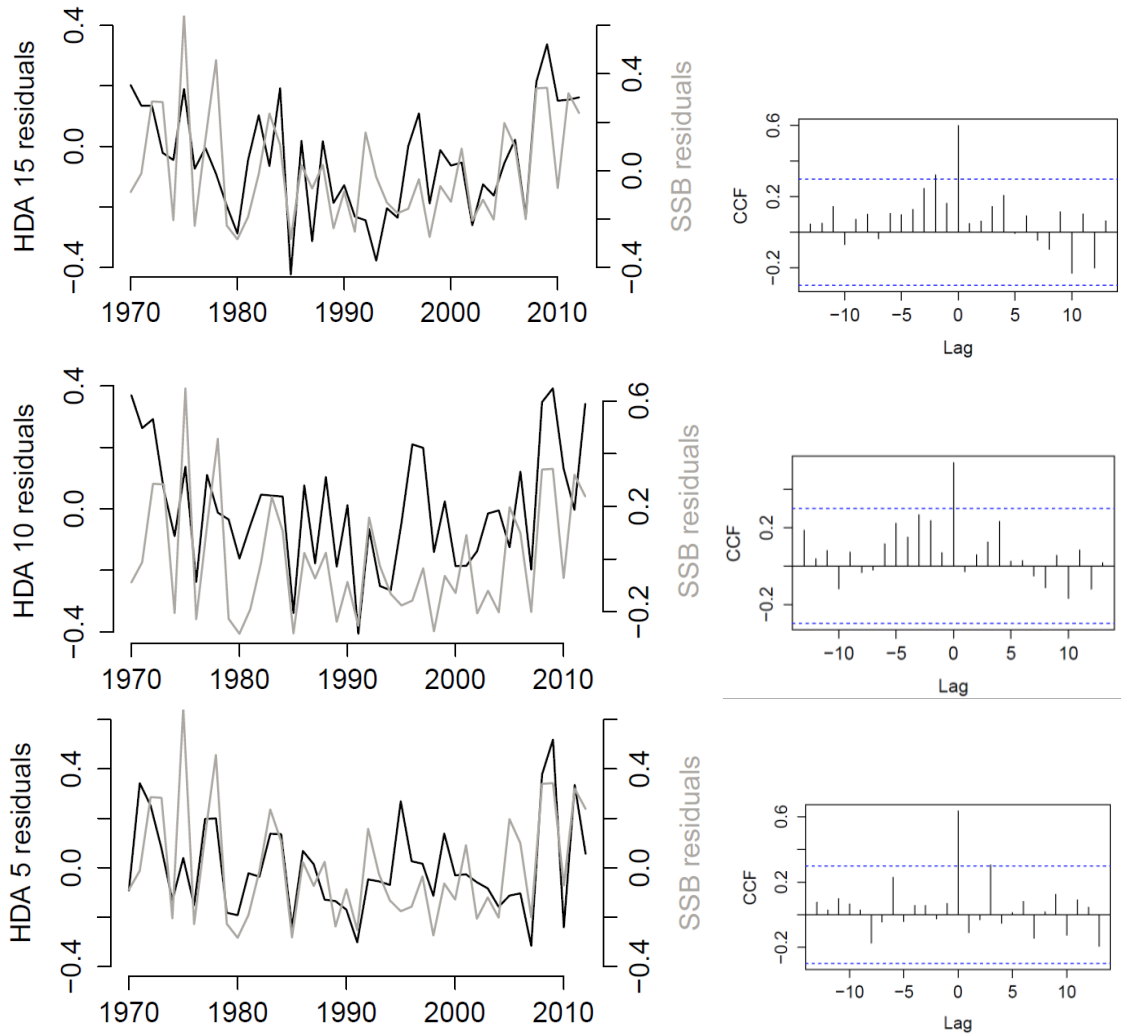
Redfish Unit 3 HDA threshold

HDA$_T$ indicated by red dot, including 95% prediction interval. Upper, horizontal green line indicates 1.0 SSB$_{MSY}$ level; lower, horizontal red line indicates 0.5 SSB$_{MSY}$ level.

APPENDIX H   Silver hake 4VWX SDM-SSB plots

Significant SDM-SSB relationships are marked with a I, II or III for a significant type I, type II or type III relationship. Absence of a mark indicates a non-significant relationship.
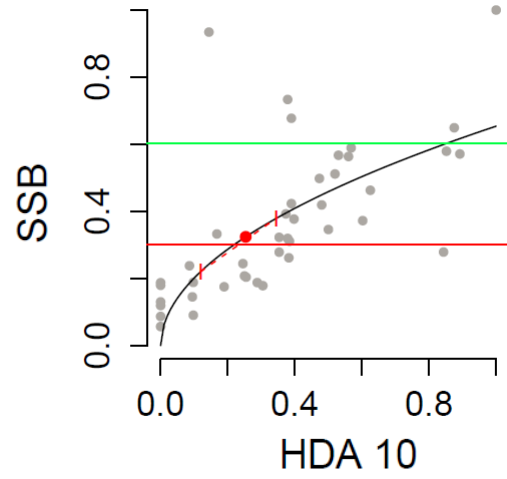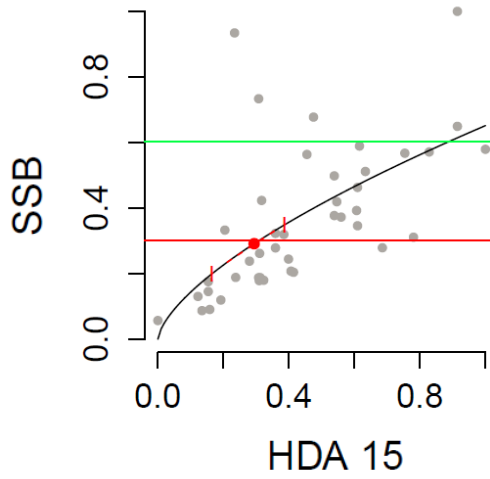
Silver hake 4VWX SDM-SSB plots (continued)

Silver hake 4VWX time series analysis

SDM and SSB residuals over time (left), with associated cross-correlation function (right)

Silver hake 4VWX HDA threshold

HDA_T indicated by red dot, including 95% prediction interval. Upper, horizontal green line indicates 1.0 SSB$_{MSY}$ level; lower, horizontal red line indicates 0.5 SSB$_{MSY}$ level.

APPENDIX I   White hake 4X SDM-SSB plots

Significant SDM-SSB relationships are marked with a I, II or III for a significant type I, type II or type III relationship. Absence of a mark indicates a non-significant relationship.

White hake 4X SDM-SSB plots (continued)

White hake 4X time series analysis

SDM and SSB residuals over time (left), with associated cross-correlation function (right)

White hake 4X HDA threshold

HDA_T indicated by red dot, including 95% prediction interval. Upper, horizontal green line indicates 1.0 SSB_{MSY} level; lower, horizontal red line indicates 0.5 SSB_{MSY} level.
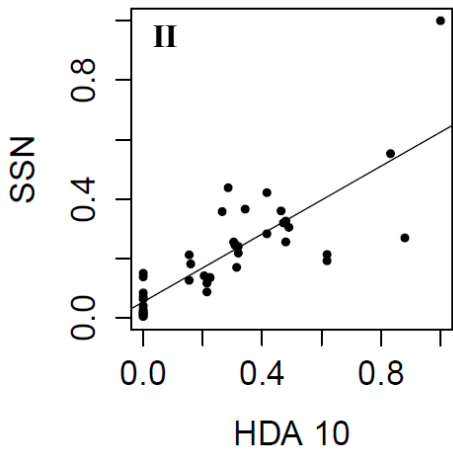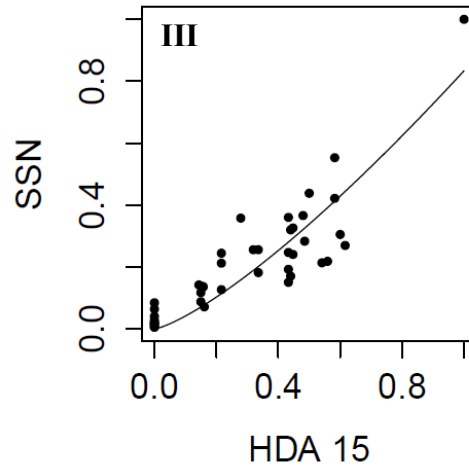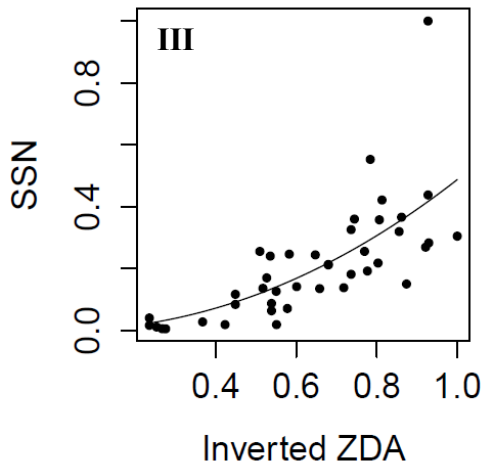
APPENDIX J   Winter flounder 4X SDM-SSB plots

Significant SDM-SSB relationships are marked with a I, II or III for a significant type I, type II or type III relationship. Absence of a mark indicates a non-significant relationship.
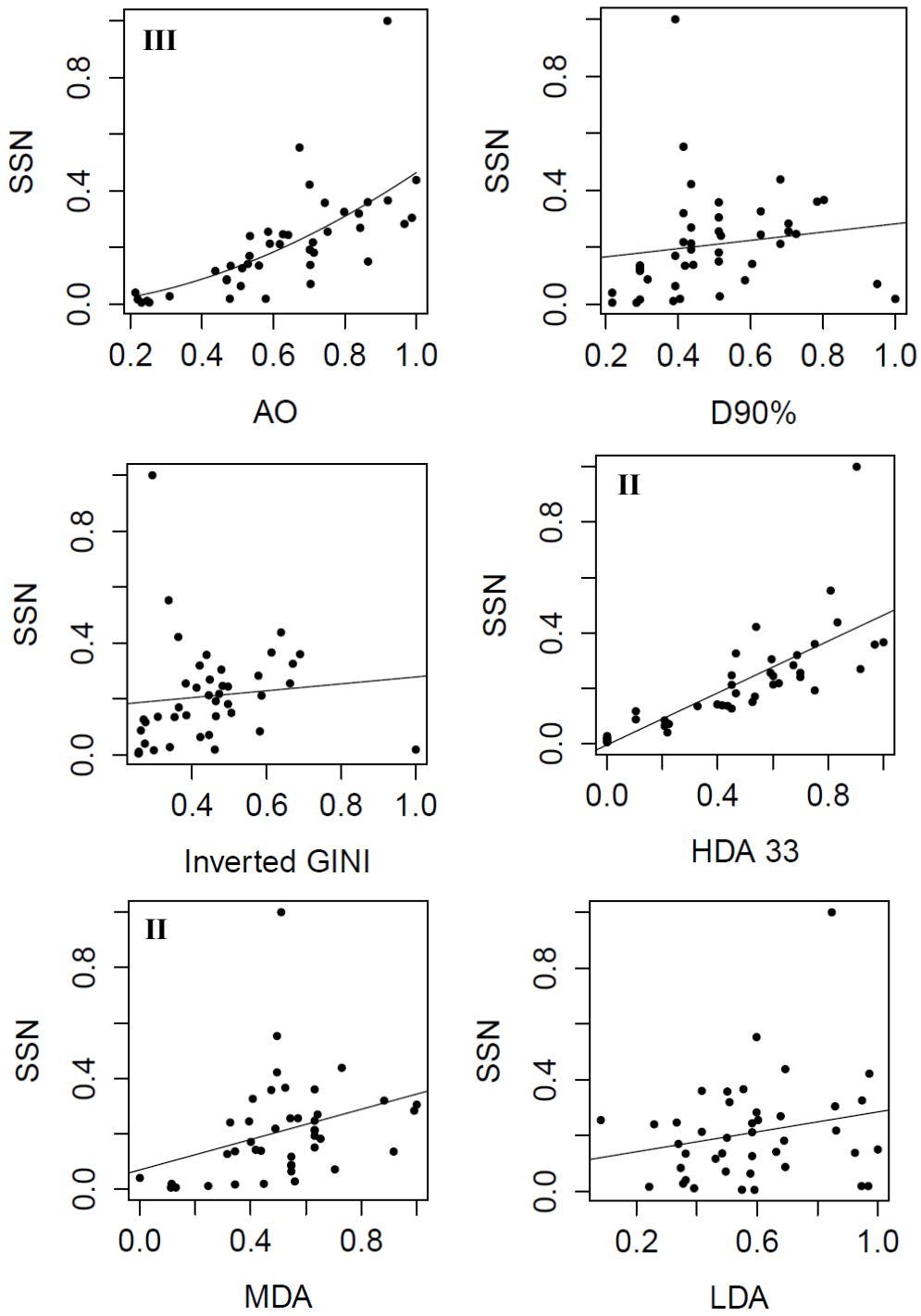
Winter flounder 4X SDM-SSB plots (continued)
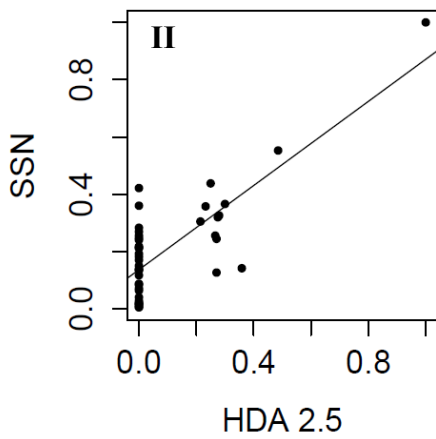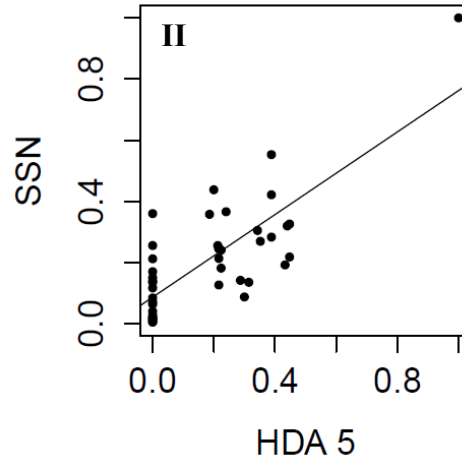
Winter flounder 4X time series analysis

SDM and SSN residuals over time (left), with associated cross-correlation function (right)