

**Conservation and management of Florida Spotted Seatrout (*Cynoscion nebulosus*).
How can a detailed understanding of the environmental and biological factors influencing population dynamics help to better manage the species?**



Dissertation
zur Erlangung des Doktorgrades
der Mathematisch-Naturwissenschaftlichen Fakultät
der Christian-Albrechts-Universität zu Kiel

vorgelegt von
Sven Kupschus
Kiel, 2010

Referent / in: Prof. Dr. D. Schnack

Koreferent / in:Second referee: Dr. J. Gröger

Tag der mündlichen Prüfung: 22 Juli 2010

Zum Druck genehmigt: Kiel 22 Juli 2010

gez. Prof. Dr. rer. nat. Lutz Kipp
- Dekan -

Author's declaration

At no time during the registration for the degree of 'Doktorgrades der Mathematisch-Naturwissenschaftlichen Fakultät der Christian-Albrechts-Universität zu Kiel' has the author been registered for any other University award. The work is original and was solely conducted by the author except where indicated in the general introduction. Chapter 2 and 3 are already published in scientific journals, and the intent is to publish Chapter 4 shortly. The work has been conducted in accordance with 'best practise' guidelines and regulations of the scientific community. No part of the dissertation has been submitted for any other degree.

Summary

Spotted seatrout populations have been historically exploited to various degrees. A recent shift from a sizeable commercial exploitation to a largely recreational exploitation has resulted in the deterioration in data quality due to the greater difficulty in obtaining suitable data for stock assessments from such fisheries. At the same time there has been increasing concern about state of the stocks from an environmental aspect, leading to increased research interest in the species to improve conservation and management.

Although the data has been collected for different and specific purposes, it frequently contains valuable additional information on the biology of the species and on trends in population dynamics over time. Extracting such information is often hampered by inconsistent or intermittent data collection and the conflict between the original sampling design needs and the requirements of long-term investigations into the population dynamics of seatrout.

This study investigates juvenile habitat requirements, reproduction, variation in growth and trends in recruitment using data from three of the main estuarine areas in Florida - Charlotte Harbor, the Indian River lagoon and Tampa Bay - to investigate what additional information can be extracted from the available data provided by the fisheries independent and fisheries dependent monitoring programs as well as data collected for additional biological studies over the last 20 years.

Generalised additive model (GAM) were chosen as an approach, because of their ability to elucidate the form of relationships for which the underlying functional form is unknown and their ability to cope with a variety of error structures. However, it is exactly this flexibility which also makes them vulnerable to inconsistencies in the sampling design. Therefore to derive robust quantitative models suitable as an evidence base for management bootstrap, independent data verification and other modelling approaches in conjunction with a rigorous analysis of model assumptions and a critical review of the biology were undertaken.

Results indicate that it is firstly possible to use GAMs to develop quantitative models of distribution and habitat usage sufficiently robust to be transferable between estuarine systems so that they can be used to evaluate the habitat value and the anthropogenic risk in estuaries currently not monitored for seatrout populations. Secondly, the reproductive models suggest that the temporal variation in reproduction between estuaries is driven by differences in the environmental conditions rather than genetic or population differences and that therefore the model should be universally applicable if environmental conditions are known. Thirdly, in contrast variation in growth, although similar between populations with regards to the effect of age sex and season does differ by cohort and year, so that neither a single growth model for a population, nor even one for different cohorts within a population should be used when assessing population dynamics in the different management units. Lastly, recruitment indices, based on the year effect from habitat models provide robust measures of relative abundance even in the presence of considerable changes in the sampling design, when models are suitably constrained.

The current stock assessment methodology is unable to accurately reflect the interannual differences in cohort strength within different populations, because management units span more than one estuary with discrete population trends and because age information is aggregated in periods greater than one year.

Generalised additive models can then extract significant amounts of additional information and provide robust management tools provided the evaluation of the model properties have been sufficiently rigorous. A more integrated approach to the management of seatrout in Florida is therefore possible, but the magnitude of the impact on management of the species is still unclear in the absence of sufficiently detailed estuarine hydrodynamic and stock assessment models.

Zusammenfassung

Spotted Seatrout Populationen wurden historisch unterschiedlichem Grade ausgebeutet. Da man kürzliche von einer beträchtlichen kommerziellen zu einer weitgehend freizeitbedingten Nutzung übergegangen ist, kam es zu einer qualitativen und quantitativen Verschlechterung der für die Bestandsaufnahme nötigen Datensätze. Zu gleich wächst die Sorge um den Zustand der Bestände aus ökologischer Sicht, was zu einem erhöhten Interesse in der Artenerhaltung und dem Management geführt hat.

Obwohl die verfügbaren Daten ueber die Jahre zu spezifischen Zwecken gesammelt worden sind, enthalten sie häufig wertvolle zusätzliche Informationen über die Biologie der Art und Trends in der Populationsdynamik ueber größere Zeiträume.

Das herausfiltrieren, dieser informationene wird of oft durch inkonsequente oder intermittierende datenerhebung behindert, und wird besonders erschweert durch den Konflikt zwischen den Beduerfnissen des urspruenglichen Sammlungszwecks und den langfristigen Anforderungen hinsichtlich der populationsdynamischen Untersuchungen.

Diese Studie untersucht separat juvenile Lebensraumnutzung, Reproduktion, Wachstumsunterschiede und Trends in der Rekrutierung mit Hilfe von Daten der letzten 20 Jahre aus drei wichtigen Mündungsgebieten in Florida - Charlotte Harbor, Indian River und Tampa Bay - um zusätzliche Information zu gewinnen aus den von der Fischerei unabhängigen und von der Fischerei abhängigen Überwachungsprogrammen sowie aus zusätzlichen biologische Studien.

Als statistische Methode wurde das verallgemeinerte additive Modell (GAM) ausgewählt. Dieses ist auf Grund seiner Flexibilität in Bezug auf die modellmäßige Adaption der funktionellen Form und seiner Fähigkeit geeignete Fehlerverteilungsfunktionen anzuwenden, besonders für diese Studie geeignet. Diese Flexibilität kann aber auch bei multicolinearen Abhängigkeiten in Datensätzen zu Komplikationen in der Modelauswertung führen, so daß hier Bootstrap, unabhängige Daten und anderen Modellierungsansätze in Verbindung mit einer strengen Analyse der Modellannahmen und eine kritische Überprüfung der Biologie der Art unternommen worden sind. Dies ist essentiell um robuste quantitative Modelle zu erstellen, die sich als sichere Grundlage für das Management der Art eignen sollen.

Die Anwendung von GAMs laesst folgende Schluesse ziehen. Die Modelle der Verteilung und Lebensraumnutzung sind ausreichend robust und übertragbar zwischen verschiedenen Mündungsgebieten, so daß sie dazu verwendet werden können um Qualität des Lebensraumes zu bestimmen und die anthropogenisch verursachten Risiken auch auf unüberwachte Gebiete in Florida zu übertragen.- Das reproduktive Modell legt nahe, dass der zeitliche Verlauf der Fortpflanzung zwischen den Mündungen von Unterschieden in den Umweltbedingungen und nicht von genetischer Differentiation geprägt wird und dass deshalb auch dieses Modell universell anwendbar sein sollte wenn die entsprechenden Umweltsbedignungen bekannt sind. - Im Gegensatz dazu zeigen die Wachstumsmodelle, populationsspezifische Trends in den Variablen Kohorte und Jahr. Deshalb kann kein einheitliches Modell für das Wachstum mehrerer Populationen noch für das verschiedener Kohorten innerhalb einer Population bei der Beurteilung der Populationsdynamik in verschiedenen Management-Einheiten verwendet werden. - Rekrutierungs Indices, basierend auf dem Jahreffekt der Lebensraum Modelle, bieten

einen robuste Maßstab der relativen Häufigkeit, selbst in Gegenwart von erheblichen Veränderungen in den Stichprobenplan, wenn die dadurch entstandene Multikollinearität eliminiert werden kann. Die aktuelle Bestandsbewertung kann die interannuelle Variation in den Kohorte nicht reflektieren, weil die Management-Einheiten mehrere Populationen mit diskreten Bevölkerungsentwicklungstrends beinhalten und weil der proportionale Populationsanteil von Altersgruppen über den Zeitraum von mehreren Jahren ausgewertet wird, so dass die Variation im Kohortensignal unterbewertet wird.

Zusammengefaßt können GAMs also wichtige, neue Information aus existierenden Datensätzen gewinnen und bieten robuste Management-Tools, sofern die Auswertung der Modell-Eigenschaften ausreichend untersucht und explizit gemacht werden. Ein stärker integrierter Ansatz für das verbesserte Management von Seatrout in Florida ist daher möglich, aber der Grad solcher Verbesserungen ist in der Abwesenheit einer hinreichen detaillierten Bestandsaufnahme und hydrodynamischen Modellen mit der nötigen räumlichen Auflösung noch unklar.

Acknowledgments

I thank the field crews in the Indian River Lagoon, Charlotte Harbor and Tampa Bay for collection and processing of samples, and the FWC-FMRI Fisheries Independent Monitoring Program as a whole for making this work possible. Notable contributors were Mandy Tyler for assisting with the measurement of 10,000 otoliths, Derek Tremain and Doug Adams for their detailed knowledge of the sampling and data protocols, Mike Murphy for his explanation of the management and assessment process, and Sue Lowere-Barbieri for her knowledge on the biology of the species and our discussions on the modelling processes.

Great thanks go to professor Schnack for his contributions to the review process and for dealing with the additional complications in taking me on as a student, such as the long distances between Kiel and my location in Florida and the UK and the extended period of completion. I would also like to thank Andy Payne for his continued support and unrelenting pressure to drive this work to completion, as well as his detailed review of the manuscript and helpful comments for improvement of the work. I would also like to thank the anonymous reviewers of the publications arising from this study for their improvements to the manuscripts and the underlying scientific approach to these complex questions.

Lastly, I have to thank my parents for my scientific schooling from an early age and the unwavering belief and support in this often difficult and laborious process.

The dissertation was supported in part by the funding from the Department of the Interior, U.S. Fish and Wildlife Service, Federal Aid for Sportfish Restoration Project Number F-96 and Florida Saltwater Fishing License Monies.

Table of Contents

Summary

Zusammenfassung

Acknowledgments

- 1 Chapter 1: General Introduction to Management and Conservation of Spotted Seatrout (*Cynoscion nebulosus*) in Florida**
- 5 Chapter 2: Development and evaluation of statistical habitat-suitability models; an example based on juvenile spotted seatrout (*Cynoscion nebulosus*).**
- 5 Introduction**
- 6 Material and Methods**
- 7 **Figure 2.1.** Definitions of the four estuarine regions over three study sites a) Tampa Bay - TB, b) Charlotte Harbor - CH, and c) the Indian River lagoon (IRN, IRS). Black areas (1-4) in c) indicate the four primary adult sampling sites.
- 11 Results**
- 12 **Figure 2.2.** Habitat-preference model of Indian River Lagoon juvenile spotted seatrout. Y-axes represent the partial effect of the independent variable on the x-axes. Classification variables are a) bottom type (M = mud, MO = mud and oysters, MX = mud and sand mix, S = sand, SO = sand and oysters or rock), b) year. Continuous variables are c) day of the year (spline with 7df) d) temperature (spline with 2 df), e) salinity (spline with 2 df), f) water depth (spline with 2 df), g) percent seagrass cover (spline with 3 df). Rug plots along the x-axis indicate the distribution of samples across each independent variable.
- 12 **Figure 2.3.** Habitat-preference model of Tampa Bay juvenile spotted seatrout. Y-axes represent the partial effect of the independent variable on the x-axes. Classification variables are a) bottom type (M = mud, MO = mud and oysters, MX = mud and sand mix, S = sand, SO = sand and oysters or rock), b) year. Continuous variables are c) day of the year (spline with 7df) d) temperature (spline with 2 df), e) salinity (spline with 2 df), f) water depth (spline with 2 df), g) percent seagrass cover (spline with 3 df). Rug plots along the x-axis indicate the distribution of samples across each independent variable.
- 13 **Figure 2.4.** Habitat-preference model of Charlotte Harbor juvenile spotted seatrout. Y-axes represent the partial effect of the independent variable on the x-axes. Classification variables are a) bottom type (M = mud, MO = mud and oysters, MX = mud and sand mix, S = sand, SO = sand and oysters or rock), b) year. Continuous variables are c) day of the year (spline with 7df) d) temperature (spline with 2 df), e) salinity (spline with 2 df), f) water depth (spline with 2 df), g) percent seagrass cover (spline with 3 df).

Rug plots along the x-axis indicate the distribution of samples across each independent variable.

- 14 **Figure 2.5.** Tampa Bay standardized relative abundance surfaces interpolated from predicted (inverse distance weighting) and observed (kriged) annual point sample abundances and subsequently standardized by mean and variance, indicating interannual differences in the distribution accounted for by the TB model: a) observed 1996, b) predicted 1996, c) observed 1997, d) predicted 1997, e) observed 1998, f) predicted 1998, g) observed 1999, h) predicted 1999.

15 Discussion

- 15 **Figure 2.6.** Charlotte Harbor standardized relative abundance surfaces interpolated from predicted (inverse distance weighting) and observed (kriged) monthly point sample abundances and subsequently standardized by mean and variance, indicating seasonal differences in the distribution in part accounted for by the CH model: a) observed May 1996-1999, b) predicted May 1996-1999, c) observed July 1996-1999, d) predicted July 1996-1999, e) observed September 1996-1999, f) predicted September 1996-1999. The outer part of the estuary was sampled only in 1996 and 1997, so the number of samples is too small for appropriate interpolation in this area.

- 16 **Figure 2.7.** Indian River Lagoon standardized relative abundance surfaces interpolated from the IR, TB and CH seatrout abundance model predictions (inverse distance weighting) and observed (kriged) 1996 point sample abundances and subsequently standardized by mean and variance. a) IR observed abundances, b) IR model predictions, c) TB model predictions, d) CH model predictions.

- 17 **Figure 2.8.** Correlation between the abundances predicted by foreign models with those predicted by the native model for the datasets from a) Indian River, b) Tampa Bay c) Charlotte Harbor. Predictions of the native model are always plotted on the x-axis, with the y-axis representing estuary foreign models. The line indicates the expected 1:1 relationship if transferability on the absolute scale were applicable.

- 22 **Table 2.1.** Catch statistics, model performance and transferability for the environmental dataset from each of the three study estuaries. (numbers in bold indicate predictions for data by foreign to the models) Numbers in bold indicate characteristics for foreign models.

- 22 **Table 2.2.** Pearson's correlation coefficients for all combinations of model to model comparisons of abundance predictions for each samples in each of the three datasets from the three Florida estuaries.

23 Chapter 3: A temperature-dependent reproductive model for spotted seatrout (*Cynoscion nebulosus*), explaining spatio-temporal variations in reproduction and young-of-the-year recruitment in Florida estuaries.

23 Introduction

- 24 **Figure 3.1.** Definitions of the four estuarine regions over three study sites a) Tampa Bay - TB, b) Charlotte Harbor - CH, and c) the Indian River lagoon (IRN, IRS). Black areas (1-4) in c) indicate the four primary adult sampling sites.

25 Material and Methods

27 Results

28 **Figure 3.2.** Partial effects of temperature (TEMP), hrs after sunset (REL-TIME), female size (TL), gonad-free-weight condition factor (C) and days past the full moon (MOON) according to the GAM model for spotted seatrout reproductive activity, describing the effect of each independent variable, assuming the others are held constant (y-axis labels: cubic spline function and degrees of freedom used; values: relative importance of each partial effect in describing total deviance; rug plot on x-axis: range and relative frequency of sampling conditions).

29 **Figure 3.3.** Estuary-specific model predictions of monthly relative reproductive effort (dashed line) and expected relative abundances of juveniles (solid line with circles) in comparison with observed relative abundances of juveniles (bars). All data are expressed as the monthly percentage of the annual total within each region.

30 **Figure 3.4.** Mean daily summer surface temperatures (1st May to 1st October) for each year (1996–1999) in the four estuarine regions CH, TB, IRN and IRS. (No data for IRS in 1996, with 1997 data from projects other than juvenile sampling)

30 Discussion

39 Chapter 4: Back-calculation to reconstruct length-at-age information based on otoliths of Florida spotted seatrout (*Cynoscion nebulosus*), and conclusions on population and individual growth dynamics

39 Introduction

41 Material and Methods

42 **Figure 4.1.** GAM plots for the 1st submodel of the increment analysis describing the partial effect on the y-axes of age a), day of the year b), sex c), and year of growth d). Age and day of the year are modeled as spline functions with 4 degrees of freedom each (notation= s(variable,4)) and year and sez are implemented as factor variables. The columns represent the respective models based on data from Charlotte Harbour (CH), Indian River (IR) and Tampa Bay (TB), indicating the similarity in the effects between the first three effects, but different trends for the year variable.

44 **Figure 4.2.** GAM model output for the 2nd submodel of the increment analysis describing the relationship between a) radius (linear), b) age (s(Age,4) = spline with 4 degrees of freedom), c) day of the year (s(Day of the Year,4) = spline with 4 degrees of freedom), d) sex (factor) and e) cohort (factor) and the partial contribution to the linear predictor of each variable on the y-axes with approximate confidence limits. In columns the models from the three populations in Charlotte Harbour (CH), Indian River (IR) and Tampa Bay (TB) are compared indicating similar trends for all variables except cohort.

47 Results

49 **Figure 4.3.** GAM model output for the direct length-at-age analysis describing the relationship between a) age (s(Age,4) = spline with 4 degrees of freedom), b) day of the year (s(Day of the Year,4) = spline with 4 degrees of freedom), c) sex (factor), d) cohort (factor) and e) year(factor). The

magnitude on the y-axis describes the partial contribution to the linear predictor of each variable with approximate confidence limits. In columns the models from the three populations in Charlotte Harbour (CH), Indian River (IR) and Tampa Bay (TB) are compared indicating similar trends for all variables except cohort and year.

50 **Figure 4.4.** Indian River yearly-mean length against mean cohort length-at-age estimates for the two length models and the 1:1 line (dot and dash). Continuous and dashed lines are the smoothed estimates of the 95% inter-quartile range in bootstrap results to provide approximate 95% confidence limits. Estimates of both analyses for males at age 7 of the 1993, 95, 97 (annotated) are based on an individual fish.

52 **Figure 4.5.** Comparisons of the empirical standard error estimates at age over cohorts of the 500 random bootstrap samples at different sample sizes (50 – 300 top to bottom) for Indian River data illustrating the convergence of estimates at higher sample sizes.

53 **Figure 4.6.** Comparison of the median cohort length-at-age and box plots of the variation in estimates between bootstrap samples from a) the increment analysis and b) the direct length-at-age analysis. In each plot females are on the left, males on the right from ages 0 to 9 where applicable. The range of predicted values increases at age 6 and for the 1998 cohorts, particularly for the direct analysis. The inter-quartile range is large for ages 8 and 9 for both methods.

54 **Figure 4.7.** Number of estimates provided for each cohort at each age and sex by each method for the 500 bootstrap samples as a percentage of the total. The left column in each plot represents females with 1984 to 2000 cohorts going left to right subdivided into ages 0 to 9, right column represents males. Bootstrap samples size increases left to right over plots.

55 Discussion

56 **Figure 4.8.** Number-at-age in each of 500 bootstrap sample against the estimates of the population standard deviation by age for three different bootstrap sample sizes (300, 100 and 50) in columns, noting the differences in the extent of the x-axes for the different sample sizes. Black lines indicate smoothed estimates of the population standard deviation, illustrating the greater tendency of the yearly mean estimates to underestimate the deviation at small sample sizes compared to the increment analysis and to a lesser degree the direct-length-at-age analysis.

57 **Figure 4.9.** Results of the 1000 bootstrap systematically re-sampling by year. Solid line represents median jack-knifed samples containing data from a particular year, with estimates of the length-at-age estimated in the absence of a year's data shown dashed. Trends in cohort size are easily observable for both estimates up to age 5, and estimates are comparable for most years except the final year at age 0 and 1. Numbers show overall mean observed by age and year.

59 **Figure 4.10.** Figures illustrating the expected responses in otolith (solid line) and somatic growth (dashed line), left hand plots (a,c) and the resultant theoretical otolith to length relationship to resource limitation right hand plot (b and d) affecting somatic growth only (top plots, a,b) and environmental conditions such as temperature affecting otolith and somatic growth differentially (bottom plots c,d). The effect in panel d has been exaggerated for clarity and to plot the relative positions of cohorts / populations as suggested by the relationship of the cohort effect in the direct length-at-age and the back-calculation sub-model analyses.

65 **Table 4.1.** Model parameterisation and results of each model developed. Negative residual deviances for the increment models are caused by arithmetic difficulties with 0-size increments and the log-link function. This is reflected in the larger dispersion parameter for the Gamma distribution estimated by S-Plus. This invalidates the use of the deviance residual, but

not the analysis as a whole.

66 **Table 4.2.** Temporal, spatial and gender distribution of age samples indicating the imbalance in the sampling numbers between estuaries and sexes.

67 **Table 4.3.** ANOVA summary results for and pair-wise comparisons for length and otolith radius between populations

68 **Table 4.4.** Estimated mean length-at-age and standard deviation from the increment Analysis by sex, year and age for the three estuaries.

69 **Table 4.5.** Estimated mean length-at-age and standard deviation from the length GAM Analysis by sex, year and age for the three estuaries.

71 **Chapter 5: How robust are generalized additive models to changes in sampling design, and how sensitive are they to the underlying assumptions made for the purpose of management?**

71 **Introduction**

72 **Material and Methods**

74 Table 5.1. Percentage deviance explained and the residual degrees of freedom in parenthesis for the original model and the two update models for each estuary. Emboldened numbers indicate the most appropriate model comparison with the original model, given the changes to the survey designs in the different estuaries.

74 **Results**

75 **Figure 5.1.** Comparison of updated habitat models based on GAMs using bay data only (red) and bay and river data (black) for the Indian River Lagoon. The model chosen for comparison with the original models (Figure 2.2) is the bay only (red) model as sampling of rivers had not commenced in 1999.

76 **Figure 5.2.** The effect of Indian River sampling design changes in the form of different periods of observations on the year effect for bay data only. In addition, the year effect of the original model, differing in the classification of bottom type is included for comparison.

77 **Figure 5.3.** Comparison of updated habitat models based on GAMs using bay data only (red) and bay and river data (black) for Charlotte Harbor. The model chosen for comparison with the original models (Figure 2.4) is the bay and river (black) model as river data was included in the original models.

77 **Figure 5.4.** The effect of Charlotte Harbor sampling design changes in the form of different periods of observations on the year effect for bay data only. In addition, the year effect of the original model, differing in the classification of bottom type and inclusion of river data is included for comparison.

78 **Figure 5.5.** Comparison of updated habitat models based on GAMs using bay data only (red) and bay and river data (black) for Tampa Bay. The model chosen for comparison with the original models (Figure 2.3) is the bay and river (black) model as river data was included in the original models.

79 **Discussion**

79 **Figure 5.6.** The effect of Tampa Bay sampling design changes in the form of different periods of observations on the year effect for bay data only. In

addition, the year effect of the original model, differing in the classification of bottom type and inclusion of river data is included for comparison.

80 **Figure 5.7.** Relationship between the annual mean probability of capturing at least one seatrout and the sampled habitat quality (solid line: characterized as the difference between the mean abundance and the predicted abundance in a year) , and the estimated cohort strength (dashed line) for a) Indian River, b) Charlotte Harbor, and c) Tampa Bay.

85 **Figure 5.8.** Temporally interpolated mean monthly sampling temperature (left) and salinity (right) each year overlaid with means standardised catch rates (dashed line) and predicted cohort strength (solid line) for a) Indian River, b) Charlotte Harbor, and c) Tampa Bay.

86 **Figure 5.9.** Comparison of the predicted estimates of cohort strength with the means standardised catch rates, observed catch rates (circles), the indices currently used in the assessment and the estimates of recruitment from the appropriate model (dashed line) for a) Indian River, b) Charlotte Harbor, and c) Tampa Bay.

89 **Generalized additive models (GAMs): a synopsis of lessons learned**

91 **References**

Chapter 1: General Introduction to Management and Conservation of Spotted Seatrout (*Cynoscion nebulosus*) in Florida

The traditional aim of fisheries management is to ensure sustainability, i.e. to maintain populations of exploited fisheries resources at sufficiently high levels for them to replicate themselves over long periods of time, while extracting maximum benefit from the resource for this and future generations (Hilborn and Walters, 1992), with limited attention to the underlying ecological processes (Ostermeier, 1999). In contrast, the aim of conservation managers is more qualitative. The UN Convention on Biological Diversity states under its Article 2 that the aims of the convention are “the use of components of biological diversity in a way and at a rate that does not lead to the long-term decline of biological diversity, thereby maintaining its potential to meet the need and aspirations of present and future generations”. It has also been described as focusing on “the renewal of ‘broadly defined’ ecological processes” (Ostermeier, 1999) and is therefore more about maintaining a suite of populations at levels where they contribute maximally to the stability of the ecosystem in relation to a reference point, usually in recent history. In the absence of a quantitative reference point, the process uses the more qualitative measure “persistence” or anecdotal information on conditions in the past to describe its specific objectives.

Recent recognition of the value of marine resources and our need to manage them more effectively under an “ecosystem approach”, has led to a need to consolidate fisheries science within the broader aspects of an ecosystem, despite differences in the aims and objectives of fisheries management and conservation (Storer, 1992; Rosenberg et al., 2000). This conclusion was adopted into US law in 1996 by the reauthorisation of the Magnuson-Stevens Fishery Conservation and Management Act (Benaka, 1999), leading to a drive to identify and characterise essential fish habitat (EFH). This ethos and the realisation of a need to understand the ecological processes underlying the dynamics of fish populations better are largely responsible for the development of the work presented in this dissertation. In Europe, ICES has adopted a similar approach by implementing an ecosystem approach to fisheries management, although the implementation here is more difficult because of the advisory requirements of the European Commission as part of the Common Fisheries Policy (CFP).

The aims of fisheries managers and conservationists may therefore appear to be conflicting, but in practice both refer to reference levels of ecological status (Tasker and Knapman, 1999). Modern fisheries management practice, particularly in the US, tends to set quite precautionary fisheries management targets to be generally more restrictive than conservation targets, which in their simplest form hope merely to maintain a species at the single-species level (Botsford et al., 2004).

Where the two differ most significantly is in the implementation of the measures used to control abundance. Fisheries management, with the exception of stock enhancement, tries to control the rate of extraction of individuals from a population, so manipulating the fishing mortality rate, whereas conservation mainly attempts to influence stock productivity by reducing excessive abundance or assisting populations that have declined excessively to rebuild, either directly through breeding programmes, or indirectly by protecting or restoring habitat to facilitate the reintroduction of original ecological processes (Yankee et al., 1999).

The tools employed in the two processes are not mutually exclusive, nor is there a clear line, in terms of exploited resources, where conservation ends and fisheries management starts, as can be seen by recent arguments over the control of the management of bluefin tuna stocks in the Mediterranean, between CITES (Convention on International Trade in Endangered Species) and ICCAT (International Commission for the Conservation of Atlantic Tunas). Conservation can often be achieved most effectively on smaller scales by protecting or restoring habitats if populations have not yet reached critical levels where genetic or biological factors are such that the population is unlikely to recover without additional intervention. In contrast, fisheries management generally considers and manipulates fishing mortality as the primary cause of declines in exploited stocks (Hogarth et al., 2004). Although managers are starting to recognise that natural variations in natural (i.e. non-fishing) mortality and stock productivity mean that exploited stocks cannot be treated in isolation of the ecosystem in which they live (Walters and Martell, 2004), traditionally they have had few methods by which they can implement measures that control the variations.

It should be clear that despite the differences in jurisdiction, fisheries managers and conservationists cannot achieve their respective aims in isolation (Tasker and Knapman, 1999). After all, a protected area without higher level predators usually targeted by fisheries is likely of no more use than a stock that continues to decline despite a cessation of fishing because it has nowhere to reproduce effectively.

Similarly, the different data sources on which conservation and fisheries management measures are based have only infrequently been used in an integrated approach, but with recent policy changes and new statistical tools for assessment it should be possible to increase the efficiencies of both disciplines in maintaining a balanced ecosystem for both economic and social benefit.

SeatROUT have been exploited historically by native artisanal fisheries and in the 20th century commercially because of their attractive appearance and taste. Statewide estimated landings peaked in 1989 at 850 million pounds, but have decreased considerably since then below 300 million pounds since 1996. In 1990, amid concerns of overexploitation of Florida populations and increasing pressure from the recreational sector, Florida implemented a number of management measures aimed at maintaining the stock's reproductive capacity, including restrictions on commercial fishers entering the fishery, bag limits and minimum and maximum landing sizes (slot limits), with a formal assessment process initiated at the same time. In 1996 a net ban was introduced in Florida inshore waters, excluding most commercial exploitation formerly conducted using gillnets, with the same measure also introducing recreational slot limits, although there is a provision for taking one specimen above the maximum landing size. For a more detailed account of the exploitation history and management measures implemented to protect and manage the species, see Vanderkooy and Muller (2003).

Spotted seatROUT, although not of immediate concern to conservationists, are strongly associated with seagrass beds in Florida estuaries (McMichael and Peters, 1989; Chester and Thayer, 1990), which have been increasingly threatened by worsening water quality, through runoff from increasing urban and industrial development, dredging, and disturbance by those using estuaries for recreational purposes. Closer exami-

nation of the available data sources and the value of information to both fisheries and conservation managers should form an integral part of future management of Florida estuaries and the biological resources found therein.

Spotted seatrout (*Cynoscion nebulosus*) belongs to the family of drums (Sciaenidae), and are largely estuary-dependent (Vetter, 1982), but on rare occasions extend locally into the marine environment as adults. They are common in seagrass meadows in shallow bays and estuaries throughout Florida and along the eastern seaboard of the US, with sizeable populations from the Chesapeake Bay (Ihde and Chittenden, 2003) to Texas (Ward et al., 2007).

Seatrout are fast-growing and early maturing, recruiting to the fishery partially at age one, and fully selected by age 2. Reproductively they develop quickly too, with both sexes capable of reaching maturity in their first year of life (Roumillat and Brouwer, 2004), when they join small ephemeral spawning aggregations throughout estuarine areas, usually in proximity to suitable juvenile habitat mostly around seagrass beds, but also in deeper channels and adjacent to tributaries. Males set up spawning territories and advertise them to potential mates acoustically by sonifications produced using specialised muscles in the swimbladder (Mok and Gilmore, 1983). Females are indeterminate batch-spawners, under favourable conditions capable of large reproductive output (Brown-Peterson et al., 1988), but classed as “intermediate” within the drum family in terms of the r-K strategy (Waggy et al., 2006). The easily recognised buoyant eggs hatch soon after release, and larvae settle shortly thereafter (Alshuth and Gilmore, 1993), precluding their separation from suitable settling habitat in close proximity to spawning sites and disentrainment from estuaries in general (McMichael and Peters, 1989).

As adults, they are mostly piscivorous predators, but they continue to take some crustaceans, on which they feed extensively as juveniles and subadults. Among piscivores they are generalists, feeding on diverse fish species, including other members of their own species when available in high densities (i.e. cannibalism).

This work aims to elucidate some of the biological processes underlying the fisheries-independent stock dynamics, without knowledge of which it will be difficult to manage the species, particularly in an increasingly anthropogenically altered estuarine environment, but bearing in mind ways in which such findings can be more effectively incorporated in the stock assessment process used to manage the fishery currently.

Both fisheries-dependent and -independent data are used to examine temporal aspects of the species' ecology, using data from three populations to determine which aspects are population-specific and which can be modelled across populations. The three Florida populations investigated are the Indian River Lagoon on the east coast of the state, and Tampa Bay and Charlotte Harbour, both located on the Gulf coast.

Chapter 2 focuses on the definition of juvenile habitat from fisheries-independent data sources so is more focused on conservation than fisheries management per se, but it also has the potential to provide an index of relative abundance, the utility of which is examined in Chapter 5 in light of new data, along with an evaluation of the statistical methods used to analyse data from all sections of the work. I contributed significantly to

the collection of the data as a member of the fisheries-independent monitoring program and conducted the analysis out of my own initiative, culminating in the publication of the chapter in its entirety (Marine Ecology Progress Series).

Chapter 3 examines the environmental aspects of reproduction based on data collected to aid fisheries managers determine egg production as opposed to the cruder measure of spawning-stock biomass. The aim there is to evaluate whether it is possible to relate spawning intensity to juvenile abundance, and therefore to future recruitment. I was an integral part of the original sample collection, the histological information on the reproductive state and the ages of the individuals were determined elsewhere, but the methodological approach, the data analysis and the publication of most of this chapter (ICES Journal of Marine Science) were my own conception and work.

Chapter 4 combines both fisheries-dependent and -independent data to investigate differences in growth between the three populations. Back-calculation at a population level is employed to derive length-at-age information which, along with length-based assessment models, can serve to improve the accuracy of the stock assessments of Florida populations. Most of the samples in the form of otolith sections were collected and prepared historically, although I was involved in the collection of some of the recent samples. My co-author (Mandy Tyler: Florida Fish and Wildlife Conservation Commission) for this as yet unpublished paper assisted in the measurement of the 10000 otoliths used and reviewed the manuscript, but the conception of the analytical approach, the analysis and write up are entirely my own work.

Chapter 5 provides a rigorous evaluation of the performance of the models developed in the published chapter 2 with regards to the conclusions made in light of new evidence and additional data. It seeks to describe the difficulties encountered and the lessons learned when using generalized additive models in conjunction with datasets collected for different purposes. It formulates conclusions on how to ensure that the models used are robust, and how to convey the uncertainties associated with such models, and underscores the relevant results in the context of the ecology of the species, to support fisheries managers and conservationists in managing the species. The dataset used is the same as that employed in chapter 2, but uses an extended period (1988-2008) to the collection of which I only contributed over the period 1996-2002. The analysis conducted is ostensibly the same as the one I developed in chapter 2, but includes some new methodologies developed by myself to evaluate the original methodology and to test its sensitivity to model assumptions and changes in sampling design. The chapter is currently not in a form suitable for publications, but it I hope to develop a peer-reviewed paper of the evaluation at a later date.

Chapter 2: Development and evaluation of statistical habitat-suitability models; an example based on juvenile spotted seatrout (*Cynoscion nebulosus*).

This paper was published in the Marine Ecology Progress Series – see Kupschus (2003) and is reproduced here in a slightly edited for formatting consistency.

Introduction

Conservation managers need to predict the abundance and distribution of fish species in estuaries lacking fisheries-independent monitoring data and to assess the possible effects that hydrodynamic changes caused by environmental perturbations may have on fish populations. Both needs can be met by models, that accurately describe the relationship between species abundance and the local environment, given information on environmental conditions or predictions on conditions following hydrological perturbation. Attempts have been made to model fish abundance or distribution quantitatively (parametrically) or qualitatively (nonparametrically) as a response to environmental conditions (Rubec et al., 1999; Brown et al., 2000). However, these approaches fail to model the relationship between environment and abundance realistically or in a quantifiable manner (Hastie and Tibshirani, 1990).

Generalized additive models (GAMs) combine the flexibility of nonparametric models with the quantifiable statistical evaluation of error structures and model selection criteria. They represent a flexible semi-parametric modelling approach to determining the relationships between dependent and independent variables, and in contrast to traditional parametric habitat-preference models are not restricted to unrealistic monotonic multi-parameter models, or by the usual assumption of normality (McCullagh and Nelder, 1989; Neter et al., 1996). The model-free parameter estimation through multiple flexible splines and likelihood-based error estimation covering a multitude of possible error functions can overcome many of the restrictions of earlier habitat preference models (Hastie and Tibshirani, 1990). Spline functions are not monotonic or tied to preconceived notions about the relationship between dependent and independent variables and can therefore more realistically describe the multitude of physiological and behavioural effects that determine the distribution of fish. The number of possible error structures available through the use of the log-likelihood approach allows for modelling the non-normal errors typical of survey data. GAMs have already been successfully employed to elucidate complex relationships between fish abundance and environmental conditions (Swartzman et al., 1994; Bigelow et al., 1999; Maravelias et al., 2000). However, their ability to predict temporal and spatial variations in fish distributions in independent datasets has yet to be rigorously examined.

The aim of this study is not to develop the best possible model describing juvenile fish distributions in all estuaries, but rather to test the ability of GAM models developed based on data in one estuary to describe the spatial and temporal distribution of fish in other estuaries, given local sets of environmental predictors. As a proof of concept of the use of GAMs in modelling fish distributions independent of a particular estuary, this study developed spatially and temporally dynamic models describing the distribution of spotted seatrout (*Cynoscion nebulosus*) based on their habitat preferences in three different estuaries. An in-depth investigation of habitat preferences and spatial distribution

of juvenile spotted seatrout is fitting for several reasons. First, owing to its considerable recreational fisheries value to Florida (Chester and Thayer, 1990), much is known about its biology (Moffet, 1961; Iversen and Tabb, 1962; Tabb, 1966; Peebles and Tolley, 1988; McMichael and Peters, 1989; Nelson and Leffler, 2001). Such published information is critical to verifying qualitatively the model results in terms of the species ecology and to judging the suitability of models for describing habitat usage and recruitment, even though nursery habitat is poorly defined and its ultimate role in determining recruitment strength is not yet clear. Second, comparable fisheries-independent datasets are available for three Florida estuaries to facilitate quantitative comparison of models derived from fisheries-independent collections made in one estuary with the observed abundances of fish collected in other estuaries (foreign models). Third, because of the high level of fishing pressure and anthropogenically induced environmental change, there is an urgent need for tools to aid conservationists and fisheries managers in protecting these economically important resources (Helser et al., 1993; Rubec et al., 1999). Because of its limited migratory behaviour and its absolute dependence on estuarine habitats (Moffet, 1961; Iversen and Tabb, 1962; Tabb, 1966), the seatrout is threatened by localized extinction through naturally or anthropogenically induced habitat perturbations. This paper assesses the ability of GAM model to describe distributions based solely on environmental conditions and to examine where such models might help conservation managers in predicting fish distribution in estuaries lacking fisheries-independent monitoring information. In addition, an assessment was made of the year-effect from such pre-recruit models as a means of predicting future recruitment, which is important to fisheries managers.

Material and Methods

Study sites

Juvenile seatrout in three estuaries located at comparable latitudes were examined in this study, two populations on the west and one population on the east coast of central Florida (Figure 2.1b-d). Tampa Bay (TB) and Charlotte Harbor (CH) are bays separated from the Gulf of Mexico by barrier island systems. The two estuaries receive significant freshwater inflows from several mainland tributaries, creating a conventional salinity gradient, with salinities decreasing at increasing distances from the Gulf of Mexico. The Indian River Lagoon (IR), adjacent to the Atlantic Ocean, is made up of two parallel basins: the more western Indian River and the less extensive Banana River. In stark contrast to the tidally driven estuaries on the west coast, the IR hydrography is largely controlled by prevailing wind patterns (Smith, 1987). The lagoon receives freshwater, but because of the location of its tributaries and the position of man-made connections to the Atlantic, the lagoon's unconventional salinity gradient is largely perpendicular to its net flow (DaCosta et al., 1987).

Despite hydrographic and zoogeographic differences, species composition in catches and available habitat types were similar in all three estuaries. Vegetated habitats included seagrass meadows, made up of *Halodule wrightii*, *Thalassia testudinum* or *Syringodium filiforme*, and mangrove fringing forest, predominantly made up of red mangroves (*Rhizophora mangle*).

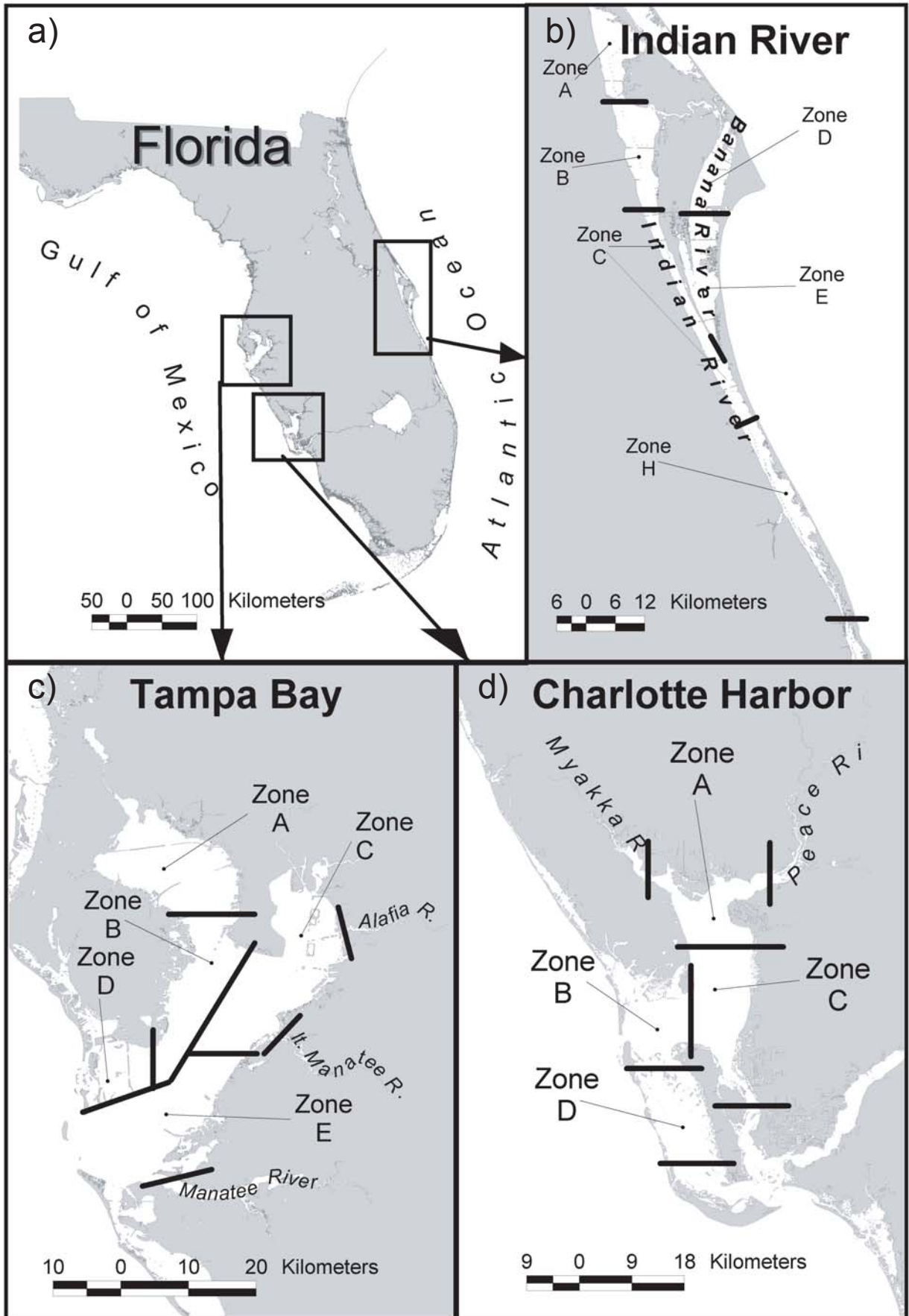


Figure 2.1. Definitions of the four estuarine regions over three study sites a) Tampa Bay - TB, b) Charlotte Harbor - CH, and c) the Indian River lagoon (IRN, IRS). Black areas (1-4) in c) indicate the four primary adult sampling sites.

Sample collection

Sampling in each estuary was conducted from January 1996 to December 1999 using a monthly, multigear stratified random sampling (StRS) design, stratified spatially by zones (Figure 2.1 b-d), proportionally stratified by habitat type within zones. Some changes to the sampling design were made over the four-year period for logistical reasons, slightly complicating interpretation of the results. The stratified random sampling design in the IR was amended in January 1998 to include the more southern zone H and to reduce the monthly sampling effort in zones A, B and E to a single fall (autumn) sampling period (Figure 2.1b). In TB, sampling in parts of zone E was eliminated during the period January to May 1998, after which monitoring in the area resumed at effort levels lower than before (Figure 2.1c). In CH, zone D was dropped from the sampling design (Figure 2.1d), and sampling effort was decreased in all other zones in 1998.

Three different techniques, boat, offshore, and beach sets, were used to deploy a 21.3-m by 1.8-m center-bag seine (3.2-mm #35 knotless nylon Delta mesh) in order to measure fish abundances effectively in a wide variety of habitats (Nelson, 2002). Sample sites were chosen randomly without replacement from a sampling universe unique to each deployment technique, consisting of 1' latitude by 1' longitude grids. Boat and offshore sets were proportionally pre-stratified, and beach sets were unstratified so that it was possible to collapse the stratified design into a simple random design for the purpose of this analysis.

Boat sets were used only in the tributaries of the west coast estuaries to sample steep riverine banks, whereas riverine habitats were not sampled at all in the IR. The net was set in a semicircle from the shore by boat and manually retrieved to shore. Beach sets sampled the estuarine shoreline and were set out perpendicular to the shore and dragged for 9.1 m parallel to the shore before being retrieved similar to the boat sets. Offshore sets were used to capture fish away from the immediate shoreline by dragging the net for 9.1 m in water <1.5 m deep and retrieving it around a pivot-pole to concentrate the sample in the bag. The area swept differed for the three techniques, covering 68 m², 140 m² and 338 m² for boat sets, offshore sets, and beach sets, respectively.

At least 40 specimens were measured to the nearest mm standard length (SL) from each set and, in case of greater sample numbers, the remainder were counted and raised to a total using the length frequency distribution. Synoptic water-quality data were collected, and additional variables on the spatial, temporal and biological properties of each sampling location were measured for each sample. For a more detailed description of the sampling design, deployment methods and environmental variables collected a full procedure manual can be obtained from the Fisheries-Independent Monitoring Program.

Numerical analysis

Three independent models of the habitat preferences of juvenile seatrout were developed, each based on the data from one of three estuaries, CH, IR and TB. Only catch data for seatrout <50 mm SL (standard length) were analysed because larger seatrout have the ability to effectively avoid the sampling gear and tend to occupy alternative habitats as a consequence of ontogenetic behavioural changes such as diet shifts (McMichael and Peters, 1989). Additionally, the initiation of schooling behaviour has

also been documented for this species at >50 mm length (Tabb, 1961). As larger fish school, they are encountered more contagiously than would be expected in a random distribution. That is, the mere presence of fish increases the probability of greater abundance, whereas the absence of fish reduces the probability of abundance. In the case of schooling fish these are better modelled as a negative binomial error distribution. In any case, mixing the assumed Poisson error distribution of the <50 mm seatrout with the negative binomial error distribution of larger schooling fish would invalidate the error distribution of the model and lead to unrealistic estimates of confidence limits for parameters and hinder model selection through improper evaluation of the deviances.

S-Plus was used to develop a separate GAM (Venables and Ripley, 1999) with an assumed Poisson error distribution for each estuary system to describe the abundance of seatrout as a response to day of the year, year, temperature, salinity, water depth at the seine bag, percentage seagrass cover, and bottom type (mud, sand, mud-sand mix, oysters with mud, oysters with sand). The choice of the environmental variables was based on either their reported performance as suitable indicators of seatrout abundance or their ability to characterize ichthyofaunal assemblages in estuaries (Kupschus and Tremain, 2001). The year effect was parametrised as a classification variable in the model in order to examine interannual changes in the abundance of seatrout in the fisheries independent survey, which were not explained by differences in the environmental conditions encountered during sampling.

The differences in effort of each of the deployment techniques associated with differences in the area swept needed to be accounted for in the analysis. Frequently this is accomplished by dividing the catch by the area to arrive at a catch per unit effort dependent variable. This approach, however, disrupts the error structure, because for very small areas the problem tends towards a binomial problem (a fish caught or not), whereas at larger areas the problem tends towards a Poisson problem (how many fish are caught). In this study, to compensate for the differences in effort between the techniques while maintaining the appropriate error structure, the area covered was divided by the largest area (338 m²), and the resulting ratios were used as an offset in the GAM analysis (Venables and Ripley, 1999).

Several of the measured environmental variables were highly correlated, because of the interplay of the sampling design and the individual hydrographic characteristics found in each estuary. This multicollinearity can complicate or invalidate the interpretation of the results of any regression analysis, particularly in linear regression models. To mitigate against this, one of a pair of correlated variables is usually excluded from models (Geary and Leser, 1968; Yeo, 1984). In the present study, correlated variables were retained, because correlation does not make them necessarily redundant (Hamilton, 1987). Instead, to avoid including truly redundant variables in the analysis yet retain all important environmental information in the analysis, the Akaike Information Criterion (AIC; McCullagh and Nelder, 1989) was used in a bidirectional stepwise procedure to select the most parsimonious model. Implementing this procedure through the S-Plus `step.gam` function (Venables and Ripley, 1999) allowed the objective selection of significant environmental variables and avoided multicollinearity problems in the development of models.

The final GAM was of the form:

$$abundance = \exp \left(\alpha + \sum_{i=1}^n \beta_i(X_i) + \sum_{j=1}^k f_j(X_j) + \epsilon \right)$$

where α is the intercept of the linear predictor, β the slope of the i th linear component, f the spline function of the j th smoothed component, and ϵ is a Gaussian error term (Hastie and Tibshirani, 1990).

Originally, the AIC was seen as an objective criterion not only for the selection of independent variables, but also the degree of freedom (df) to choose for the spline function. However, the resultant models had unjustifiably high degrees of freedom associated with only minimal deviation of the overall trend from spline functions with a lesser degree of freedom. The phenomenon was explained by Hilborn and Mangel (1997), who described the tendency of the AIC to overfit the model beyond the complexity necessary to describe the relationship between the independent variable and its partial effect when the true error distribution was more contagious (contained higher frequencies of small and large values) than expected for a Poisson distribution. To avoid overfitting, the final model was scrutinized by reducing the spline complexity (degrees of freedom for each bicubic spline smoother; Hastie and Tibshirani, 1990). If the reduction in the degrees of freedom for the individual splines subjectively changed the overall partial relationship in the new model, the original complexity of the splines was maintained, otherwise the spline complexity was reduced and tested again.

Independent validation and transferability

The flexibility of splines allows GAMs to portray complex relationships realistically between fish and their environment, but this flexibility is also their weakness. When the exact error structure is unknown, the predicted means become susceptible to the effects of outliers. The validity of each model was tested by confronting the model with independent data from other estuaries (foreign data), to evaluate its predictive utility in other systems. The expected mean abundance for each of the three survey datasets was predicted from the environmental conditions by all three models developed in this study. The summed deviances between observed and predicted values were used to calculate the explained deviance for all model and estuary combinations to give an independent measure of the accuracy and the interestuarine transferability of each of the models. Systematic bias in the transferability of models was examined by studying the correlation between the sample predictions from each of the three models for a particular estuary.

Spatial comparisons

In contrast to models, maps are static reproductions of a state at a given time. As such they cannot account for or predict changes in the spatial distribution over time and hence underestimate the fluctuations in the distribution over time. This makes them unsuitable as a management tool, or a way of statistically comparing models, but they do represent a useful visual assessment of the ability of the models to capture interannual and intra-annual changes in juvenile seatrout abundance. To examine the spatial and

temporal dynamics in years and in months over years, surfaces of the localized, model-predicted abundances were interpolated by inverse distance weighting (IDW) from all collections made in one year and all collections made in May, July, and September in all four years (the start, middle, and end of the main recruitment season, respectively). Observed abundance surfaces for the equivalent time periods were also interpolated, but rather than using the IDW method for predictions, observations were kriged (variable radius 12 nearest neighbours) in order to take into account the sample variance associated with observations. The resulting surfaces were standardized by the overall surface mean and variance in order to compare more easily the models and observations in light of differences in the mean abundances and coefficients of variations for the different surfaces.

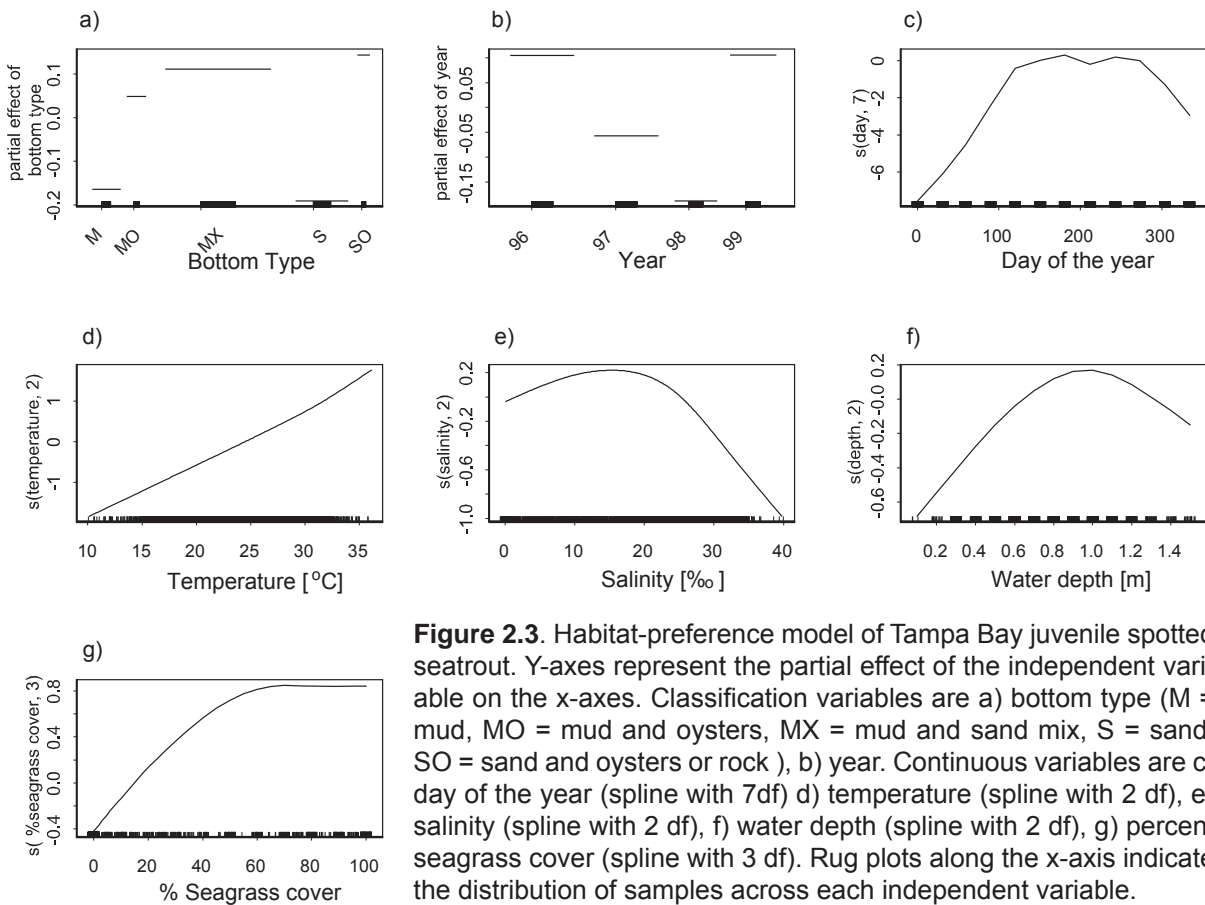
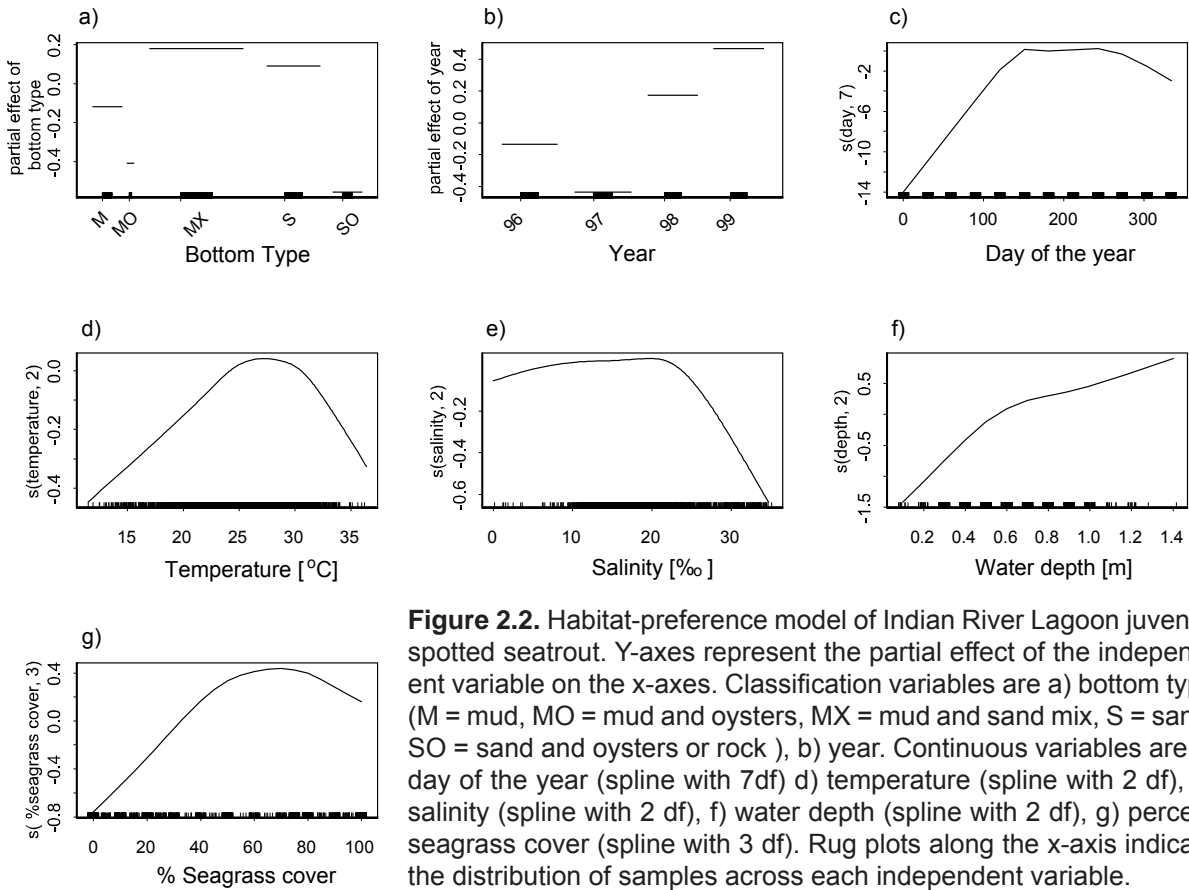
Results

Three independent GAMs predicting seatrout abundance were developed, each based on the data from one of the three Florida estuaries. The variables chosen by the stepwise model selection procedure for inclusion were the same in all models, and the degrees of freedom chosen for each spline function were the same and their shapes similar (Figures 2.2 – 2.4). The models explained 36.64% (IR), 42.54% (CH), and 44.04% (TB) of the deviance in the data from which they were derived (native data) (Table 1).

Environmental variables

The partial effects of temperature indicated an increased abundance of seatrout as water temperatures increased to 28°C for all estuaries, after which abundances declined in the IR (Figure 2.2d), continued to increase in TB (Figure 2.3d), and remained constant in CH (Figure 2.4d). The scale (range on the y-axis) of the partial effect, and hence its importance, was smaller in the IR than in TB or CH. The partial effect of salinity implied a unimodal relationship between salinity and seatrout abundance in all estuaries with a maximum of 20 ppt (IR, 20 ppt.; TB, 17 ppt.; CH, 18 ppt: Figures 2.2e-2.4e). As for temperature, the scale of the salinity effect was smaller in the IR than in the other two estuaries (Figures 2.2e-2.4e). The partial effect of depth was unimodal in TB and CH, rising to a maximum near 1 m in both estuaries, whereas in the IR, it continued to rise beyond the range of the sampled depths. The scale of the effect of depth was largest in the IR, smaller in TB, and smallest in CH (Figures 2.2f-2.4f). The partial effect of percentage seagrass cover rose from 0% to about 60% cover in all estuaries, after which it declined in the IR and CH and remained constant in TB. The percentage-seagrass-cover partial was comparable in size in all models (Figures 2.2g-2.4g). Of the frequently sampled bottom types (sand, sand-mud mix, mud), sand-mud mix was the most productive bottom type according to both the IR and TB models, whereas sand was the most productive bottom type in CH (Figures 2.2a-2.4a). The effect of bottom types containing rock or oysters, irrespective of the presence of mud or sand, fluctuated widely between models. These differences may indicate behavioural differences between populations, but it is likely that the overall scarcity of the latter two substrata and the differences in their prevalence in each estuary account for the disparity. The relative importance of bottom type was significant but small in all models.

Temporal variables



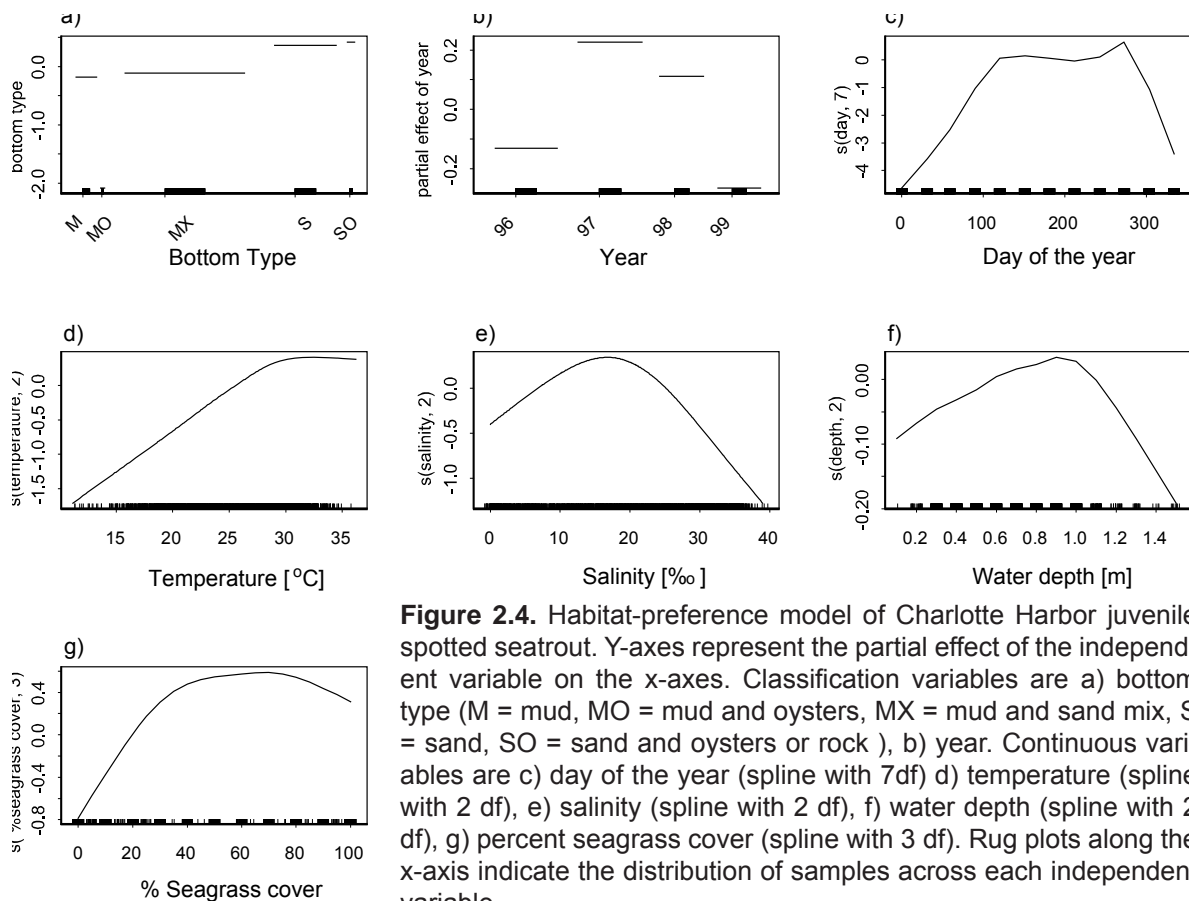


Figure 2.4. Habitat-preference model of Charlotte Harbor juvenile spotted seatrout. Y-axes represent the partial effect of the independent variable on the x-axes. Classification variables are a) bottom type (M = mud, MO = mud and oysters, MX = mud and sand mix, S = sand, SO = sand and oysters or rock), b) year. Continuous variables are c) day of the year (spline with 7df) d) temperature (spline with 2 df), e) salinity (spline with 2 df), f) water depth (spline with 2 df), g) percent seagrass cover (spline with 3 df). Rug plots along the x-axis indicate the distribution of samples across each independent variable.

In all models, the partial effect of day (1 January = 1 through 31 December = 365) implied a general seasonal increase in abundance of seatrout from May through August (Figures 2.2c-2.4c). The timing and exact form of the effect, however, was different between the models. The IR model indicated a plateau of greatest abundance lasting from day 125 to day 250 of the year, with abundances declining sharply outside that period (Figures 2c). Charlotte Harbor and TB models both indicated longer periods of maximum abundance, lasting from day 100 to day 280 (Figures 3c,4c). The effect of day was bimodal in both estuaries, with local maxima around day 180 and day 230, but in CH, the second peak was larger than the first, whereas in TB the peaks were symmetrical. The day partial represented the most important variable describing the abundance of seatrout in each model, with the greatest importance implied for the IR model.

The interannual patterns of abundance were specific to each estuary. Indian River abundances declined from 1996 to 1997 but have risen since (Figure 2.2b), whereas TB seatrout abundances continued to decline until 1998, recovering in 1999 to levels seen in 1996 (Figure 2.3b). Charlotte Harbor abundances increased from 1996 to 1997 but have declined since (Figure 2.4b). The partial effect of year was small, yet significant, in all estuaries.

Spatial comparison between catches and predictions

Distinct interannual differences in the spatial distribution of seatrout in each estuary were predicted by the models derived from their respective data (native models), as indicated by the interpolated surfaces produced from observed and predicted point data (Figure

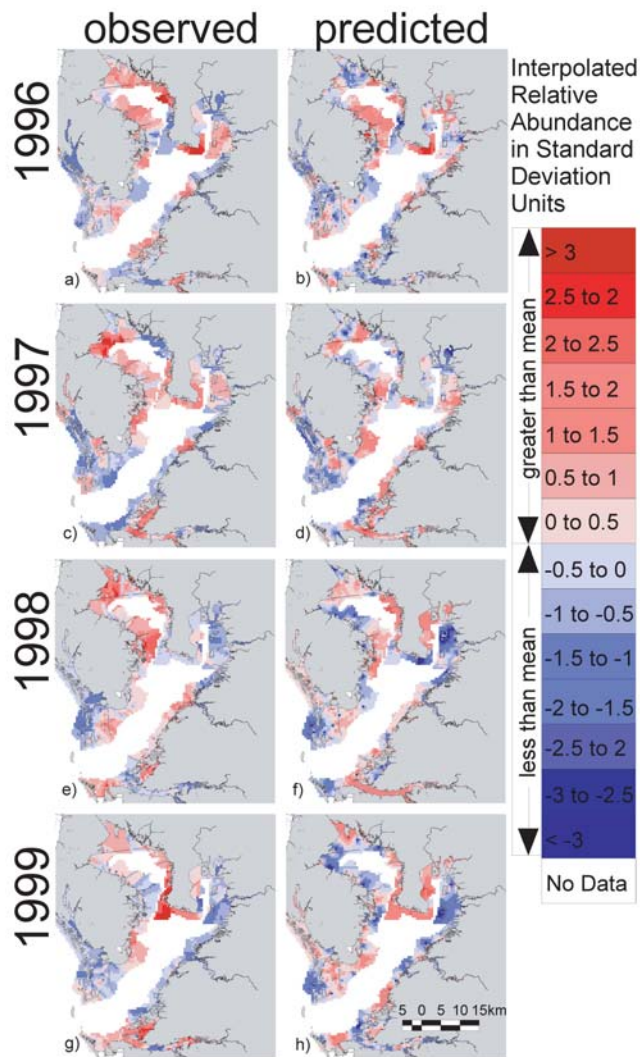


Figure 2.5. Tampa Bay standardized relative abundance surfaces interpolated from predicted (inverse distance weighting) and observed (kriged) annual point sample abundances and subsequently standardized by mean and variance, indicating interannual differences in the distribution accounted for by the TB model: a) observed 1996, b) predicted 1996, c) observed 1997, d) predicted 1997, e) observed 1998, f) predicted 1998, g) observed 1999, h) predicted 1999.

linity regime is strongly influenced by the presence of the Canaveral locks in the area, resulting in unusual salinity fluctuations, so the discrepancies are likely a reflection of the unusual conditions experienced there.

Validation and transferability

Seatrout abundances predicted for each of the estuaries by their respective native model were significantly correlated ($\alpha = 0.05$) with abundances predicted for the same samples by foreign models (Figure 2.8, Table 2). Although the IR model fared worst in explaining deviance in the native data, it transferred best between estuaries, explaining 28.14% and 15.69% of the deviance in the TB and CH data, respectively (Table 2.1). The CH model only accounted for 7.96% of the deviance in the IR data and 23.79% of the deviance in the TB data. The TB model produced the worst fit for foreign data

2.5-2.7). Predictions matched not only the spatial pattern in the relative abundance but also the actual magnitude of mean catches (e.g. TB 1996–1999; Figure 2.5). Intra-annual variations in the spatial distribution of seatrout within CH (Figure 2.6) and TB were also obvious. In CH and TB, these spatial dynamics could largely be explained by native and foreign models, as caused by monthly changes in the environmental conditions, although the CH model consistently overpredicted the abundance of seatrout in the lower part of estuary (Figure 2.6) owing to an insufficient sampling density associated with the changes in sampling design to Zone D. Despite good interannual correlation between the observed and predicted abundances in the IR, monthly spatial comparisons were less consistent. The IR model demonstrated poor predictive ability, particularly in the Banana River region (Figure 2.7a, 2.7b), indicating that there was some spatially systematic bias not explained by the environmental conditions included in the model. This part of the estuary

is a wildlife refuge, and the sa-

(IR data 8.40%; CH data 19.41%), but explained the largest amount of deviance of any model for its native data (44.04%).

Comparisons of the standardized kriged model predictions by year and month showed spatially consistent distribution patterns between models (Figure 2.7). The model prediction surfaces, although not dissimilar to surfaces derived from observed data from each estuary, usually resembled each other more than they resembled the observed data. As with the native model, the foreign models were inconsistent predictors of the spatial distribution of seatrout in the Banana River region of the IR (Figure 2.7c, 2.7d), again confirming the unusual status of this area.

Discussion

Models of seatrout habitat preferences independently developed for three Florida populations showed that juvenile spotted seatrout responded similarly to salinity, temperature, depth, and percentage sea-grass cover. Habitat preferences were alike for all three estuary populations and were similar to documented habitat preferences of this species. The GAMs described the relationships between species abundance and environment and supplied a robust measure of the interannual variation in abundance. However, based on published information of the biology and detailed examination of the sampling designs used in this study, it was

clear that the models were susceptible to misinterpretation when independent variables were correlated. The predicted spatial distribution of juveniles based on the spatial configuration of habitat characteristics in the estuaries closely matched the observed distribution of catches. What follows is a detailed review of biological inferences from the models and how the results compare with previously reported findings for this species. This review is critical in order to aid in model interpretation, assessing transferability, and judging model utility in conserving and managing fish stocks.

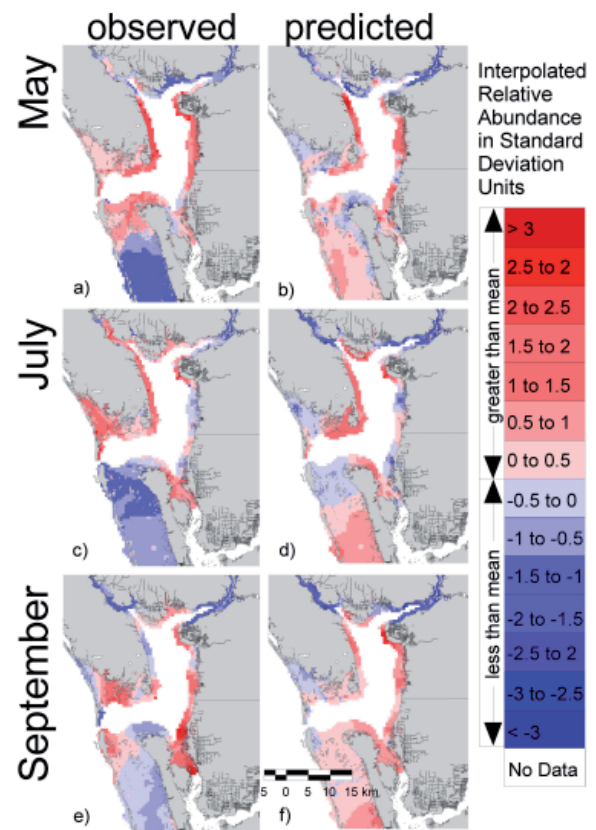


Figure 2.6. Charlotte Harbor standardized relative abundance surfaces interpolated from predicted (inverse distance weighting) and observed (kriged) monthly point sample abundances and subsequently standardized by mean and variance, indicating seasonal differences in the distribution in part accounted for by the CH model: a) observed May 1996-1999, b) predicted May 1996-1999, c) observed July 1996-1999, d) predicted July 1996-1999, e) observed September 1996-1999, f) predicted September 1996-1999. The outer part of the estuary was sampled only in 1996 and 1997, so the number of samples is too small for appropriate interpolation in this area.

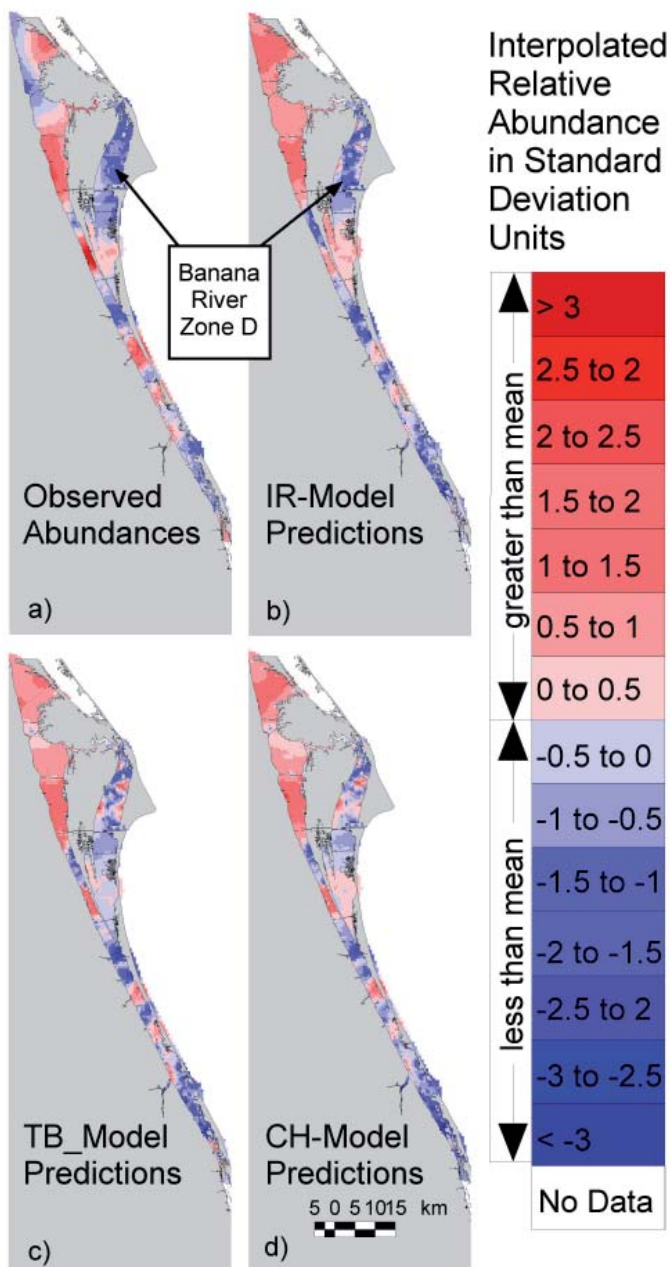


Figure 2.7. Indian River Lagoon standardized relative abundance surfaces interpolated from the IR, TB and CH seatrout abundance model predictions (inverse distance weighting) and observed (kriged) 1996 point sample abundances and subsequently standardized by mean and variance. a) IR observed abundances, b) IR model predictions, c) TB model predictions, d) CH model predictions.

of temperature, the relationship between temperature and abundance, at first glance, appeared to differ between populations. The optimum temperature for the species is around 28°C (Wohlschlag and Wakeman, 1978), consistent with the predicted abundance increases up to this temperature in all models. Higher temperatures were reported to affect the physiology of this species adversely, leading to stress and eventually death (Vetter, 1977), so declining abundances would be expected at such temperatures. The anticipated decline in abundance was only observed in the IR model, with unrealistic increases in abundance predicted by the CH and TB models. The differences in the

Day was a prominent descriptor of seatrout abundance in all models, despite the protracted spawning period reported by Moody (1950), Tucker and Faulkner (1987), Peebles and Tolley (1988), and McMichael and Peters (1989). The CH and TB models showed a bimodal relationship between day and abundance, which was similar to reports of temporal fluctuations in juvenile abundance in Florida by McMichael and Peters et al. (1989) and Rutherford et al. (1989). Seatrout spawning intensity was reported to be similarly bimodal elsewhere along the Gulf coast (Hein and Shepard, 1979). Presumably, the bimodality in juvenile abundance within a year reflected temporal variations in reproductive activity (Nelson and Leffler, 2001). In contrast, the IR model indicated a unimodal seasonal pattern of juvenile abundance, concordant with unimodal reproductive patterns reported from the Indian River Lagoon (Crabtree and Adams, 1998). The importance of the intra-annual variation in larval supply, whether caused by variation in reproductive effort or differential survival of larvae, greatly limits the abundance of juveniles, which was reflected in the primary importance of day in all models.

The dominance of day in the model was diminished in the CH and TB models, which were associated with concurrent increased importance of temperature. In addition to the quantitative differences in the importance

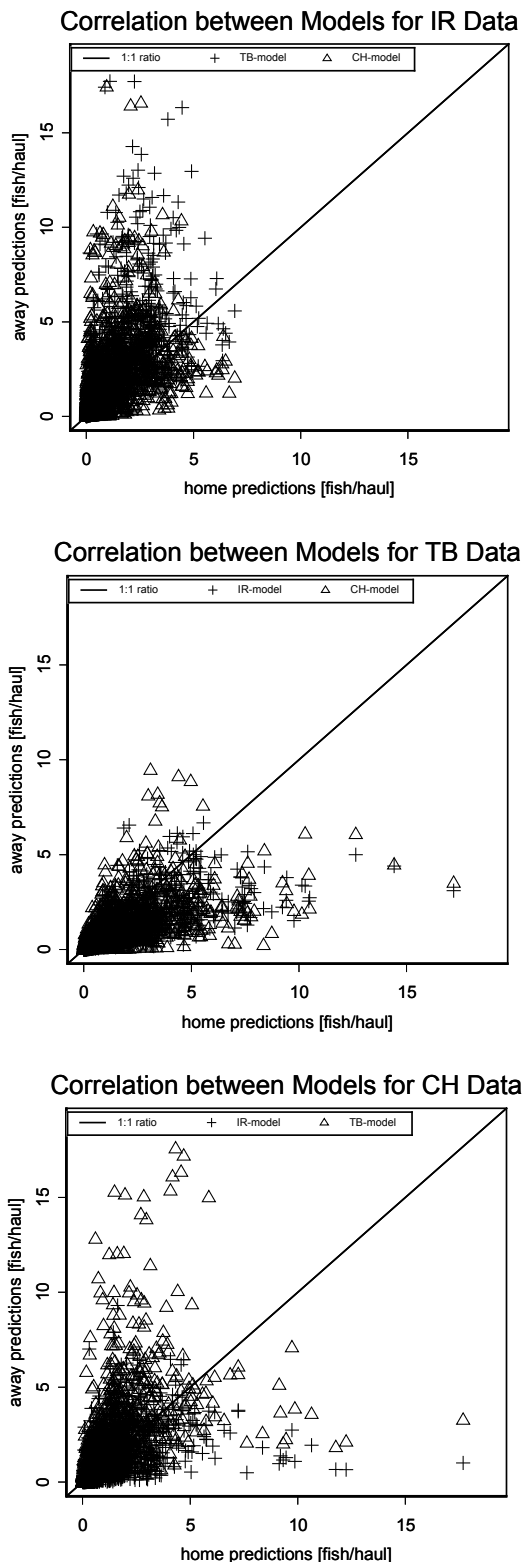


Figure 2.8. Correlation between the abundances predicted by foreign models with those predicted by the native model for the datasets from a) Indian River, b) Tampa Bay c) Charlotte Harbor. Predictions of the native model are always plotted on the x-axis, with the y-axis representing estuary foreign models. The line indicates the expected 1:1 relationship if transferability on the absolute scale were applicable.

importance and shape of the temperature partial between the west coast estuaries and the IR can be explained by differences in the extent of correlation between temperature and day within each estuary. The large latitudinal expanse and shallow depth of the IR (Smith, 1987) leads to greater temporal variability in temperatures, resulting in less of a correlation between temperature and the day of the year in the IR than in the other bay systems. Therefore, the IR model can correctly attribute the deviance to day, whereas the CH and TB models associate some of the deviance attributable to day to the temperature effect. The predicted high abundances at high temperatures are scaled back by an excessive dip in the day effect during the summer period when temperatures are $>28^{\circ}\text{C}$. Multicollinearity between day and temperature, rather than differences in the biology of the populations, was the most likely cause for the difference in the day and temperature effect, particularly given the evidence of fatalities at high temperatures.

Percentage seagrass cover was positively correlated to seatrout abundance in all models, second only to day in influence on seatrout distribution after accounting for the colinearity between temperature and day. The prominence attributed to seagrass cover in these models was consistent with reports by Gilmore (1977), McMichael and Peters (1989), and Chester and Thayer (1990). Despite the predicted high-ranking importance of seagrass, juvenile seatrout have also been frequently encountered in areas devoid of seagrass, usually in protected backwaters and tributaries over muddy bottom (Peebles and Tolley, 1988; Peebles et al., 1991; Llansó et al., 1998). Even estuaries apparently lacking seagrass completely have sustained viable populations of seatrout (Darnell, 1958). This is evidence that seagrass itself is not a facultative requirement of seatrout but rather that percentage seagrass cover served as an indirect measure of the ability to find

food (Orth et al., 1984) and avoid predators (Hindell et al., 2000), because of habitat complexity. This function may be facilitated in other estuaries by shallow backwaters (Ruiz et al., 1993; Halpin, 2000; Paterson and Whitfield, 2000). Quantitative measures of food availability and protection from predators offered by different habitats would be necessary in order to accurately predict the distribution of seatrout in estuaries lacking seagrass.

All three models largely concur on the shape and the importance of the salinity partial, indicating maximal seatrout abundances at 20 psu. This value is also close to the physiological optimum of this species (Wohlschlag and Wakeman, 1978). The divergence of the IR model from the other estuaries at low salinities results from the lack of sampling in the suboptimal riverine habitats (Peebles et al., 1991) in the IR, but that are frequently sampled in TB and CH. The few IR samples taken in low-salinity environments are more representative of short-term conditions incidental to sampling and not true long-term oligohaline conditions. Consequently, the IR model overpredicts the abundance of seatrout in mesohaline environments when compared with the other models. In contrast, the CH and TB models correctly predicted few seatrout at low salinities, but unfortunately, the low-salinity river sites in these estuaries also yielded samples from the deepest water because of the boat-set technique employed solely in that habitat. Inevitably, this led to the low abundance associated with low salinity also being associated with increasing depth in the west coast models. In contrast, the depth partial in the IR, where rivers were not sampled, continued to increase for the entire length of the depth gradient, as reported elsewhere (Rutherford et al., 1989). It is likely that the observed differences between models in the salinity and depth effects were again a result of sampling-design-induced multicollinearity and not behavioural divergence of the populations. The high degree of correlation of salinity and depth in the CH and TB data, the ecological evidence, and the transferability performance of the IR model all attested to the greater plausibility of the latter model and demonstrated that multicollinearity is hampering the effectiveness of the CH and TB models when predicting abundances in the IR data.

Transferability

Transferability in this case is the ability of a model derived from data in one estuary to predict the abundance of seatrout in a second estuary based solely on measured environmental conditions in the latter estuary. The developed models were able to achieve reasonable transferability when confronted with non-native environmental data, explaining significant portions of the total deviance in the data from other estuaries. Observed abundances were significantly correlated to predicted abundances for all foreign models, although the relationship was temporally biased and the overall relationship between model predictions always differed from the expected one-to-one relationship.

The three models implied three distinct estuary-specific year effects, indicating three independent populations, each with its own specific population dynamics. This type of information gleaned from these models has important implications for fisheries managers who must ultimately consider such effects in producing coastwide stock assessments in order not to allow localized populations to collapse. It might be argued that the sampling-design changes implemented at the end of 1997 invalidate the use of the year effect as a measure representative of estuarine recruitment dynamics. The year effect was smallest in TB, the estuary that has had the most modest sampling

design changes, and was largest in the IR, the estuary with the most significant design changes. In CH only small changes in abundance were observed across the sampling design transition --1997 and 1998 data were more similar to each other than to the 1996 and 1999 data. Consequently, differences could not be attributed solely to changes in the sampling design, and abundances must at least in part be controlled by differences in the population dynamics between estuaries. The unique interannual trends meant that models were not useful in predicting the number of seatrout found in an area of a foreign estuary but could be an invaluable tool in grading the suitability of habitats in a foreign estuary.

The multicollinearity unique to the sampling designs within each estuary represented a hindrance to transferability, as indicated by the better ability of the IR model, the model with the least correlation among independent variables, to explain the most deviance in foreign datasets. Presence of multicollinearity in itself does not seriously impede model predictability, provided that it is constant over the period and area of interest (Neter et al., 1996). In the absence of sampling design changes, we can assume this to be the case within an estuary but certainly not between estuaries, as shown here by the poorer transfer performance of the CH and TB models. It is important to consider the sampling design in light of the species' ecology during the development phase of these complex models and to remember that changes to the design will potentially invalidate the use of the indices of abundance across such changes.

Implications for conservation management

In order to protect and conserve species, conservation managers need information on the resource requirements of all life stages of a species, especially the vulnerable juvenile stages. The models described here allow quantitative evaluation of the important habitats of juvenile seatrout for their native estuaries based on actual environmental data. All models clearly indicated areas of high seatrout abundance (high suitability) as well as areas of low seatrout abundance (low suitability) in non-native estuaries. The suitability of specific estuarine regions was consistent between all models and all estuaries, despite considerable dynamics in space and time. Because the location of optimum conditions (e.g., nursery habitat) varies dynamically in space and time, protection of a specific locale will unlikely suffice to ensure the survival of the species. Generalized additive models can clearly aid conservation managers in reviewing proposed changes to the environment and deciding on options with the least deleterious effects on populations.

For conservation managers it is important to identify the areas of most suitable habitat within an estuary lacking fisheries independent sampling data. Despite the high residual deviance in these models, it is clear from the maps presented here that when environmental conditions are sampled in suitable density in space and time, all models were capable of identifying the areas of most suitable habitat in native and foreign estuaries. This justifies the use of low explanatory power models by conservation managers. Preference should always be given to those models with least correlation of the independent variables in order to avoid multicollinearity issues during transfer of models, even if it is thought to be at the expense of explanatory power in native estuaries.

Although transferable on a relative scale, the models discussed here were not transferable on the scale of absolute abundances caused by the significant contribution of the population-specific year effect. Therefore, the current models would not be capable of assessing the absolute number of fish affected by environmental alterations or disasters in foreign estuaries. However, this might be different for species with a well mixed population or one that recruits from a single ocean spawned pool of larval recruits.

Implications for fisheries management

Fisheries managers are interested in obtaining information on the abundance of juveniles before they enter the fishery in order to predict future stock sizes and implement management changes early. In the past, the most important factor in determining the size of recruitment was thought to be the size of the spawning stock as reflected by the spawning-stock biomass (SSB) benchmark currently used for Florida's spotted seatrout stocks. It has become increasingly clear, however, that recruitment can only be poorly linked to SSB, particularly for species restricted to very specific juvenile habitats, because of the variance-dampening effect enforced by its limited availability (Iles and Beverton, 2000; van der Veer et al., 2000). A poor spawner-recruit relationship has been observed for Florida spotted seatrout. Therefore, it is expected that the variance-generating function of the reproductive part of the life cycle was overshadowed by the variance-dampening function of the other life stages. Assessment of habitat quality and availability should produce better estimates of recruitment than information solely on spawning-stock size. The year effect described by the models represents a robust measure of native juvenile seatrout abundance or future recruitment, assuming a consistent sampling design, stable environmental conditions, and constant niche breadth. Interannual fluctuations were estuary specific, indicating the different seatrout populations are less well mixed than assumed by current stock assessments, and quantitative predictions of recruitment for foreign estuaries is not possible from these models. In contrast to conservation managers, fisheries managers using the models purely in the native estuaries would place greater emphasis on the explanatory power of the models, rather than on their transferability.

Conclusions

The prohibitive costs of intense fisheries-independent surveys has led conservation managers to look for models that can be used to predict fish abundances in systems lacking suitable surveys (Rubec et al., 1999; Brown et al., 2000). This analysis suggests that considerable savings can be made by the development of environmentally driven models of species distribution based on modern regression techniques. Generalized additive models are also sure to be valuable tools for fisheries managers in determining useful recruitment indices for implementation in stock assessments provided that the time-series are sufficiently long and uninterrupted by large-scale changes in the sampling design.

The ability of GAMs to deal statistically with non-normal data and weighting of different environmental variables as well as the flexibility of the splines used to more sensibly model the relationship between abundance and environment means that in data-rich situations, these models provide a temporally and biologically more accurate picture of seatrout distributions than habitat suitability models (Rubec et al., 1999). However, the

susceptibility of the models to multicollinearity issues means special attention needs to be paid to the sampling design under consideration of the biological and ecological characteristics of a species, in order to produce robust distribution models.

Chapter 2 Habitat models

Table 2.1. Catch statistics, model performance and transferability for the environmental dataset from each of the three study estuaries. (numbers in bold indicate predictions for data by foreign to the models) Numbers in bold indicate characteristics for foreign models.

Indian River	Data Characteristics			
	number of samples	1603		
	sum of fish caught in all samples	1465		
	mean catch [fish / haul]	0.91		
	percent occurrence	19.15		
	total deviance	6606.36		
	Model Characteristics	Indian River Model	Tampa Bay Model	Charlotte Harbor Model
	mean predictions [fish / haul]	0.91	1.88	1.55
	residual deviance	4185.61	6051.40	6080.55
	% deviance explained	36.64	8.40	7.96
Tampa Bay	Data Characteristics			
	number of samples	2605		
	sum of fish caught in all samples	2556		
	mean catch [fish / haul]	0.98		
	percent occurrence	21.00		
	total deviance	10409.35		
	Model Characteristics	Indian River Model	Tampa Bay Model	Charlotte Harbor Model
	mean predictions [fish / haul]	0.62	0.98	0.63
	residual deviance	7479.90	5824.85	7932.81
	% deviance explained	28.14	44.04	23.79
Charlotte Harbor	Data Characteristics			
	number of samples	1862		
	sum of fish caught in all samples	1593		
	mean catch	0.86		
	mean catch [fish / haul]	0.86		
	percent occurrence	19.33		
	total deviance	6969.47		
	Model Characteristics	Indian River Model	Tampa Bay Model	Charlotte Harbor Model
	mean predictions [fish / haul]	0.76	1.35	0.86
	residual deviance	5851.97	5616.98	4004.84
% deviance explained	15.69	19.41	42.54	

Table 2.2. Pearson's correlation coefficients for all combinations of model to model comparisons of abundance predictions for each samples in each of the three datasets from the three Florida estuaries.

	IR-data	TB-data	CH-data
IR-model x CH-model	0.515	0.589	0.564
IR_model x TB-model	0.674	0.767	0.751
TB-model x CH-model	0.609	0.700	0.608

All correlations were significant at the $\alpha = 0.05$ level.

Chapter 3: A temperature-dependent reproductive model for spotted seatrout (*Cynoscion nebulosus*), explaining spatio-temporal variations in reproduction and young-of-the-year recruitment in Florida estuaries.

This paper was published in the ICES Journal of Marine Science – see Kupschus (2004) and is reproduced here in a slightly edited format with an updated review section not included in the original publication.

Introduction

Spotted seatrout (*Cynoscion nebulosus*, Cuvier 1830) range along the east coast of the US from Virginia south to Florida and along the Gulf coast up to Mexico, where they are exploited both as recreationally targeted sportfish and commercially exploited foodfish. In Florida, conservation measures to protect the species have largely focused on catch-at-age analysis, but an important and yet poorly understood component of the stock dynamics are the factors driving recruitment to the fished stock. The stock-recruit relationship is poorly defined, suggesting that environmental factors play an important part in the recruitment process.

Reproduction, as part of the recruitment process, has been documented to be highly variable, temporally and spatially. Texas populations have been characterized as having two spawning peaks based on histological examination of ovarian tissue (Brown-Petersen et al., 1988) and gonadosomatic indices (GSI; Colura et al., 1988; Maceina et al., 1987). Bimodal reproduction patterns were also indicated for Louisiana populations by gonadosomatic indices (GSI; Hein and Shepard, 1979; Helser et al., 1993) and by hydrophone investigations of spawning aggregations (Saucier and Baltz, 1993). In contrast, a unimodal reproductive pattern was evident in a hydrophone study of a South Carolina population (Saucier and Baltz, 1992) and in a combined histological/hydrophone study of a Georgia population (Lowerre-Barbieri et al., 1999). In addition to differences in reproductive modality, distinct differences in the length of the spawning season were also apparent, with the length of the spawning period generally inversely related to latitude (Hein and Shepard, 1979).

Both unimodal and bimodal reproductive patterns have been documented for Florida populations. Nelson and Leffler (2001) inferred two spawning peaks from juvenile abundances in Charlotte Harbor (CH) and Tampa Bay (TB), and suggested unimodal reproduction for Choctawatchee Bay. Similarly, Tucker and Faulkner (1987) found unimodal and bimodal reproduction in pond experiments under ambient conditions in the Indian River Lagoon (IRL) in two consecutive years. GSI values of spotted seatrout populations in Florida's Panhandle region (DeVries et al., 1997) and in Cedar Key (Moody, 1950) as well as juvenile abundances in Naples Bay (Peebles and Tolley, 1988) indicated only a single spawning peak.

The estuary-specific pattern and lengths of the spawning season might suggest that reproduction locally is governed by genetic differences and that endogenous reproductive rhythms evolved to maximize survival and growth of juveniles under long-term average

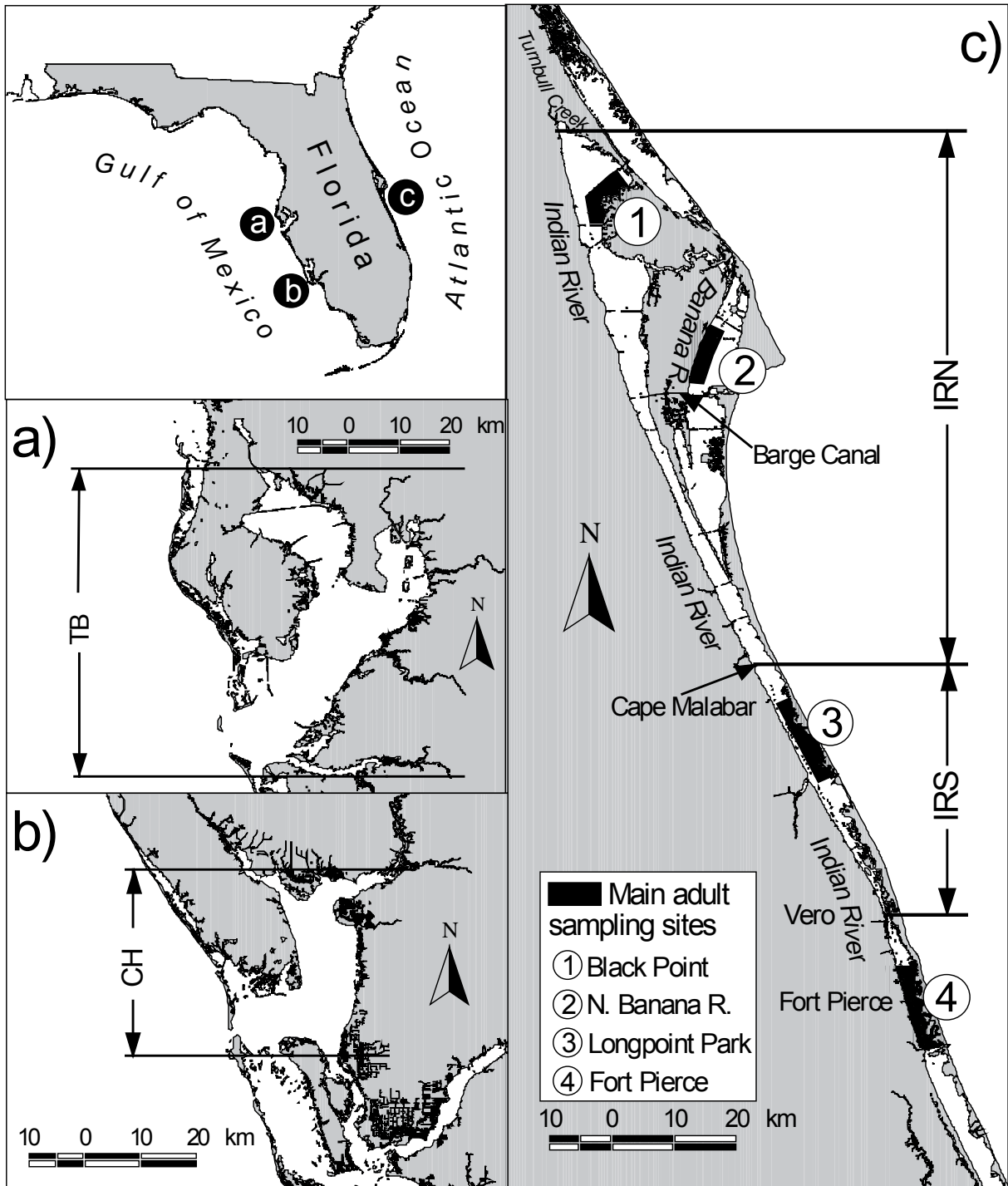


Figure 3.1. Definitions of the four estuarine regions over three study sites a) Tampa Bay - TB, b) Charlotte Harbor - CH, and c) the Indian River lagoon (IRN, IRS). Black areas (1-4) in c) indicate the four primary adult sampling sites.

environmental conditions (Bye, 1990). However, observed differences may equally well be explained by the direct influence of variable environmental conditions on reproductive activity, allowing for a single model to describe reproductive timing for the species.

This study sets out to examine the effects of temperature on reproduction, and to investigate whether predicted egg production from such a model projected forward can explain regionally highly variable temporal trends in recruitment.

Material and Methods

Sampling

Mature females were sampled at four documented spawning sites in the IRL (Fort Pierce, Longpoint Park, the northern Banana River and Black Point) on the east coast of central Florida (Figure 3.1) from January 1996 to December 1997. Sampling consisted of 3–5 dedicated gillnet trips per month during the spawning season (April–October) and fewer trips during the rest of the year (November –March). Nets used were one or more of the following: a) 550 m × 2.4 m monofilament net with equal sections of 76, 98, and 101 mm stretch mesh, b) 550 m × 2.4 m monofilament net with equal sections of 76, 89, and 101 mm stretch mesh, and c) 274 m × 1.8 m monofilament net constructed entirely of 114 mm stretch mesh. Deployment was predominantly around dusk (the reported time of maximum spawning; Saucier and Baltz, 1992; Lowerre-Barbieri et al., 1999) over areas of seagrass-covered shoals in the proximity of topical relief, and retrieval took place between one and three hours later. Samples not collected at dusk were used to estimate the daily periodicity of reproductive activity and consisted of two 24-h sampling events in the Banana River, with gear being retrieved and reset every 2 h. Additionally, samples collected by other methods and during other studies were incorporated into the analysis.

Date, time of day (recorded in Eastern Standard Time, EST), location, and surface water temperature (°C) were recorded for catches of mature females. If suitable temperature data were unavailable, samples were eliminated from the analysis. Photoperiod (day length in h) and hours after sunset were calculated from information on latitude, longitude, and EST.

Females caught were placed on ice and returned to the laboratory, where total weight (g), gonad weight (g), and total length (TL in mm) were measured. To provide a measure of the energy reserves, a gonad-free-weight (W-g) condition factor (C) was calculated as

$$C = 10000(W-g/TL^3).$$

Sections from the right ovary were fixed in 10% buffered formalin, soaked in water, and stored in 70% ethanol prior to histological preparation. Subsequently, glycol-methacrylate-stained histology sections were prepared using a modified periodic-acid-Schiff's technique, with Weigert's iron hematoxylin as nuclear stain and metanil yellow as counterstain (Quintero-Hunter et al., 1991). The ovarian tissue was microscopically examined and samples were sorted in eight reproductive stages in accordance with the classification used by Lowerre-Barbieri et al. (1996). Only females with hydrated oocytes (Stage 4) were classified as spawning on the day of capture and all others as not spawning.

Juvenile collections were made from January 1996 to December 1999 by the Fisheries-Independent Monitoring (FIM) Program in three estuaries (TB, CH and IRL; Figure 3.1). Because of its latitudinal expanse (120 km), IRL was split into a northern (IRN) and a southern region (IRS) at Cape Malabar, coincident with the reported temperature-induced zoogeographic boundary (Gilmore, 1995; Kupschus and Tremain, 2001). Sampling for juveniles did not commence in IRS until 1999.

A monthly multigear (trawls sampling depths >1.8 m; seine depths <1.5 m), stratified-random sampling design, proportionally stratified by the presence or absence of bottom and shore vegetation and logistically implemented zones, was used to establish relative abundances of juvenile fish. Seines were deployed in one of three different ways: boat sets, beach sets, and offshore sets (Nelson, 1998). From each randomly collected sample, spotted seatrout >15 mm and ≤50 mm standard length (SL) were used in the analysis. Catches from both types of gear were summed over each calendar month for each estuary or estuarine region distinguished. Changes to spatial and gear effort allocations have been implemented in all three estuaries, invalidating absolute inter-annual comparisons of juvenile abundances. However, effort was constant within any one year, so intra-annual abundances relative to total annual catches for each estuary can be used to reflect relative seasonal dynamics of juveniles. Impartial measures of the surface temperature regime in each estuarine region were developed to predict its relative reproductive output independently. The average daily surface temperature was estimated using a cubic spline smoother with 15 degrees of freedom from all stratified-random samples collected by the FIM program over the period January 1996 (January 1997 for IRS) to December 1999.

Models

The probability of a female being in spawning condition (P) was modelled as a generalized additive model (GAM) using a logit link function. This allowed for the examination of the binomial response variable (spawning or not spawning on the day of capture), at the same time allowing for multiple relationships with nonlinearly related independent variables (Hastie and Tibshirani, 1990). The general form of the GAM was

$$P = \exp(\beta)/(1+\exp(\beta)),$$

where

$$\beta = \alpha + \sum_{i=1}^k f(X_i) + \varepsilon$$

and α is the intercept of the additive predictor, f is the spline function of the i th smoothed dependent variable (X) and ε is a Gaussian error term. Surface temperature, days past the full moon, photoperiod, time after sunset, TL, and gonad-free-weight condition factor were included as independent variables in the initial model.

The final form of the model was selected by increasing and decreasing the degrees of freedom of the spline functions in a bi-directional manner, using the Akaike information criterion (AIC) to determine the most parsimonious model (McCullagh and Nelder, 1989). The model selected was then used to predict temporal changes in the reproductive potential of an average female (398 mm SL, condition factor = 0.892) in each estuarine region at the peak daily spawning time based on the interpolated regional temperature for that day.

Comparing predicted reproductive output with observed abundances of juveniles of a certain size requires an adjustment for the growth experienced during between spawning and sampling. To this aim, a temperature-dependent growth model was developed from data published in Alshuth and Gilmore (1994). Growth was modelled as a GAM describing TL as a function of age in days (a) and water temperature (T) using an identity link function (assuming a normal error distribution):

$$TL_t = \alpha + \sum_{i=1}^k f(X_i) + \varepsilon$$

where symbols are used as before.

From the model, a matrix of daily growth increments was created, starting with an initial length of 1.5 mm at the day of hatching, i.e. the day following spawning (Alshuth and Gilmore, 1993). The growth of individual daily cohorts of juveniles was then simulated in each estuarine region based on the smoothed temperature estimates for each day. For comparison with juvenile catches, predicted TL was converted to SL using the formula provided in Hein et al. (1980).

Simulated relative reproductive output and juvenile growth were combined to predict relative intra-annual dynamics in spotted seatrout abundances in each region, assuming a fixed natural mortality over all months and in all regions. The daily spawning probability was calculated to cover the entire period during which juveniles were predicted to be available to the gear ($15 \text{ mm} < \text{SL} < 50 \text{ mm}$). Each daily cohort was then discounted by the mortality rate ($M = 5.11 \text{ year}^{-1}$; monthly mortality of 34.7%) taken from an Everglades National Park study (Rutherford et al., 1989). The resulting daily measure of juvenile abundance was summed by month and expressed as a percentage of the total abundance over all months. To compare predicted and observed relative abundance, monthly catches were analogously expressed as a percentage of total annual catches. Significance of the correlation between observed and predicted values were tested by Spearman rank correlation.

Results

Reproduction

In all, 1674 female spotted seatrout, collected on 133 successful sampling days, were sacrificed for histological examination. All females were mature, and the 195 reproductively active females (8.6% of all females and 18.4% of the females caught during between April and September) were caught between April and September in water temperatures ranging from 24.0 to 32.5°C.

The most parsimonious GAM model, as selected by the AIC, explained 38.2% of the total deviance with 15.8 model degrees of freedom. Dependent variables included in the model in decreasing order of importance were water temperature, hours after

sunset, condition factor, TL, and days past the full moon (Figure 3.2). The model reached a maximum spawning probability of 0.42, suggesting that during optimum spawning conditions, females on average spawn every 2.38 days. The temperature partial peaked at 29°C, declining at both higher and lower temperatures, indicating spawning probability peaks at 29°C. The partial effect of hours after sunset was also unimodal, reaching a peak about two hours before sunset. The gonad-free-weight condition factor and TL partial effects indicated that fish with a high weight-to-length ratio, as well as larger fish in general, were more likely to spawn on a given date than more poorly conditioned or smaller females were. The model also indicated an almost linear decline in the propensity to spawn during the entire lunar cycle following the full moon, a result supported by the raw data.

Photoperiod, in the absence of temperature, explained a significant portion of the total deviance in the model, but it was dropped by the selection procedure when temperature was included. Temperature, rather than photoperiod, was included in the final model because it explained a larger portion of the deviance, suggesting that there was an effect of temperature beyond the component shared by the two correlated variables.

Predicted seasonal patterns of juvenile abundance

The model clearly predicted seasonally bimodal reproduction in CH and IRS, with the temporary decrease in reproductive activity corresponding to the warmest months (July and August) of the year (Figure 3.3). In IRN and TB, the predicted summer reproductive hiatus was generally much less pronounced in all years, and it was completely absent in cooler summers (IRN: 1999; TB: 1996, 1999; Figures 3.3, 3.4). Temperature data for the four estuarine regions examined in this analysis indicated that CH and IRS generally had higher temperatures than TB and IRN. However, local estuarine conditions do not nec-

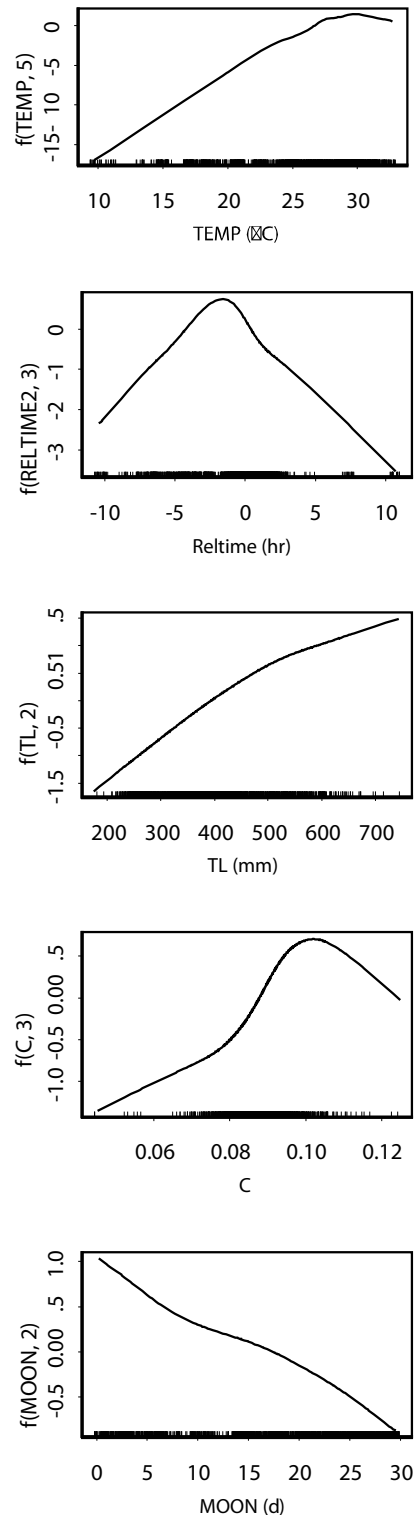


Figure 3.2. Partial effects of temperature (TEMP), hrs after sunset (RELTIME), female size (TL), gonad-free-weight condition factor (C) and days past the full moon (MOON) according to the GAM model for spotted seatrout reproductive activity, describing the effect of each independent variable, assuming the others are held constant (y-axis labels: cubic spline function and degrees of freedom used; values: relative importance of each partial effect in describing total deviance; rug plot on x-axis: range and relative frequency of sampling conditions).

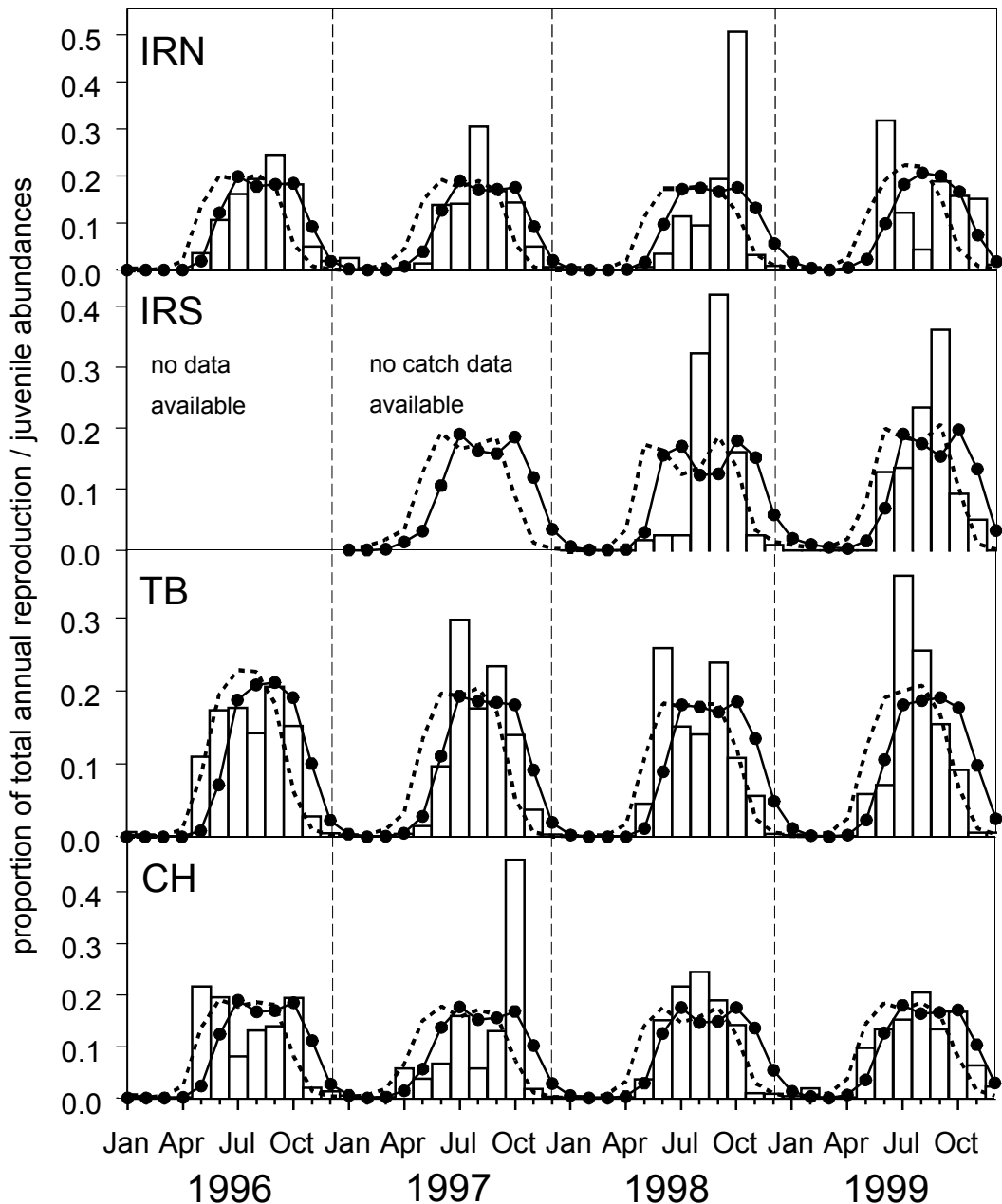


Figure 3.3. Estuary-specific model predictions of monthly relative reproductive effort (dashed line) and expected relative abundances of juveniles (solid line with circles) in comparison with observed relative abundances of juveniles (bars). All data are expressed as the monthly percentage of the annual total within each region.

essarily follow the overall regional trend, which in itself is variable over time. All regions in all years experienced temperatures in excess of the predicted optimum reproductive conditions during summer (Figure 3.4).

Comparison of observed and predicted juvenile abundance

During stratified-random sampling 1994 (CH), 1685 (IRN), 265 (IRS), and 3450 (TB) juvenile spotted seatrout $15 < SL \leq 50$ mm were collected over the study period 1996–1999. The greatest monthly abundance of juvenile spotted seatrout were roughly one month after the highest predicted relative reproductive effort (Figure 3.3), with juveniles being available to the gear for between 43 and 69 days, dependent on temperature.

The period during which juvenile spotted seatrout <50 mm SL were predicted to occur in each estuary coincided well with the period during which catches of juveniles were made, suggesting that the model predicted the spawning season accurately (all Spearman rank correlation coefficients significant at $P=0.05$: 0.82, 0.82, 0.62 and 0.83 for CH, IRN, IRS and TB, respectively). Additionally, the juvenile abundances predicted from the model overall resembled the types of temporal recruitment patterns observed in the three estuaries. Within the spawning season, the timing of increases and decreases in reproductive activity appeared to be predicted well particularly in TB and CH, although the amplitude of the fluctuations during the spawning season was underestimated.

Discussion

Temperature was the most important predictor of spotted seatrout reproductive activity in the IRL, as reported for other species, particularly those occurring in low latitudes (Taylor, 1990; Wieland et al., 2000). However, unlike the linear relationship hypothesized for spotted seatrout by Brown-Petersen and Thomas (1988), temperature was unimodally related to reproductive activity. The likelihood of encountering reproductively active females increased until the optimum water temperature of 29°C was reached, then declined at higher temperatures. Consequently, the model implied that spotted seatrout populations in estuaries with daily mean summer temperatures below the optimum would have only one spawning peak, and that those populations experiencing

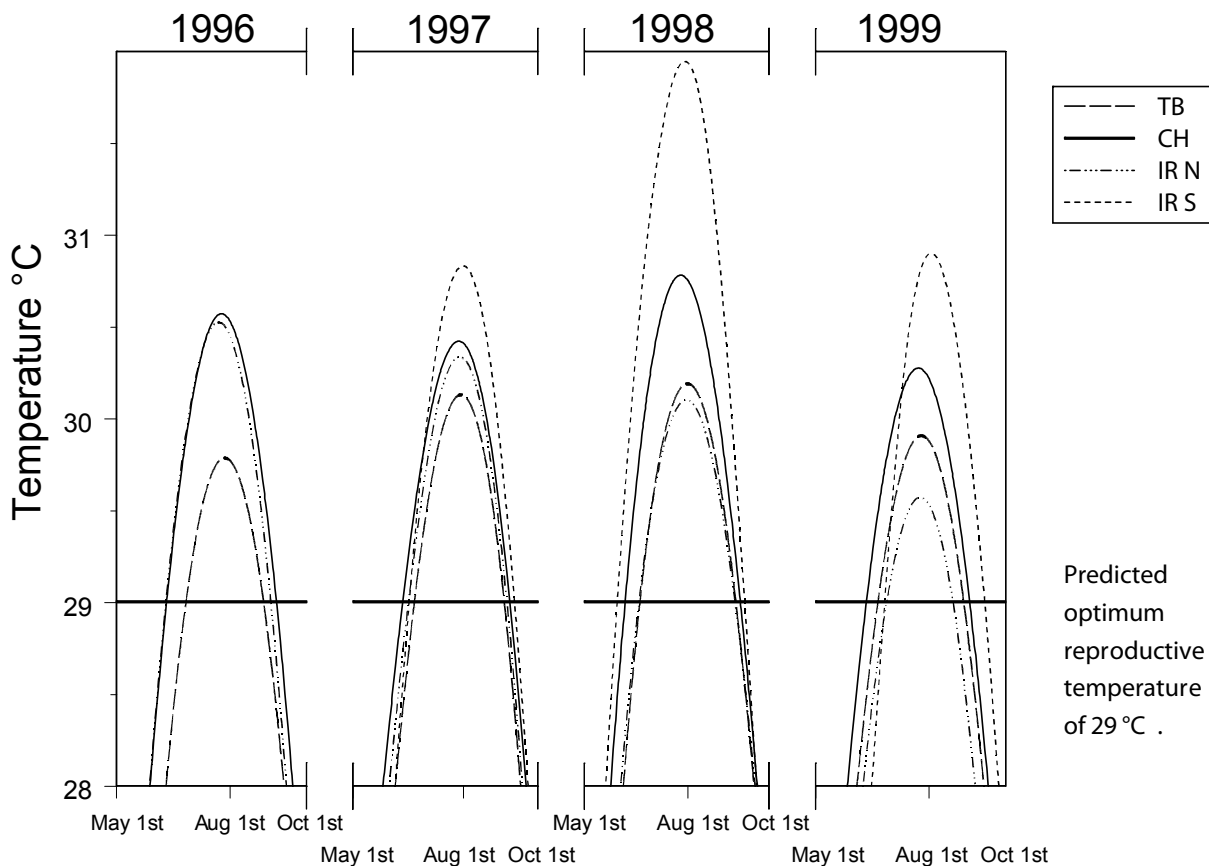


Figure 3.4. Mean daily summer surface temperatures (1st May to 1st October) for each year (1996–1999) in the four estuarine regions CH, TB, IRN and IRS. (No data for IRS in 1996, with 1997 data from projects other than juvenile sampling)

water temperatures consistently above the optimum would exhibit a temporary decline in reproductive effort during the warmest months of the spawning season. In addition, conditions suitable for spawning should be reached earlier in the year and be maintained longer in warmer estuaries or during warmer years, leading to a generally more protracted spawning season in the southern part of the species' range (Bye, 1990).

These findings are generally consistent with the documented patterns of reproduction in Florida spotted seatrout (Moody, 1950; Tabb, 1958; Stewart, 1961; Janke, 1971; Tucker and Faulkner, 1987; Peebles and Tolley, 1988; DeVries et al., 1997; Nelson and Leffler, 2001) and were also largely in agreement with the reproductive patterns of spotted seatrout populations throughout the range of the species (Hein and Shepard, 1979; Maceina et al., 1987; Brown-Petersen et al., 1988; Colura et al., 1988; Saucier and Baltz, 1992; Lowerre-Barbieri et al., 1999;). Tucker and Faulkner, (1987) and Nelson and Leffler, (2001) found differences in the seasonal reproductive trends within populations that supported the notion that genetic differences cannot be solely responsible for the observed regional differences in spotted seatrout reproduction. Therefore, as was concluded by Beaumarige (1969) and Tabb (1966), environmental conditions, at least in part, regulate spotted seatrout reproduction.

The predicted optimum reproductive temperature of 29°C was also in general agreement with the temperature reported for optimal hatch rates (Gray et al., 1991; 25–30°C), highest larval survival (Taniguchi, 1981; 28°C; Alshuth and Gilmore, 1994; 25–30°C), and juvenile habitat preference (chapter 2).

The principal diel spawning period of seatrout extends from two hours before to one hour after sunset, as indicated by the maximum rate of decrease in the partial effect of hours after sunset. This is consistent with estimates by Brown-Petersen et al. (1988), who reported a peak in spawning activity from one hour before to two hours after sunset. Tucker and Faulkner (1987) and Saucier and Baltz (1992) reported probable peak spawning times from 21:00 to 22:30 and 20:02 to 23:31 local time, respectively. Other studies reported spawning of specific events within a longer time-frame, Lowerre-Barbieri et al. (1999) described male spawning sonifications lasting from 18:30 to 23:00. Saucier and Baltz (1993) recorded a spawning event as lasting from 16:30 to 23:30, with spawning more generally between 17:00 and 01:00. Therefore, the model is very much consistent with the reported times of the diel spawning period reported in seatrout studies along the Gulf and Atlantic coasts.

The model indicated strongest spawning during the first few days following the full moon, with a decline in activity towards the following full moon. This slightly unusual cyclical pattern has been reported anecdotally by fishers as a response to a combination of specific light and current requirements, and has been observed by Tucker and Faulkner (1987) and McMichael and Peters (1989).

The expected effects of condition and length of individuals were produced by the model. Although these variables were largely included as covariables to account for differences in the sampling gear, it was clearly indicated that larger fish and those in better condition are more likely to spawn (and hence more frequently) than smaller fish or those in poorer condition.

Photoperiod was not a significant predictor in the model in addition to temperature. In contrast, laboratory-based reproductive studies have relied on a combination of temperature and photoperiod manipulation to induce spawning of seatrout (Capo et al., 1997) or to correlate spawning events to environmental conditions (Tucker and Faulkner, 1987). Bye (1990) suggested that under natural conditions, photoperiod might not be an important cue to reproduction, but photoperiod may just be too strongly correlated with temperature to see the effect.

In general, much of the current knowledge on reproduction could be combined into a single quantitative model that explained a significant portion (38.2%) of the deviance in the reproductive status of IRL spotted seatrout. In addition, the results were largely consistent with the regional differences observed in reproductive timing throughout the species' range.

Projecting the predicted reproductive output from the model forward to the juvenile stage resulted in temporal patterns of recruitment similar to the patterns observed in Florida estuaries, confirming reproduction as one of the major determinants driving recruitment, as inferred by Nelson and Leffler (2001). The model, based upon temperature differences in space and time, could explain the observation of unimodal and bimodal recruitment, as well as the differences in the protraction of the recruitment period. Although the output matched the relative trends in recruitment across time reasonably well, the observed fluctuations in recruitment were amplified over those predicted by the projection.

This amplification may be caused by the interactions of at least three factors. First, reproductive activity itself could modulate as the number of individuals on spawning sites fluctuates. Migration in response to lunar cycles, as exploited by fishers, may reflect a more general movement to spawning sites during favourable conditions and away from spawning sites during unfavourable conditions. Second, egg production could modulate, because both the quantity and the quality of the eggs produced varies with changes in length or condition of females spawning, as observed for other species (Santiago and Eltink, 1988; Secor, 2000; Wieland et al., 2000), or through variation in the fraction of mature females during the spawning season, as seen in species such as *Cynoscion regalis* (Lowerre-Barbieri et al., 1996, 1998), *Engraulis encrasicolus* (Santiago and Eltink, 1988), and *Penaeus semisulcatus* (Crococ and Van der Velde, 1995). Third, processes following egg production such as hatching rates and juvenile survival are influenced by environmental conditions (Taniguchi, 1981; Gray et al., 1991; Helser et al., 1993; Alshuth and Glimore, 1994). If the effects on these processes are similar to those on reproduction, as indicated by the effect of temperature on the survival of adults (Vetter, 1977; Wohlschlag and Wakeman, 1978), the variation in the reproductive signal would be amplified in the recruitment pattern. All three factors would have a tendency to amplify the variation in observed recruitment patterns compared with the model signal.

Reproductive output certainly is determined to a large extent by environmental conditions, so variability in recruitment pattern and strength between estuaries and years is to be expected. Fisheries managers need to take this variability into account, particularly when employing tuning indices of recruitment based on an amalgamation of data from a combination of estuaries. To understand more fully the recruitment processes, data on variations in abundance on spawning grounds, on temporal trends in size composition

and condition, and on fluctuations in larval and juvenile mortality, are required. Without this understanding, it is doubtful whether a meaningful stock-recruitment relationship can be established for this species.

Implications for management (*Review section not part of published manuscript*)

The contribution that this model could make to improving estimates of recruitment within the assessment model is qualitatively evaluated, and the results are reviewed with respect to recently published studies on reproduction in seatrout, particularly those using passive acoustics to determine spawning activity (Luczkovich et al., 2008; Walters et al., 2009). There is also a need for conservation managers to consider spawning habitat as part of the lifecycle of any species within the framework of essential fish habitat (EFH) under the Magnuson-Stevens Act and its protection in the form of temporal or spatial closures (Powell, 2003; Porch et al., 2004; Powell et al., 2004; Tremain et al., 2004; Reyier et al., 2008), and a wider need to understand the ecology of the species with reference to its long-term reproductive strategy (Waggy et al., 2006) in order to prioritise efforts of to conserve this and other species in the ecosystem.

Although the results from the model itself are quantitative, they are so only at the level of the individual. It is not possible quantify the overall effect as it relates to stock as a whole external to a stock assessment model, nor is it possible to quantify the effects of habitat degradation or restoration in the absence of high resolution hydrodynamic models. In many ways the model then provides more question than answers, but can certainly help guide managers in assessing sensitivities. It is the design of the data collection, rather than the model itself that is at fault. An important message here is that integrating monitoring is likely to be even more important than integrating management. If such data were available in many cases the integration would follow much more naturally.

Fisheries management

Murphy et al. (2006) included a function in their latest model that represents estimates of recruitment on the basis of the number of eggs produced at age by an individual female over a single spawning event, multiplied by the average number of spawning events in a 184-day spawning season, summed over the number of individuals in the stock in the previous year. Such a function reduces the model's ability to respond to rapid changes in the stock dynamics, as might be expected from more realistic interannual variation in recruitment. The extent to which the constraint is active depends on the scale of the contrast in the data and the relative weighting of the objective function, but in the case of variable data sources, is likely to drive the model to stasis at the overall mean level of population abundance.

In reality, estimates of spawning frequency, fecundity and maturity vary considerably over the range of spotted seatrout populations (Holt et al., 1985, Brown-Peterson et al., 1988; Coloura et al., 1988; Lowerre-Barbieri, 2004; Roumillat and Brouwer, 2004) as does the extent of the spawning season, suggesting that there may be significant environmental factors affecting the spawning activity directly, and indirectly through differences in growth rates. The estimates of relative abundance produced in Chapter 2 also suggest that variation in cohort strength is affected by factors other than the effect of environmental conditions on the survival of juveniles, represented as the year-effect

despite relatively stable adult age structures in the short term. Whether this variance-generating function is a result of variation in larval survival or reproductive output is unclear, but its existence does underline the need to include environmental effects in the reproductive component (Luczkovich et al., 2008), of the assessment model if such a component is to be included at all.

The reproductive model is able to represent spawning frequency at the biological level more realistically. It showed that spawning frequency is related to temperature, which will affect the average spawning interval over the spawning season as well as limit the length of the spawning season itself, so acting on reproductive output on two levels. Using temperature effects to differentiate the spawning activity in individual stocks does require representative measures of temperature at spawning locations, which unfortunately are less poorly defined and more ephemeral than originally thought (Walters et al., 2009).

In addition the reproductive model suggested that length of a female is a better measure of reproductive activity than age, with larger females spawning more frequently. Assessment models using length information, which are also better at resolving the effects of size-based management when there is variability in growth (Chapter 4), will be able to provide more accurate measures of reproductive output than possible with the currently employed age-based method.

Given the significant contribution of one-year-old female seatrout to the total reproductive output in the southern portion of the range (Crabtree and Adams, 1998; Lowerre-Barbieri, 2004; Roumillat and Brouwer, 2004), accurate estimates of the most recent cohort are necessary to assess future recruitment. In reality, the current model is unable to provide such estimates because of the practice of merging age-length keys over several years. It is questionable whether incorporation of such information is useful or even possible in the current assessment structure.

Knowledge of the interannual variation in reproduction beyond the component of the standing stock does, however, call into question the use of a recruitment function at least in periods where direct measures of recruitment are available. In that case the reproductive function ignores the environmental conditions, whereas the index models it explicitly. Including such knowingly conflicting information in a model that has difficulty in resolving cohort strength renders the choice of weighting in the objective function subjective. In the current model, recruitment indices contribute little to the estimates of F (fishing mortality) or stock numbers, yet they could still provide more-reliable evidence off future recruitment, especially in light of the uncertainty regarding survival at egg and larval stages.

What is clear, however, is only that we will continue to require quantitative models of reproduction if such a function is to be incorporated into assessment models. Claims by Luczkovich et al., (2008) that sound production can be used as a quantitative measure of the spawning stock or reproductive activity in lieu of quantitative models of reproductive activity are difficult to justify, because sound is produced by males, whereas reproductive effort is usually considered by fisheries managers to be limited by the female contribution. Nor is the relationship between sound production and reproductive success likely to be straightforward. Males call for mates, but presumably once mating has been initiated, calling will cease, so a group of males with little success in attracting mates may well produce more sounds than one with more success.

Conservation

The delineation of spawning habitat is important for conservation managers with regards to spatial planning issues, particularly in estuarine environments, which are frequently well developed. In addition, national directives in the form of the Sustainable Fisheries Act oblige fisheries scientists to provide such information for exploited stocks (Benaka, 1999). For sciaenids, it is claimed that an effective method of doing so is the use of passive acoustic information (Saucier and Baltz., 1992; Luczkovich et al., 2008; Walters et al., 2009). Indeed, Mok and Gilmore (1983) first verified the link between reproduction and sound in seatrout in the Indian River Lagoon. Luczkovich et al. (2008) also recognized the need to describe the habitat identified in terms of its environmental conditions, and provided estimates of the temperature and salinity range, as well as depth and dissolved oxygen conditions.

A precise evaluation of the requirements is useful to identify habitat beyond those sites actually sampled for sound. Although Walters et al. (2009) provided a more detailed analysis of the temporal variability in spawning activity in Tampa Bay and related the activity to habitat on a more basic level, such as the presence of seagrass or structure and depth/environmental conditions), these factors are not specifically linked to the presence or absence of spawning activity at a particular location. The conclusions were that the majority of spawning locations were ephemerally used only on occasion, rather than being permanent sites attended by individuals throughout the spawning season. Neither is it clear if individuals attend a single location or only when conditions are suitable, or select between different locations based on the conditions prevailing at each.

All this is important to assess the impact that changes on the environment might have on the reproductive capacity of seatrout. The model developed here is in good agreement with the data provided by Luczkovich et al. (2008) in terms of temperature and time of day. The habitat characteristics in which reproductively active female seatrout are found in the IR is consistent with those described by Walters et al., (2009). The fact that sites are inconsistently used suggests that the biology of seatrout has evolved to concentrate reproductive activity in areas likely to provide optimal conditions for juvenile survival and settlement, presumably based on environmental cues experienced by adults, because broadcast spawners have no ability to assess their own reproductive success.

The information presented by Waggy et al. (2006) identifying seatrout as “intermediate” between sciaenids that are small, short-lived, attain maturity quickly and have a short spawning season with frequent reproduction, and those that are large, mature late and live longer and have a lower relative fecundity. Relatively large individual eggs provide a better strategy in variable environments (Hutchings, 1997), but also imply significant investment in an individual offspring. A short larval phase (Alshuth and Gilmore, 1993) and selection of reproductive sites based on current environmental cues expected to maximize future reproductive success in addition to the adaptation of seatrout to thrive in a wide range of environmental conditions (Vetter, 1982) suggest that random variation in recruitment should be small. Batch spawning allows the spreading of risk, because future environmental conditions are not entirely predictable on the basis of current conditions. This suggests that seatrout are in some way adapted to bet-hedging, weighing the risk to adult survival against the benefits of increased reproductive success as and when such information becomes available, unlike single-event spawners that have to apportion investment based mainly on the basis of the condition of an individual.

It appears then that seatrout are well adapted to maximizing their reproduction in variable environments, and should be able to adapt to changes in the environment as development of estuarine areas continues as postulated by Walters et al. (2009). Although this may be true for the survival of the species in the genetic or persistence sense and therefore possibly sufficient for conserving a species, this adaptation is unlikely to fulfil the aims of fisheries managers interested in ensuring maximum benefit from the resource (Tasker and Knapman, 1999).

Selection of a spawning site is almost certainly non-random, and presumably an individual will use those sites deemed most likely to produce progeny. Displacement from sites deemed to be optimal under the prevailing conditions would result in a net reduction in progeny, irrespective of whether reproduction is still successful elsewhere. For example, dredging channels for navigation destroys the productivity of seagrass beds (Sheridan, 2004). Although the area affected may be small in relation to the total available seagrass coverage and consequently in terms of its direct effect on the survival of juveniles, it is exactly those sites with seagrass in close proximity to deeper water that have been shown to be of substantial importance in seatrout reproduction (Mok and Gilmore, 1983; Luczkovich et al., 2008)

Evaluating the impact of future alterations to the ecosystem will require not only the spatial location of sites, but also a more detailed assessment of the hydrographic environment and the conditions likely to influence spawning success or at the very least the likely impacts on spawning behaviour as a proxy for spawning success. Ignoring this component may lead to surprising results when considering placement of marine reserves in order to protect spawning habitat.

Although not specifically designed to protect spawning aggregations, the Merritt Island National Wildlife refuge (Johnson et al., 1999) refuge on the east coast of Florida has been shown to be a spawning site for spotted seatrout, yet the evidence is that there is little if any benefit of this refuge in terms of a source of reproductive potential directly (Reyier et al., 2008), or in terms of the protection of spawning stock (Tremain et al., 2004), despite claims that it direct linked to the abundance of trophy-sized fish (Roberts et al., 2001), which in reality is much more likely to have been linked to the faster growth rates in the IR (Chapter 4).

Similarly, evaluating the effects of restoration projects needs to consider the reproductive biology. Powell (2003) identifying spawning habitat in the Everglades national park, postulated that the proposed restoration would influence seatrout unpredictably through an increase in juvenile habitat with a potential decline in spawning habitat. Powell et al. (2004) and Porch et al. (2004) call for the use of seatrout as an indicator to assess the restoration of the Everglades.

In general though, the danger of using such an environmentally tolerant species (Vetter, 1982) or one specifically adapted to survive in variable estuarine environments to evaluate restoration projects, is substantial. More sensitive species are likely to produce much more easily detectable evidence of the impacts of the restoration program than seatrout, requiring smaller sample numbers and hence lower costs than those suggested by Porch et al. (2004).

Specifically, the models examined here suggest that juvenile seatrout are well adapted to surviving in more variable environmental conditions beyond the changes likely to occur as part of Everglades restoration, so this may have much less of an impact than supposed. Similarly, the theory that spawning habitat may be limiting in a restored Florida Bay is based almost solely on the premise that seatrout eggs require salinity >15 psu. to float (Alshuth and Gilmore, 1993). Spawning activity (Luczkovich et al., 2008) and recently hatched larvae (Powell, 2003) have been found with some regularity at lower salinity. Given the reproductive strategy of seatrout, it seems unlikely that the species would continue to spawn if reproductive success was certain to be zero, so seatrout may be able to adapt the buoyancy of their eggs to the prevailing environmental conditions, through allocating a higher fat content. From an evolutionary perspective, this would be consistent with their high investment in individual offspring and their adaptive reproductive behaviour.

The impact of restoration on seatrout may well be much less serious than postulated by Powell et al. (2004). The effects of restoration on seatrout abundance are much more likely to be determined through its effect on productivity in Florida Bay through changes in oxygen levels, and through ecosystem impacts such as alterations in the distribution of seagrasses and altering productivity conditions through nutrient input rather than the more direct effect of salinity on reproduction. These statements are no less speculative than suggesting that seatrout might be suitable as an indicator of restoration success, and are made merely to underscore the importance for quantitative models of reproduction and juvenile habitat requirements, rather than playing down the value of monitoring seatrout in Florida Bay.

Chapter 4: Back-calculation to reconstruct length-at-age information based on otoliths of Florida spotted seatrout (*Cynoscion nebulosus*), and conclusions on population and individual growth dynamics

Introduction

Spotted seatrout fisheries in Florida represent a locally important economic resource in various estuaries and coastal waters around the state. Historically, many of these populations have been exploited by artisanal fisheries, tending towards commercial exploitation during the 20th century. During the latter stages of the 20th century, and increasingly so after the implementation of the net ban in Florida inshore waters in 1996 and a drive to conserve recreational fisheries, a substantially greater proportion of the landings has come from the recreational sector, resulting in reduction in the precision of landings estimates and more importantly in the relative age composition of catches (Vanderkooy and Muller, 2003). The current and previous assessment methodology for the regional stock assessment carried out by the Florida fish and wildlife conservation commission (Murphy, 2003; Murphy et al., 2006), so it combines age-length keys over some periods. This practice brings with it the danger of underestimating the true variability in cohort strength and ultimately biasing the parameter estimation in the model.

An alternative approach is to develop length-based models, or models that use length information in conjunction with what little age information is available. Several modern stock assessment methods for example MULTIFAN-CL (Fournier et al., 1998) and stock synthesis (Methot, 1990) successfully use information on size-at-age and the associated population variance-at-age either in lieu of, or in addition to, age-based information to determine stock trends (Fournier et al., 1990, 1998; Maunder and Watters, 2003). These models are constrained by the addition of a growth function in order to attribute catches parsimoniously to a particular cohort and age based on their lengths, employing the available age information to determine the appropriate growth model. However, for species such as seatrout with a substantial overlap in length between ages and sexes (Murphy and Taylor, 1994; DeVries et al., 1997) and / or for species with significant variability in growth, either between years or between cohorts, such models will ultimately still suffer from an underestimation of cohort strength variability. A more detailed and complete understanding of the growth histories, the variation and the factors influencing growth in conjunction with the ability to deliver historical information during the period not sampled will ultimately lead to more accurate and parsimonious assessments if the time-series can be extended reliably.

A solution to the problem is to develop estimates of trends in size at age as well the variability external to the model, but brings with it the need to bridge data-poor periods or ages by the use of back-calculation. The choice of the appropriate back-calculation methodology and whether any of them work at all is hotly contested in the literature, because the relationship between otolith radius and fish length has increasingly been shown to be variable over time, at inter- and intra-annual scales and at different ontogenetic stages of life, the onset of which differs among individuals (Živkov 1996; Shafer 2000; Hüsey and Mosegaard, 2004). In addition, otolith growth in a radial dimension is

frequently allometric, so the relationship is affected by both the shape of the otolith as it grows (Gagliano and McCormick, 2004) and the direction chosen when measuring it (Chauvelon and Bach, 1993; Shafer, 2000).

In general, the focus of back-calculation has been to determine the size of an individual at a previous time given its current size and some relative growth scale, such as that provided by the size of interannual increments seen in otoliths or other hard structures in fish. Unfortunately, the underlying functional form of the relationship between body size and increment size is unknown, so a number of back-calculation methodologies have been developed and compared in a number of studies on different species or stocks, based upon a number of incomparable evaluation criteria (Secor and Dean, 1992; Hare and Cowen, 1995; Smedstad and Holm, 1996; Sirois et al., 1998; Escot and Granado-Lorencio, 1999; Shafer, 2000; Vigliola et al., 2000; Klumb et al., 2001; Morita and Matsuishi, 2001; Schaalje et al., 2002; Finstad, 2003; Brevian et al., 2006). Consequently, there are almost as many “most suitable” methods as there are studies; for examples, see the reviews by Francis (1990, 1995) and Campana (2005).

In contrast, at a population level, given that “there can be little doubt that the dimensions of marks in the scale (or other hard parts) contain some information on the growth history of a fish” (Francis, 1990), it should be possible, choosing an appropriate model, to describe the average length-at-age in the population despite the complications encountered when trying to reconstruct individual growth trajectories (Brothers, 1995; Živkov, 1996; Schirripa, 2002; Hüsey and Mosegaard, 2004). Indeed, several studies have reconstructed historical population mean lengths-at-age (Schirripa and Trexler, 2000; Sinclair et al., 2002; Bolle et al., 2004), although they have been unable to verify the results with independent data.

The approach applied here is to predict the average increment size based on factors known to affect otolith growth, informed by the available data. The sum of these predicted increments through the cohort up to a specific age represents the average population otolith radius in a given year at that age. Conversion of the average radius into an average length is performed by modelling the degree of non-linearity, or decoupling, between otolith growth and changes in length caused by differences in the conditions experienced by groups of individuals, assuming that individual variability in length is independent of the individual variability in the relationship between otolith radius and length.

In the back-calculation step, flexible spline functions are used to model the decoupling effects of season and age, while accounting for differences in the conditions experienced by cohorts and sexes as factors, as suggested by Morita and Matsuishi (2001) and Finstad (2003) and as shown to be important in a number of species (Smedstad and Holm, 1996; Shafer, 2000; Hüsey and Mosegaard, 2004). The increment analysis is applied to datasets from spotted seatrout (*Cynoscion nebulosus*) in three Florida estuaries, Charlotte Harbor, Tampa Bay, and the Indian River lagoon, where sampling has been intermittent or at least temporally unbalanced.

Model efficiency, the ability to provide the greatest number of useful estimates of size-at-age from the smallest number of samples, and model robustness, the ability to provide unbiased estimates of size-at-age in the absence of any samples from a particular year, were examined by bootstrapping the largest of the three datasets from the Indian River Lagoon in a random, systematic approach. The random approach

selected a subset of (50, 100, or 300) fish from the sampled population to determine the precision at different sampling levels (Efron and Tibshirani, 1993) and the number of useful estimates provided. The systematic approach used all samples from randomly selected years only, to determine whether the method was robust to information gaps or biases in a timeseries.

Material and Methods

Sample collection

Growth in three Florida populations of spotted seatrout, Charlotte Harbor (CH: 552 otoliths), Indian River (IR: 6295 otoliths) and Tampa Bay (TB: 2866) were determined from samples derived from a number of different projects with various possible sources of bias in terms of gear selectivity, but also in terms of spatial, gender or temporal biases. Most data prior to 1996 consisted of samples taken from commercial catches made by gillnet or splatter-pole fisheries. Many samples taken after 1997 were collected for reproductive studies, biased towards females, collected using experimental gillnets or hook-and-line sampling (mainly 1997–1999 in the IR and 2000 on in TB). The remaining samples were collected in a stratified random design by the Fisheries Independent Monitoring Program as part of their routine monitoring of estuarine fish populations using mainly seine gears, but those sample sizes were considerably smaller than from other sources of sampling.

Both sagittae were collected from each fish, and length, weight, date, and location of capture were recorded. The left sagitta was cut transversely using a slow-speed isomed saw, and sections were mounted for age determination. For a detailed description of the technique the reader is referred to Lowerre-Barbieri et al. (1994). Unclear sections or those not passing through the nucleus were discarded and if possible replaced with sections from the right sagitta.

Sections were viewed using transmitted light and a clear field under a dissecting microscope. Digital images of each otolith were captured using a video camera and PC video capture board, and measurements of the radius and the distances between the nucleus and each annulus were made radially along the ventral arm of the sulcal groove using Optimas V8.0 software. Two experienced readers had previously determined the ages for stock assessment purposes with a high degree of agreement. Samples that did not show agreement between the expert derived ages and the number of annual increments measured for this study were excluded from the analysis. Generally agreement was very good, and few samples had to be excluded. Given the time of annulus formation and the extended spawning period, starting around March and continuing into September (Chapter 3), in relation to the time of annulus formation, mostly November–February (Murphy and Taylor, 1994), the period of the first increment could be significantly less than one year.

It was difficult for readers consistently to determine whether a mark had started to form, was forming, or was complete when near the edge of the otolith. Nieland et al. (2002) found annuli in Louisiana spotted seatrout to be deposited between November and April, values that appear appropriate for Florida populations investigated here (Murphy and

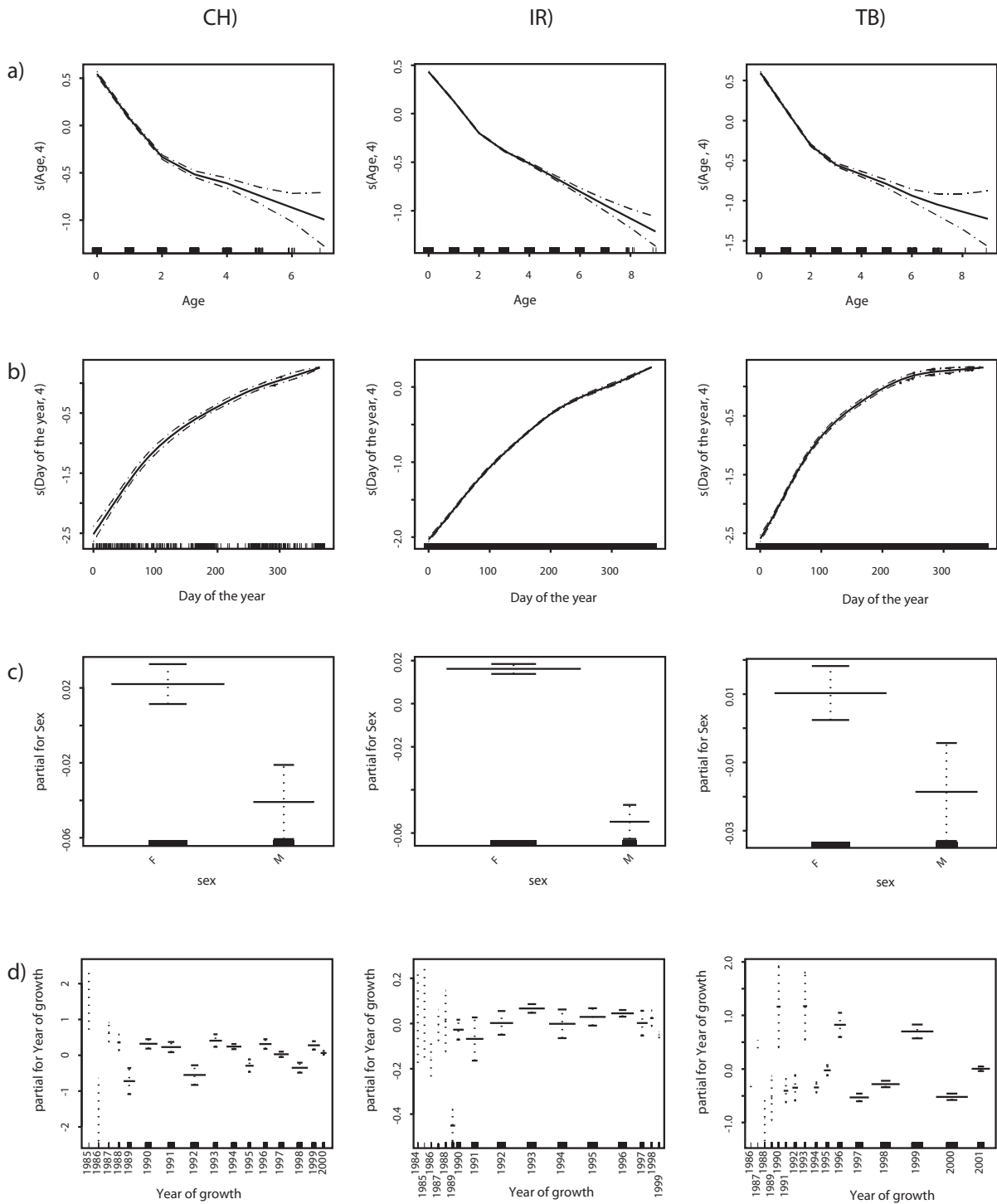


Figure 4.1. GAM plots for the 1st submodel of the increment analysis describing the partial effect on the y-axes s of age a), day of the year b), sex c), and year of growth d). Age and day of the year are modeled as spline functions with 4 degrees of freedom each (notation= $s(\text{variable},4)$) and year and sex are implemented as factor variables. The columns represent the respective models based on data from Charlotte Harbour (CH), Indian River (IR) and Tampa Bay (TB), indicating the similarity in the effects between the first three effects, but different trends for the year variable.

Taylor, 1994). This asynchronicity in annulus formation between individuals complicated the age assignment of increments in the final year. To avoid the problem of having to detect and measure very small increments, edge interpretation (Francis, 1995) was used to convert annulus count to age. For fish with more than one increment, the size of the final partial increment (from the last annulus to the edge) was expressed as a ratio of the previous increment. When the ratio was <0.3 and the date of capture was after 1 November, it was deemed that an annulus was deposited prior to the assumed median date of annulus formation on 1 January. In the latter case, age was determined as the annulus count $- 1$ and the final increment was ignored. Conversely, if the ratio was >0.4 prior to 1 May, it was assumed the annulus would be formed after the assumed date of formation. In those cases, age was assumed to be the annulus count $+ 1$ and the increment size for the partial year was set to 0. Fish without a first annulus were assumed to be age 0 if captured prior to 1 January, and age 1 thereafter.

The analyses conducted in this study mostly focus on the properties of otolith and somatic growth specific to a given population. To provide some interpopulation comparisons, ANOVAs (Analyses of Variance) using bay, sex and age as grouping variables were carried out to examine differences in the size of otoliths and length, followed by Tukey's pairwise comparison tests between the three estuarine systems.

Increment analysis

The increment analysis represents a two submodel approach. The first submodel determines the average increment size independently in each population for a given sex, age and year combination, using all measured increments with the day of the year variable, taken as 365 for complete increments (after annulus formation). Annual increments were estimated independently for each estuary using a GAM (generalized additive model) considering age and day of the year of capture as bicubic spline effects with 4 degrees of freedom, with sex and year as factors. The model employed no interactive terms and the form for the additive predictor was:

$$\text{Increment}_{\text{size}} = \exp\left(\alpha + \sum_{i=1}^n \beta(X_i) + \sum_{j=1}^k f(X_j) + f(\epsilon)\right)$$

where α is the intercept of the linear predictor, β the slope of the i th linear component (categorical variable represented as dummy linear predictors), f the spline function of the j th smoothed component, and $f(\epsilon)$ is the local error term linked via a Gamma link function to the scale of the data. The mean predicted size of the increment at the end of each year was summed over the cohort at each age less than the full age and added to predicted increment size midway through the final year, to provide an estimate of the mean otolith radius in the population for each age, year and sex combination.

The second submodel relating fish length to its otolith radius was applied by way of a basic linear relationship on a log scale with cohort and sexes having different conversion rates on the scale of the response fitted as factors in the additive predictor. Further deviations from the linear form take into account differences in age and time of year of sampling. The effects of the last two independent variables are unknown, so they were fitted as smoothed terms in a GAM to determine the shape of the relationships. The functional form of the model is therefore similar to that used to determine increment

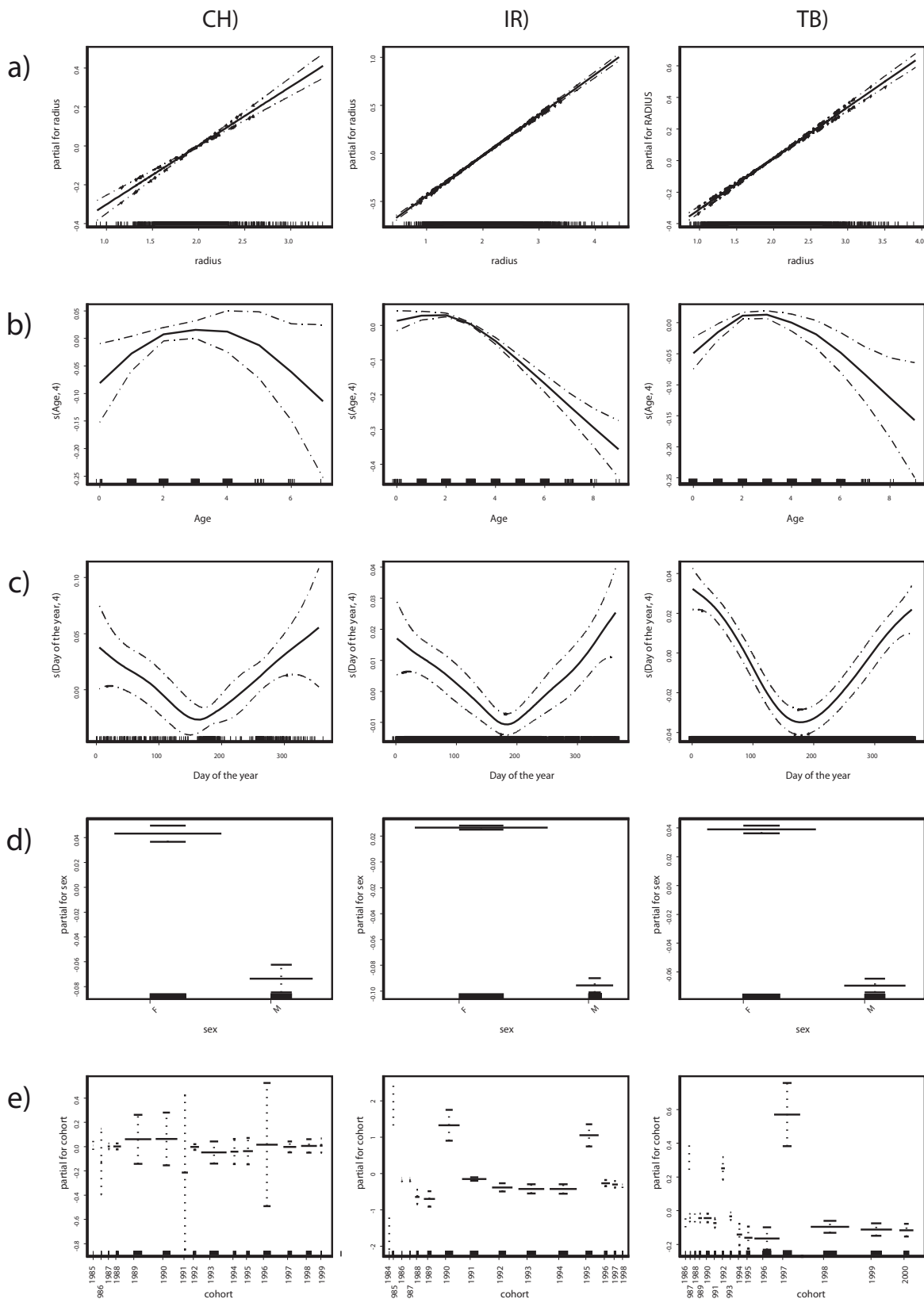


Figure 4.2. GAM model output for the 2nd submodel of the increment analysis describing the relationship between a) radius (linear), b) age ($s(\text{Age}, 4)$ = spline with 4 degrees of freedom), c) day of the year ($s(\text{Day of the Year}, 4)$ = spline with 4 degrees of freedom), d) sex (factor) and e) cohort (factor) and the partial contribution to the linear predictor of each variable on the y-axes with approximate confidence limits. In columns the models from the three populations in Charlotte Harbour (CH), Indian River (IR) and Tampa Bay (TB) are compared indicating similar trends for all variables except cohort.

size (see formula above), but includes a linear effect of radius and cohort as a factor instead of the year variable. Using the model parameter estimates as determined from the observed data, predictions of the mean population length-at-age for each sex and cohort were made based on the predicted mean radius of each cohort, sex and age combination.

The ultimate choice of model complexity of all GAMs was a somewhat subjective process, employing experience with GAMs, the findings of otolith researchers, and knowledge of the biology of the species as a qualitative measure of model parsimony. Using purely quantitative criteria such as the AIC (Akaike Information Criterion) leads to a tendency to imply higher degrees of freedom than appropriate, when the true error distribution is overdispersed compared with the implemented error distribution, as may be expected for such data with only a limited number of covariables, especially when the latter are correlated (Hastie and Tibshirani, 1990). An overfitted model would attribute random sample variability to systematic differences in length-at-age, so greater variation in both the trends themselves and the size of effects between subpopulations would be expected.

Model were seen as improbable when the same settings implied substantially more variation in the additive predictor over part of the age range or between sexes for different populations, because some variables, such as sex and age are largely expected to be species specific. In contrast, interannual or intercohort trends in growth are likely population-specific and driven by local environmental conditions so models suggesting cross population differences. In these factors were retained. In all instances, the final model chosen was more constraining in terms of the smoothed terms than would have been the case using the AIC as the sole criterion. All categorical variables included in the model also demonstrated to be significant explanatory variables by the AIC. The GAM form selected is summarized in terms of its independent variable, degrees of freedom for spline functions and deviance explained in Table 4.1.

Direct length-at-age analysis

Murphy and Taylor, (1994) and DeVries et al. (1997) found not only differences in growth rate but also in growth models between estuaries and sexes. Consequently, it was likely that a pan-population length-at-age model may oversimplify the true growth dynamics, so individual models were developed for each bay system consistent with the approach taken for the increment analysis. The main aims of this work were to identify possible biases in the increment analysis, to determine the additional information that could be generated by performing the more labour-intensive latter analysis and to assess independently the degree and form of decoupling associated with the back-calculation submodel of the increment analysis.

Trends in length-at-age were examined by relating total length to a number of available covariates, again in the form of an additive model. The GAM used spline functions for day of the year and age, with year, sex and cohort implemented as factors. The model form was therefore identical to the GAM in the back-calculation step of the increment analysis, with the linear effect of radius being replaced by a year effect.

Model comparison

The results of the increment and direct length analyses were compared with the simple annual means. The last was the least restrictive in that it made no assumptions about previous growth and forced no relationship between length at-age at different ages or through a particular cohort. The direct length analysis makes some assumptions about the relationship between length at one age and subsequent age, as well as about length within previous years at different ages. The increment analysis makes the same assumptions, but not on the basis of overall length, but of otolith radius. In addition, it assumes that otolith growth can be linked to somatic growth and that this relationship is specific to a particular cohort. Unlike traditional growth models, no model was sufficiently constrained to avoid shrinking of a cohort over time.

The models represent very different degrees of constraint, requiring a statistical criterion such as the AIC to make sound inference on a model's ability to differentiate between true variation in growth and the effect of sample variability at small sample sizes. Unfortunately, such a criterion could not be applied across length models, because the true underlying error structure is not known, nor is it applied consistently across the models, because the increment analysis has two submodels using additional information to calculate additional parameters. Instead, the residual sum of squares in length from each model was used as a proxy measure for goodness-of-fit of each length model. Although an approximation, this was thought to provide useful comparative information, because the overall residuals in lengths of all the analyses approximated the normal distribution over the range of -2 to $+2$ standard deviations, despite the fact that the residuals estimating increment size were distinctly heteroscedastic.

Estimates of the variation in length are often as important as estimates of the central tendencies in statistical stock assessment or length-based models. However, the increment and direct analyses are based on a daily time-step out of synch with the traditional annual time-steps of assessment models and the yearly means model, so to compare annual variance estimates, the predicted mean size-at-age half way through the year was estimated. The population standard deviation from the mean estimates was calculated to compare the robustness of the variance estimates between methods.

Bootstrap analysis

Bootstrapping was carried out only on the IR dataset, because sample numbers in the other estuaries were not considered large enough to approach representation of the true variance in the population. For each of the 1000 bootstrap samples, the mean length-at-age for each cohort and sex, and the estimated population standard deviation by sex and age, were estimated for yearly means, the direct length-at-age analysis, and the increment analysis.

Two subsampling approaches were taken. A subsample from the total of 6298 IR samples was selected either entirely at random, taking a fixed number (50, 100, or 300) of otoliths, or systematically by taking all samples from 5 (out of 8) randomly selected years. The trend in median estimates across cohorts between the different models was examined to determine whether they showed the same trends, which if so would suggest that the methods were unbiased estimators of the true trends in size, or at least within the sampled population.

The results from the different models for a given simulation would not contain the same number of estimates because of the difference in their efficiencies. Comparisons between models were made qualitatively in terms of the number of valid estimates of length-at-age for a particular cohort, sex and age combination, and quantitatively by calculating the standard deviation of mean estimates (empirical standard error) for those cases where estimates were obtained from all methods for each of the three bootstrap sample sizes.

Results

The summary of the age results by bay, sex, age and year (Table 4.2) highlights the sparseness, particularly at older ages, and temporal imbalance of the available data. This is also the reason why the current stock assessments pool the age-length keys over periods of more than one year (Murphy, 2003; Murphy et al., 2006). Despite the sampling imbalance and substantial variation in length-at-age, the ANOVA revealed significant differences in the size and otolith radius-at-age between the different systems. Pairwise comparisons showed that fish from the IR were the largest, followed by fish in CH and TB. In contrast, CH fish had the largest otoliths, with IR and TB otoliths not differing significantly (Table 4.3).

Increment analysis

The first submodel in the increment analysis determined the average size of the year's increment. The models explained >75% of the deviance in the data for all three estuaries, estimating 23 parameters. Trends were coherent between estuaries for the continuous covariables age and day of the year, both in trend and the relative importance in explaining variance, despite differences in the number of samples available. Increment size was affected seasonally in all estuaries in an asymptotic manner. It increased most rapidly in the early part of the year, slowing considerably towards the later portion of the year, more so in Gulf coast estuaries than in the Indian River lagoon (Figure 4.1). The size of the increment decreased with age in all three estuaries, with what appears to be a faster change in increment growth rate at age 2, following which the growth rate returns to a more linear decline at older ages.

Factor covariables indicated important differences between the estuaries. Females had larger annual increments than males, but the magnitude of the difference was larger in CH and IR fish, compared with TB fish. Year effects indicated the greatest difference between the models, in terms of both scale and direction. Although data are sparse in many years, the model indicates a three-year periodicity, which is persistent where samples are most abundant. The effect in the IR can be described as an upward trend for three years before returning to a lower level. The year effects in CH and TB were of a similar magnitude, whereas TB increment growth increased over a three-year period before returning to previous levels, and as in the IR, it decreased in CH. On the whole, over the period of the available data, there appear to be no long-term trends in increment accretion rate.

The second submodel relating otolith radius to length explained around 80% of the deviance in length in the observed data within each of the populations (CH 81%, IR 79%, TB 82%). The relationship primarily assumes a linear relationship between otolith radius and total length, but one that deviates from the strict linear relationship by age, season, sex and cohort (Figure 4.2).

The slope of the linear relationship is similar in all three systems, as is the effect of sex, with females attaining a greater total length given a particular radius. Radius on its own is the best predictor of fish size in all estuaries, contributing about 85% of the deviance explained by the full model. A significant part of this explanatory power is shared, however, with the other variables (55% in TB and CH, and 25% in IR) through colinearity between the independent variables.

Given a specific radius of otolith, a fish aged 2–4 will be larger than a fish with the same otolith radius, but younger or older. This reflects the faster increment accretion rates at younger ages, whereas at older ages, the decline in growth is faster than the apparent linear decline in otolith growth.

The seasonal effect has a midyear minimum (day 180 in CH and IR, day 200 in TB), which can be interpreted as a seasonal decoupling of otolith and somatic growth, with otolith growth outstripping somatic growth during the declining part of the curve, and somatic growth in turn outstripping otolith growth on the ascending portion.

The cohort effect, though small, is responsible for the biggest difference between populations in the increment submodels. The model for IR indicates the greatest variation in decoupling between years, but appears to have a five-year periodicity, in common with the other estuaries, where cohort seems to explain less of the variation in size.

Direct length-at-age analysis

The direct length models from all three estuaries explained marginally less deviance (CH, 77%, IR 70%, TB 78%) in length than the back-calculation submodel based on individual otolith radii. The scale of the effect of age differs between the systems, being largest in the IR and smallest in CH, and the trend is similar at younger ages, although it becomes increasingly asymptotic at older ages, from IR to TB to CH (Figure 4.3). Females are larger than males, and there is little or no growth in the first half of the year, followed by rapid growth in the second half of the year in all populations. There are small, but important, effects of sex and season on length, and these are similar between estuaries. As in the increment analysis, year and cohort effects, again small, imply differences between the estuaries with cohort, indicating a five-year periodicity in the TB and IR systems. Year effects demonstrate an asynchronous three-year periodicity in growth rates between the systems, most apparent in CH and the IR, and less so in TB.

Model comparison

The increment analysis explained roughly 80% of the deviance for 24 degrees of freedom (in the back-calculation submodel), about 5% more than the direct length analysis for with 29 degrees of freedom. The increment analysis provides more accurate results and is more parsimonious, because it performs better with fewer degrees of freedom.

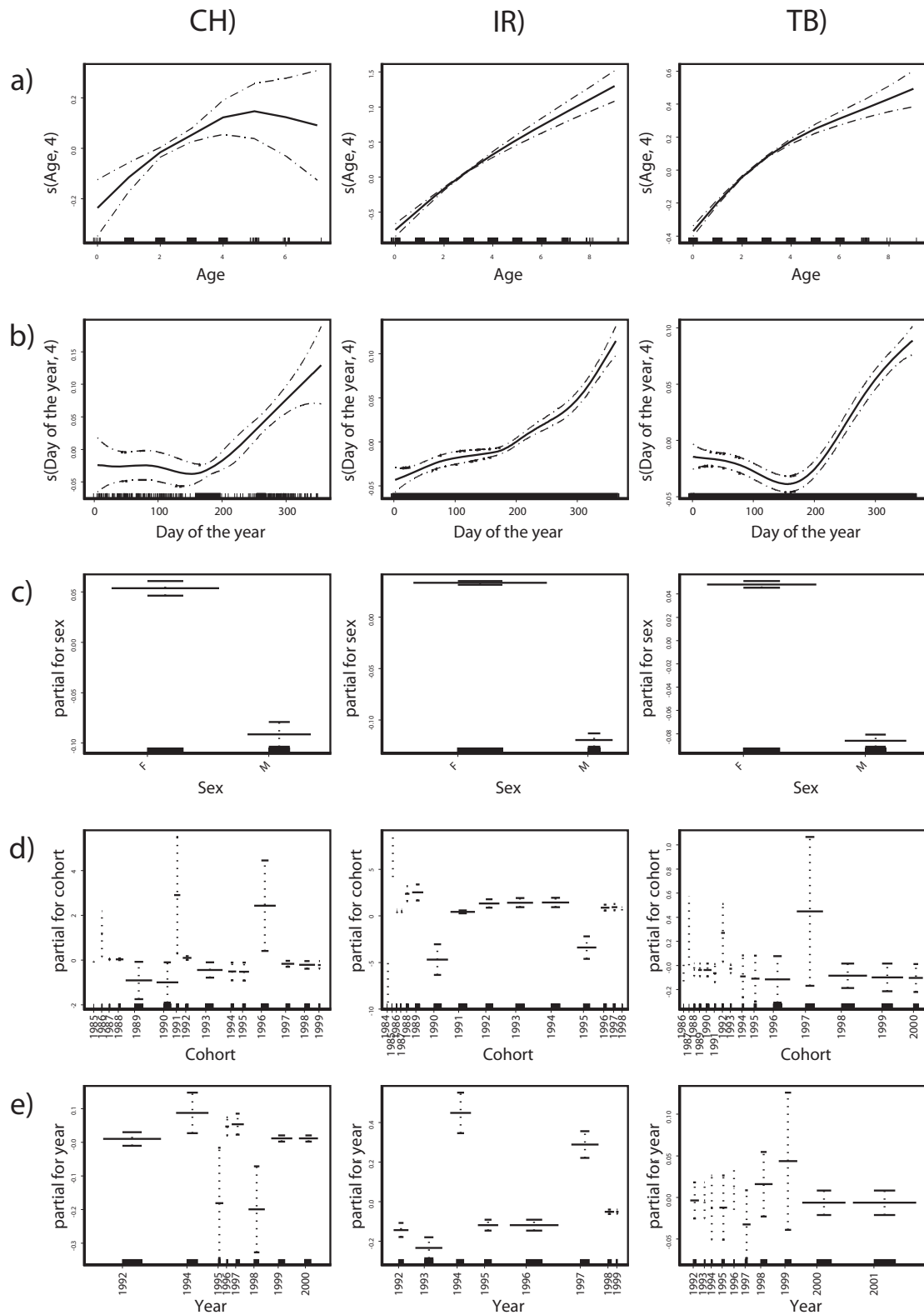


Figure 4.3. GAM model output for the direct length-at-age analysis describing the relationship between a) age ($s(\text{Age}, 4) = \text{spline with 4 degrees of freedom}$), b) day of the year ($s(\text{Day of the Year}, 4) = \text{spline with 4 degrees of freedom}$), c) sex (factor), d) cohort (factor) and e) year (factor). The magnitude on the y-axes describes the partial contribution to the linear predictor of each variable with approximate confidence limits. In columns the models from the three populations in Charlotte Harbour (CH), Indian River (IR) and Tampa Bay (TB) are compared indicating similar trends for all variables except cohort and year.

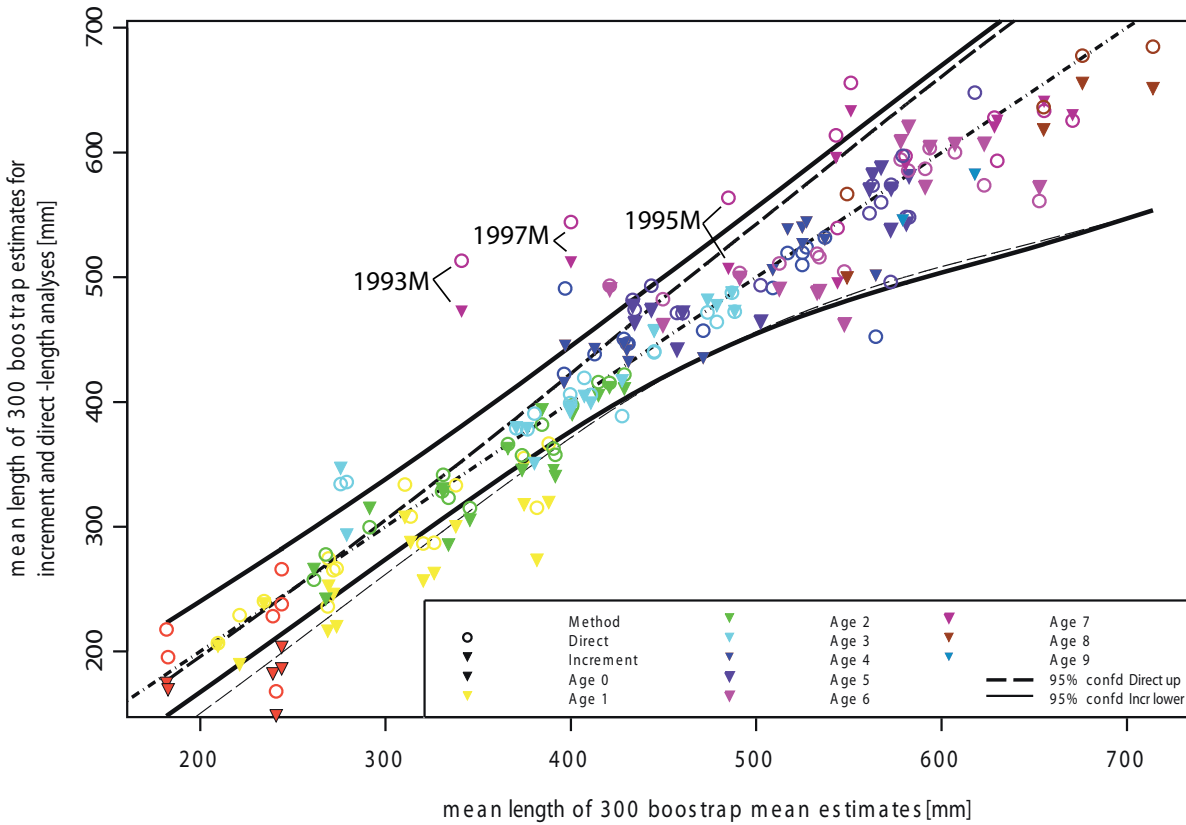


Figure 4.4. Indian River yearly-mean length against mean cohort length-at-age estimates for the two length models and the 1:1 line (dot and dash). Continuous and dashed lines are the smoothed estimates of the 95% inter-quartile range in bootstrap results to provide approximate 95% confidence limits. Estimates of both analyses for males at age 7 of the 1993, 95, 97 (annotated) are based on an individual fish.

Mean length predictions for each year given the sex and age are given in Tables 4.4 and 4.5 for the increment and direct analyses. The biggest differences between the two analyses are at age 0 and at older ages, where sample numbers are scarce.

Seasonal, age and sex effects are consistent between the analyses, though less so for the cohort effects particularly in CH. Cohort correlated between the two analyses negatively in IR, suggesting that large fish (e.g, IR 1990 and 1995 cohorts, Figures 4.2 and, 4.3) have large otoliths for their size. In contrast, TB correlations are positive, so small fish (e.g. TB 1992 and 1997 cohorts) have small otoliths relative to their size. The picture in CH is less clear, but the well estimated small cohorts (1989 and 1990) have small otoliths for their size, whereas the intermediate cohorts (1993–1995) have large otoliths, and subsequent smaller cohorts (above average size) have otoliths of average size.

Standard deviation estimates for the increment analysis and the direct length-at-age analysis are listed in Tables 4.4 and 4.5. They indicate differences between bays and sexes, with the IR having greater variation at age than TB and CH, and with females generally displaying greater variation than males in all systems. Variation increases with increasing age and tends to level off at the older ages. At the oldest ages in some of the bays, there is a sharp decline in the standard deviation.

Bootstrap analysis

The aim of the bootstrap analysis was to examine the characteristics of three methods of estimating length-at-age in terms of empirical variation in the estimates, the possibility of bias, and the efficiency of the different model in providing information from small samples.

Random bootstrapping of the IR data indicates that the direct length-at-age and the increment analyses when compared with the yearly means estimates provide unbiased estimates of length-at-age for most ages, even at small sample sizes, with similar median and mean estimates, the latter plotted in Figure 4.4. Empirical standard error estimates by age and sex show that at a sample size of 300, estimates of the standard error are stable across most ages. Estimates overall are smallest for yearly means, followed by the increment analysis, and largest for the direct length-at-age analysis, with standard error estimates of means in males being smallest at around 90 and largest for females in the increment analysis at roughly 150 (Figure 4.5). Male length-at-age is estimated more precisely than female size in all methods, reflecting the greater variation in growth of females.

As the empirical standard error stabilizes with increasing sample size, it indicates the number of samples required to attain a consistent estimate of the population variance from the sample variance. At an overall sample size of 50, the bootstrap results show population mean estimates reasonably precisely only for ages up to about 4 for the direct length-at-age method and about 6 for the increment analysis. With increasing sample size, the consistency improves at older ages. However, at ages 8 and 9, no asymptote is reached at sample sizes of 300. Given that these ages are very rare in the sampled population (4 fish only, ~0.1% of the total) it seemed unlikely that an empirical estimate for any of the methods would be able to describe the true population mean.

Median results of the increment and direct bootstrap analyses are plotted for the 1992–1999 cohort and sex combinations in Figure 4.6, along with the box plots representing the standard error. In general, estimates of length-at-age for ages <6 years are less variable for the increment analysis than for the direct length analysis. Precision decreases with age, and in recent years, as sampling levels in the IR declined.

The three different methods of estimating length-at-age make different assumptions about the linkages between length across ages and years. Consequently, there are differences in the number of length-at-age estimates provided by the different methods for a given bootstrap sample. The difference in efficiency is shown quantitatively in Figure 4.7 for 1000 simulations at different sample sizes. The area covered by each of the bar graphs is proportional to the efficiency of the methods. The direct length-at-age analysis always provides more information for each cohort than the yearly means model, particularly so at the smallest sampling size, where there are few estimates available for males because these were particularly poorly sampled in the IR dataset. There is an increase in the density of available estimates with increasing sample size for both methods, but more substantial in the direct means method. The increment analysis always provides the same number of estimates over the sampling period as the direct means analysis, but additionally provides substantial information prior to the period of sampling.

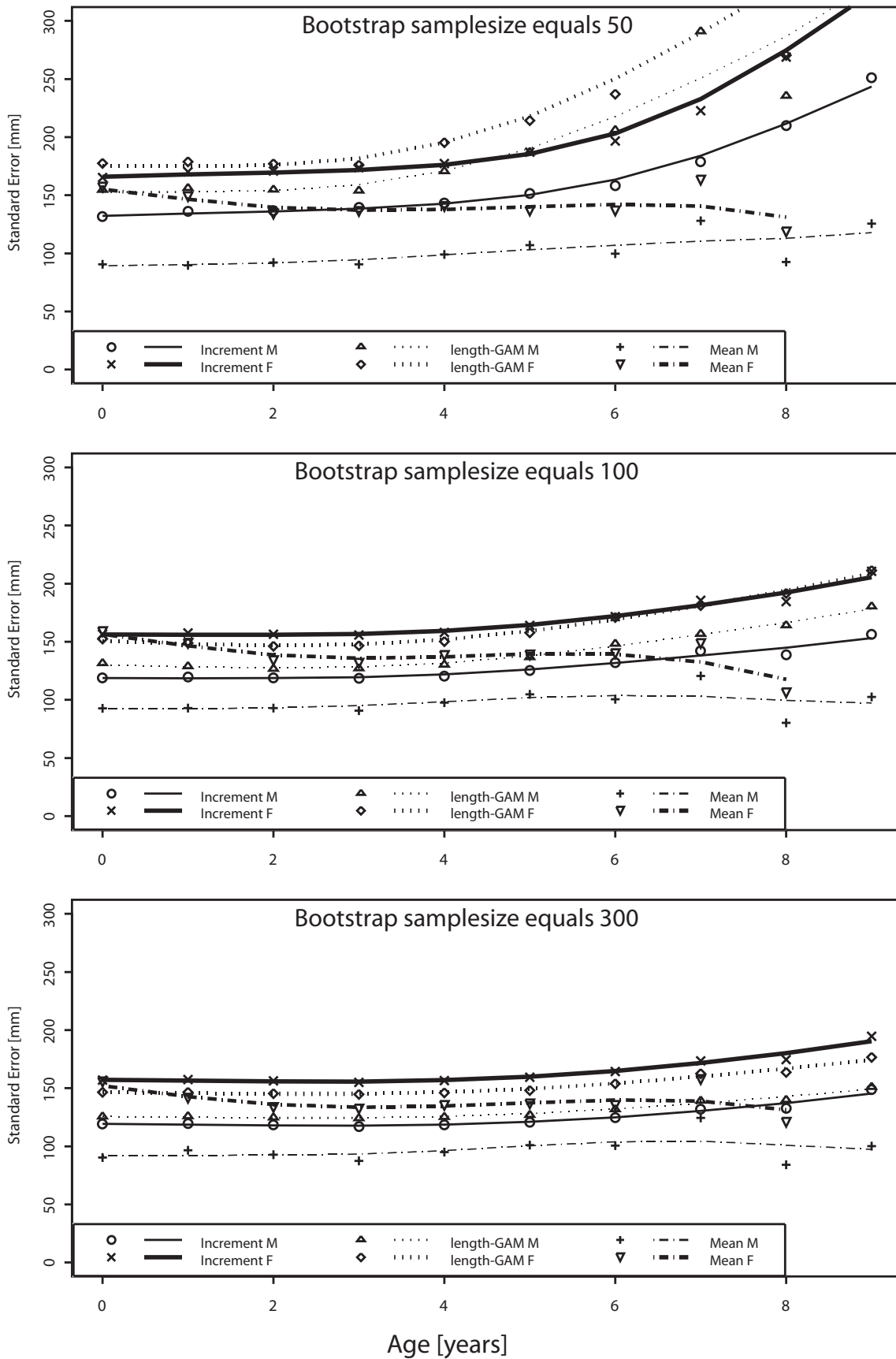


Figure 4.5. Comparisons of the empirical standard error estimates at age over cohorts of the 500 random bootstrap samples at different sample sizes (50 – 300 top to bottom) for Indian River data illustrating the convergence of estimates at higher sample sizes.

The bootstrap estimates of the population standard deviation calculated by age and sex for the whole of the IR dataset are plotted by method in Figure 4.8. The bootstrapped yearly means estimates of variance generally underestimate the true variance at the youngest and oldest ages, i.e. where sample numbers are few or bootstrap samples are small. It suggests that some 40 fish of a given age are required in the analysis to

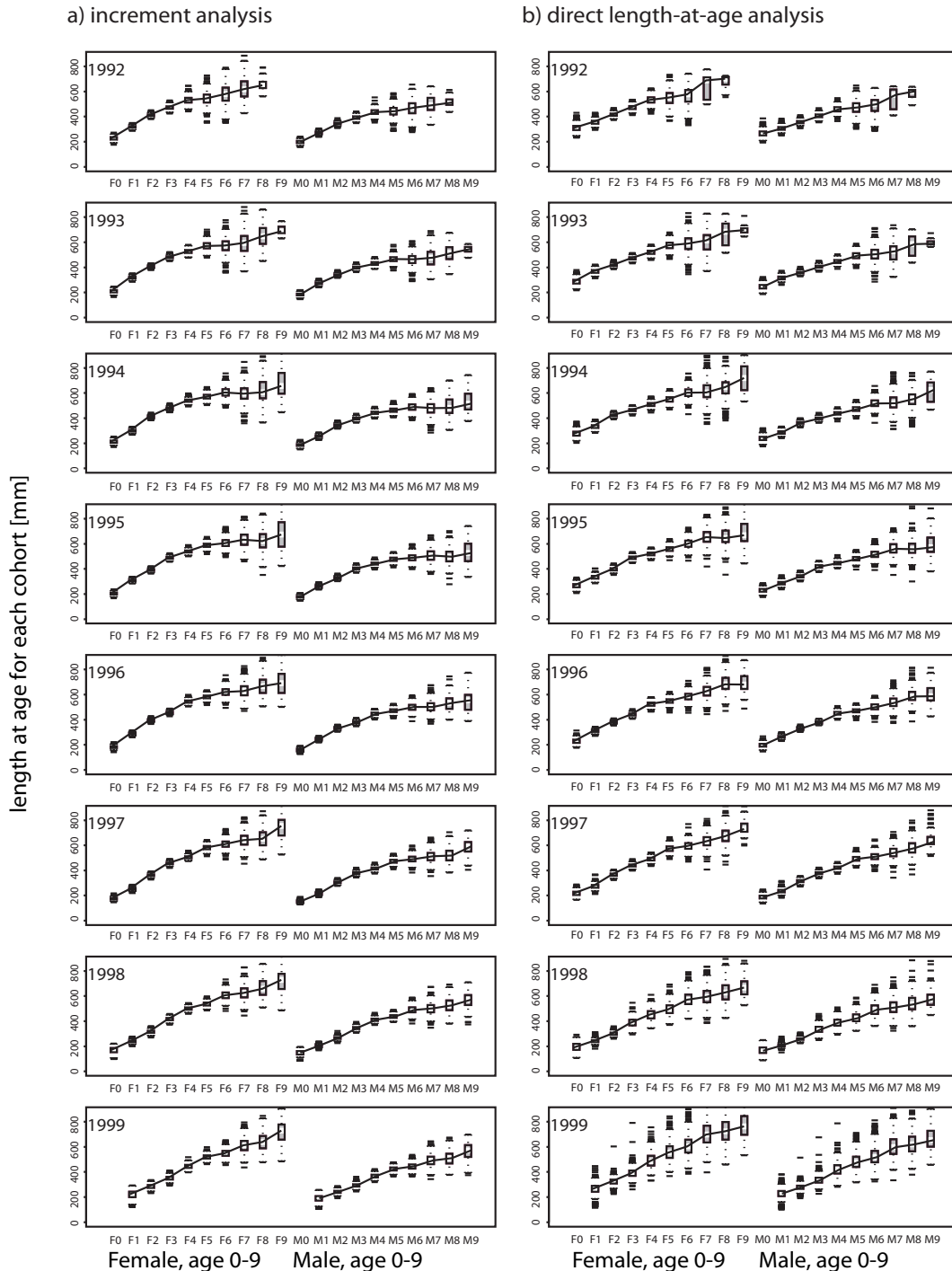


Figure 4.6. Comparison of the median cohort length-at-age and box plots of the variation in estimates between bootstrap samples from a) the increment analysis and b) the direct length-at-age analysis. In each plot females are on the left, males on the right from ages 0 to 9 where applicable. The range of predicted values increases at age 6 and for the 1998 cohorts, particularly for the direct analysis. The inter-quartile range is large for ages 8 and 9 for both methods.

provide unbiased estimates of population variance. The direct length-at-age analysis performs better at older ages, but shows that at sample numbers below 20, the variance estimates are biased downwards for younger individuals. The increment analysis provides the least biased estimates of population standard deviation at all ages, but part of the cost of this is that at small sample sizes, the precision of the standard deviation estimates is significantly lower.

The systematic bootstrap analysis, subsampling by year, was designed to determine whether it was possible to provide unbiased estimates of length-at-age in the absence of data from a particular year using the increment analysis. The other methods investigated could not provide estimates in such an extreme case of small sample size, so are not examined here. Figure 4.9 indicates the difference in the estimates of length-at-age between the results of the increment analysis containing a particular year's data with those that did not (jackknife). For the older ages there is very little difference in the mean estimates, as is the case for ages 0 and 1 in all but the most recent years. Furthermore, the estimates follow the trend in the overall mean observed values at ages <6. Observed age 0 and 1 fish have substantially larger size-at-age than estimated by either including or excluding data from a particular year, but this effect had declined by age 2, as had the divergence of the jackknife estimates in the most recent year.

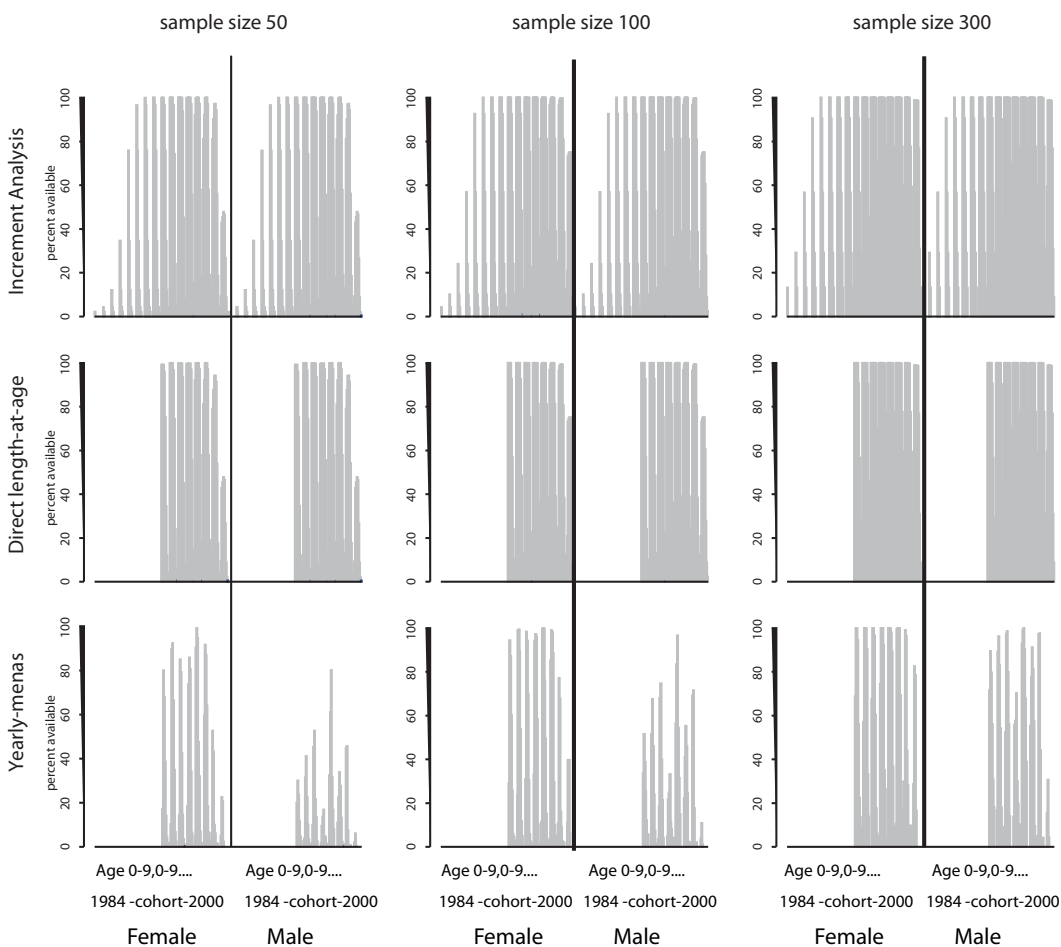


Figure 4.7. Number of estimates provided for each cohort at each age and sex by each method for the 500 bootstrap samples as a percentage of the total. The left column in each plot represents females with 1984 to 2000 cohorts going left to right subdivided into ages 0 to 9, right column represents males. Bootstrap samples size increases left to right over plots.

Discussion

A new methodology was examined to see whether it was possible to extract information on the variation in length-at-age the otolith records and to reconstruct the average growth history of historic cohorts. Given the uncertainty regarding the underlying factors driving the processes of otolith growth and somatic growth, the aim was to see whether the results are consistent between populations, between methods where such information exists, and by bootstrapping in order to determine the relative level of bias and precision between methods. Finally, the results are related to current knowledge of the growth of seatrout and its biology in general.

Increment analysis

The growth dynamics of seatrout otoliths were studied to determine factors that affect otolith accretion within an increment. Growth is most rapid during the first quarter of the year, slowing to its lowest level at the end of the year, consistent with the assumption of maximum growth as environmental conditions, particularly temperature, increase in the ecosystem. Annual increment width decreases with increasing age, and this decline is most rapid in the first two years of life, more or less the period of immaturity in spotted seatrout. With a seasonally asymptotic trend in increment accretion, overall radius development follows the classical annually stepped asymptotic growth pattern, with female increments larger than male increments for a given age. These patterns are independently revealed in the datasets from the three estuaries, increasing confidence in the validity of the results and indicating a cross-population effect. In addition, a year effect suggests that otolith growth varies between years though with unexplained three-year periodicity, but the exact pattern differs between the three systems. The year effect used here is just a pooled effect reflecting the integral of the environmental and biological conditions in a particular year, so periodicity in this effect is at the least surprising.

Given that otolith growth in seatrout very much follows somatic growth in other species of fish, a simple linear or at least monotonic function might be expected, to relate the size of the otolith radius to the length of the fish. Instead, the relationship between otolith radius and length in seatrout illustrates distinctly seasonal, age-, cohort- and sex-specific deviations from such a monotonic relationship. These variables also drive changes in length in the direct length-at-age analysis, so there is some danger of introducing potential redundancy in the increment analysis. However, if otolith growth rate is non-linearly related to somatic growth, for example when energy expenditure on reproduction occurs after maturity or maintenance metabolism increases at larger body size while otolith growth is unaffected, then those factors affecting somatic growth rate must also affect the otolith to length relationship, which is also the theory behind the time-variant model (Sirois et al., 1998).

The age effect in the second submodel can be approximated by two linear trends, so that a more parsimonious model than the spline function related to maturation or other ontogenetic stage transition may be possible as found by other authors (Hare and Cowen, 1995; Vigliola et al., 2000; Brevian et al., 2006). Here, as in Živkov, (1996), Finstad, (2003), and as suggested by Francis (1990), age was found to be a suitable predictor. Given the asynchrony in maturation (Nieland et al., 2002), the perceived

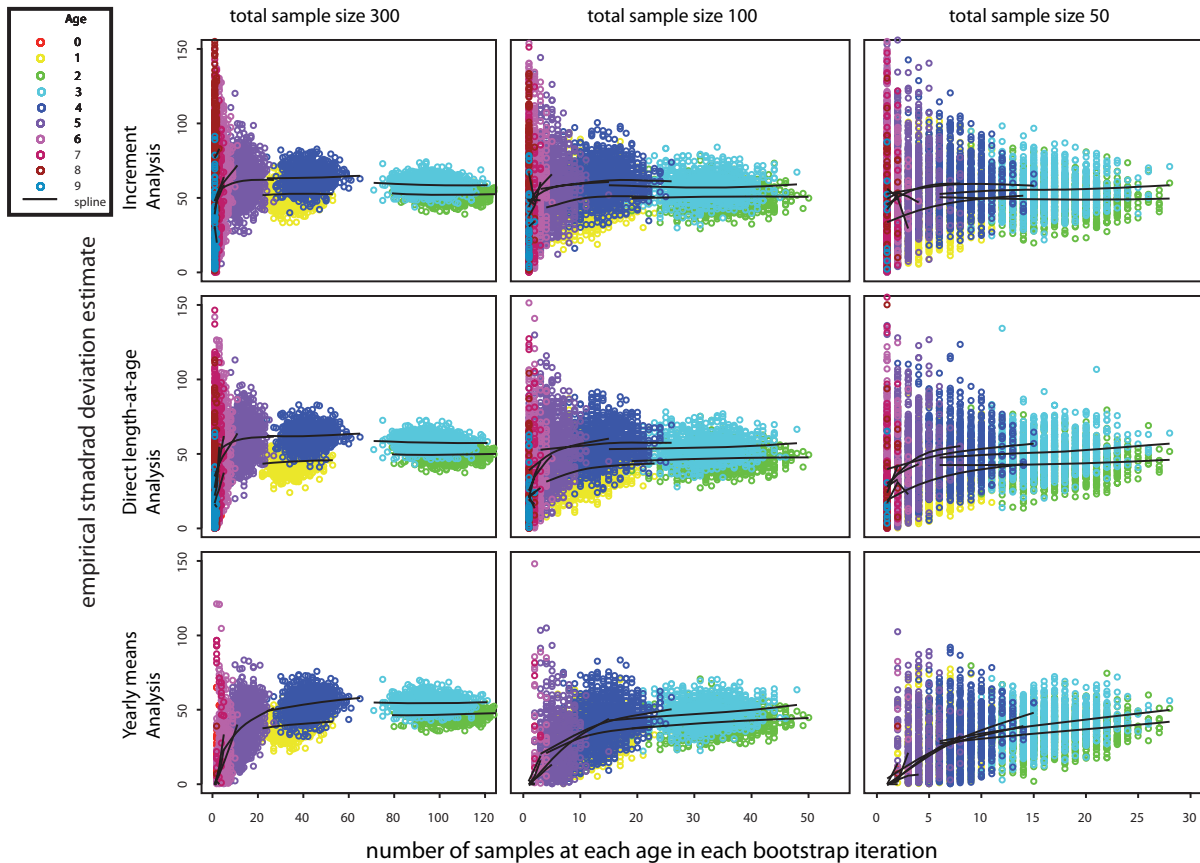


Figure 4.8. Number-at-age in each of 500 bootstrap sample against the estimates of the population standard deviation by age for three different bootstrap sample sizes (300,100 and 50) in columns, noting the differences in the extent of the x-axes for the different sample sizes. Black lines indicate smoothed estimates of the population standard deviation, illustrating the greater tendency of the yearly mean estimates to underestimate the deviation at small sample sizes compared to the increment analysis and to a lesser degree the direct-length-at-age analysis.

change in growth rate in the population would tend to smoothed compared to that of the in the individual making a spline function more appropriate in the absence of known dates of maturation for a mature individual.

The back-calculation effect of season declines from a high at the beginning of the year to a minimum midyear, before increasing again at the end of the year. It implies that seasonal growth seen in the otolith is not reflected in the seasonal trajectory of length. In the first half of the year, otolith growth is at its fastest and outstrips increases in length, but in the second half of the year the relationship reverses as length increases most rapidly and otolith growth achieves some of it slowest rates. Therefore back-calculation for samples taken at different times of the year can only be applied after taking account of the time of year, particularly at an individual level.

For a given otolith radius, males were smaller than females, as were both sexes during the middle of the year, compared with either the beginning or end of the year. Shafer (2000) found similar differences in the extent of decoupling between sexes and rearing temperature. In this analysis, temperature differences may be reflected in both the seasonal trend and the cohort effect, where annual differences are integrated over the life

of the cohort. If temperature is the underlying cause of this decoupling, and seasonal trends in temperature differ between years, then the orthogonal model used here can only express the average seasonal trend, not the trend specific to a particular year.

Reproductive activity is another likely underlying cause of decoupling of somatic growth, particularly given the high reproductive output of this species (Chapter 3). Again, the decoupling effect of sex is orthogonal across season and age in the model. Given that reproductive strategies for sexes differ seasonally, and across ages because the sexes mature at different ages (Brown-Peterson et al., 1988) the model is likely to suffer from a lack of interactive terms. The shape of the function shown here therefore represents the average over all years and both sexes, but it does seem to provide a useful approximation, particularly given the similarity of the effect between estuaries.

The full increment analysis suggests a late autumn or early winter growth spurt, with little growth throughout the rest of the year. Unfortunately, there is little in the literature on the seasonal growth cycle of the species, although Lowerre-Barbieri et al. (1994) commented that the mean length-at-age in the congener *Cynoscion regalis* appeared not to increase or even decrease slightly during the warmer months of a year. They suggested that this may be due to size-selective migration, but seatrout do not undertake seasonal migrations outside estuaries, at least not on the Atlantic coast, and just a small percentage of the population on the west coast migrate (Iversen and Tabb, 1962). Nor would we expect to see the pattern in the back-calculation, because an individual would still continue to grow asymptotically throughout the year. The fact that almost the identical pattern is repeated in all estuaries means that this is not an artefact of sampling bias, but rather a reflection of the biology of the species.

In general then, there is good agreement between the results of the increment analysis and current understanding of the differences in the relative strength of environmental and energetic effects on the processes of otolith and somatic growth (Francis, 1990; Xiao, 1996; Hüsey and Mosegard, 2004).

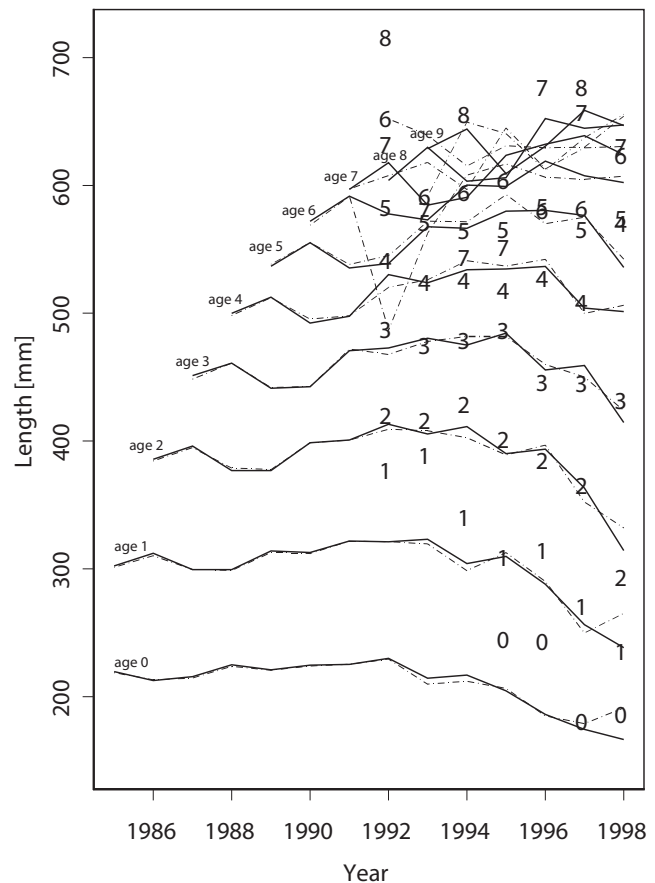


Figure 4.9. Results of the 1000 bootstrap systematically re-sampling by year. Solid line represents median jack-knifed samples containing data from a particular year, with estimates of the length-at-age estimated in the absence of a year's data shown dashed. Trends in cohort size are easily observable for both estimates up to age 5, and estimates are comparable for most years except the final year at age 0 and 1. Numbers show overall mean observed by age and year.

Direct length-at-age analysis and model comparison

The direct length-at-age analysis was carried out to estimate the bias in the increment analysis where comparable information is available. It also revealed that sex and age are the most important variables affecting the size of spotted seatrout, with females being larger in all estuaries and with increases in size slowing as fish grow older. Growth is also almost exclusively confined to the second half of the year in all estuaries, and cohort and year effects seem to indicate a roughly 5-year and 3-year periodicity, respectively.

Mean length-at-age estimates from the increment and direct length-at-age analyses are in good agreement. This should not be seen as particularly surprising, because it is exactly those variables that affect growth that seem to contribute most significantly to the departure from linearity of the otolith-to-length relationship such as age, sex and seasonal effects. Comparison of the year variable between the analyses is inappropriate, because the year variable in the direct length-at-age model relates only to the year of capture, whereas in the increment analysis it is indicative of the growth of the otolith in a single year.

The cohort effect, here originally considered to be a density-dependent decoupling effect, represents the most interesting findings with regards to better understanding the relationship between otolith radius and length. When resources are limited, an increasing proportion of those available is spent on maintenance, resulting in fish of a given size having larger otoliths than those with unlimited resources. As resources increase, growth first increases rapidly, but it then slows as chemical processes limit the utilization of the resource, leading to the classical sigmoid relationship between growth and resources.

The increment analysis detected significant decoupling effects for specific cohorts. TB 1992 and 1997 and IR 1990 and 1995, were large given the size of their otoliths, but most of the remaining cohorts have roughly similar otolith-to-length relationships. In CH again, most cohorts are similar, but the 1991 and 1996 cohorts at least contain some fish that are small given the size of their otoliths, although the effect overall is poorly estimated there given the considerably smaller sample size. However, if resource limitation influenced somatic growth alone, one would not expect to see correlation between the cohort effects of the two analyses (Figure 4.10a, b), positive in TB, negative in IR. Hüssey and Mosegaard (2004) surmised from an energy budget evaluation that otolith accretion was linked to total metabolism, whereas somatic growth is determined by the excess of metabolites above those required for maintenance, yet they represented maintenance metabolic cost as constant across temperatures, which is unlikely (Wuenschel et al., 2004). Experimentally, it is difficult to isolate the functional forms of energy use with the environment, because the independent variables interact, nor is it possible to provide accurate environmental information for individuals sampled from natural populations, so the direct energy budget approach to decoupling seems some way off.

Instead, the relationship can be simplified into a simple linear component based on the chemical processes alone, accounted for in the increment analysis by the radius variable, and a more complex decoupling process driven by the differences in the limitations of the biological processes (Shafer, 2000) interacting with variable environmental conditions represented by the proxy variable cohort. Somatic growth has a dome-shaped

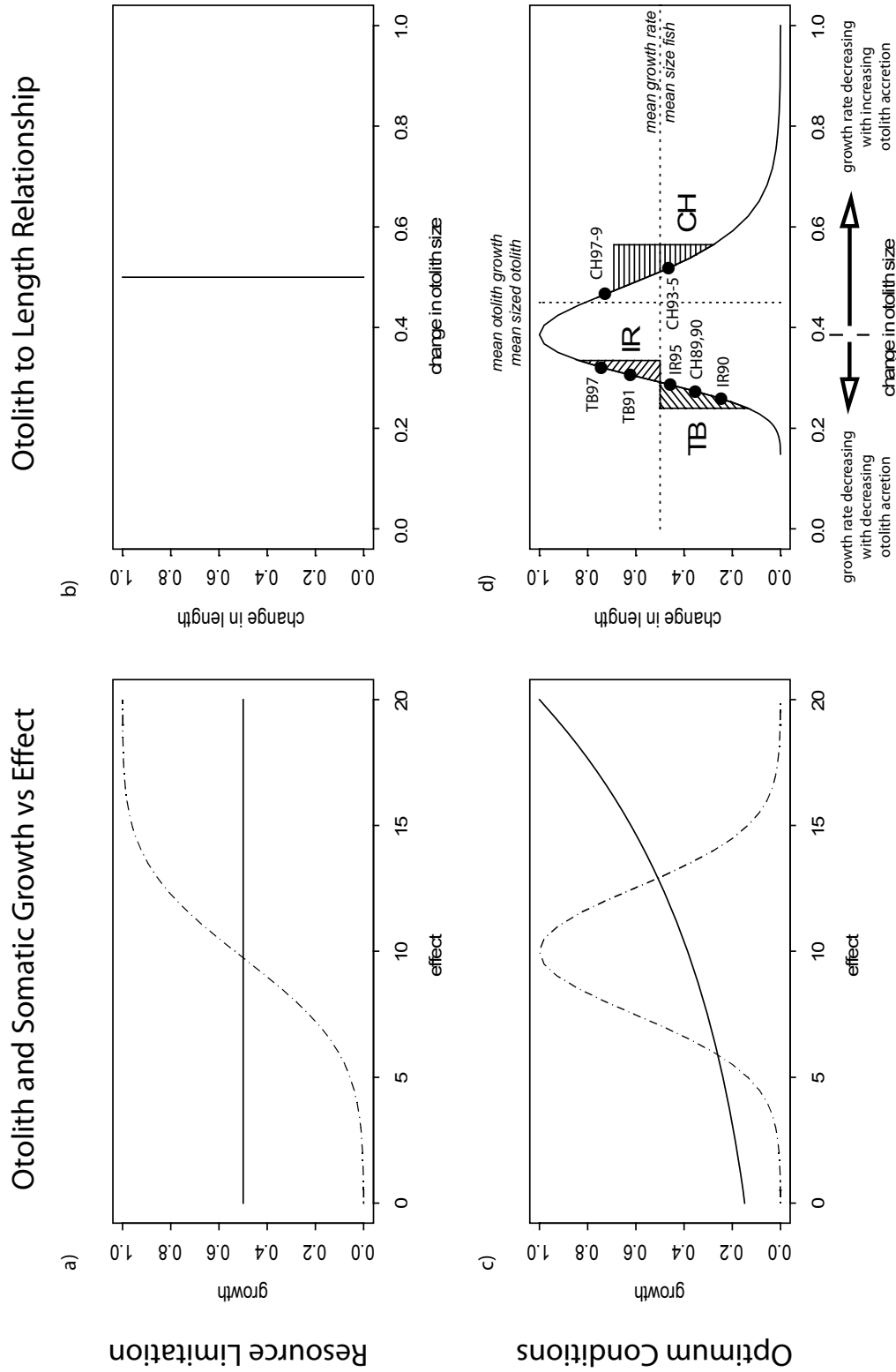


Figure 4.10. Figures illustrating the expected responses in otolith (solid line) and somatic growth (dashed line), left hand plots (a,c) and the resultant theoretical otolith to length relationship to resource limitation right hand plot (b and d) affecting somatic growth only (top plots, a,b) and environmental conditions such as temperature affecting otolith and somatic growth differentially (bottom plots c,d). The effect in panel d has been exaggerated for clarity and to plot the relative positions of cohorts / populations as suggested by the relationship of the cohort effect in the direct length-at-age and the back-calculation sub-model analyses.

curve, restricted at the lower end by effects such as membrane permeability restrictions and enzyme deformation beyond the general slowing of chemical processes at lower temperatures and at the upper end by biological constraints such as increased metabolic maintenance costs through more rapid protein degradation and metabolite transport limitations (Figure 4.10c). The resultant otolith-to-length decoupling effect then indicates a skewed dome-shaped relationship (Figure 4.11d).

Comparing the results of the cohort effects in the direct and increment analyses, it is possible to make some inferences on the conditions experienced by the different cohorts in the three systems. In the IR, short cohorts (1990 and 1995) not only had small otoliths, but also otoliths smaller than expected for a linear relationship, whereas in TB, oversized cohorts (1995 and 1997) had large otoliths, but which were small for the size of fish. This allows by inference, relative to otolith and body size, placement of the remaining cohorts in Figure 4.10. In CH, the classification is more difficult because of the greater uncertainty about the size of what appears to be some very large fish in the 1991 and 1996 cohorts. If those cohorts are ignored and emphasis is instead placed on the cohorts for which larger sample sizes exist, then 1989 and 1990 can be placed with the TB fish on the left side of the graph, 1997 and 1998 with the majority of the IR cohorts in the central section, and 1993–1995 with the largest otoliths, but smaller than expected for their size, in the descending portion of the otolith-to-length relationship. The fact that a particular otolith growth rate implies two possible somatic growth rates explains the frequent occurrence of fish of equal size, but differing otolith radii. The poorly estimated 1996 cohort is consistent with the conclusion above, but the 1991 cohort is the largest, but also has the largest otoliths, which would imply that it should be placed in the central section in which case it is not possible to arrange the remaining CH cohorts consistently with the environmentally induced decoupling theory presented here.

On average then, IR fish should be the largest, but have otoliths of intermediate size, whereas TB and CH fish should be smaller, with the latter having the largest otoliths at age. The ANOVAs comparing the raw data between estuaries confirm that IR fish are the largest, followed by CH and the TB. There is no significant difference in the size of the otoliths between IR and TB, but CH otoliths are significantly larger at age (Table 4.3).

Differences in the direct response of somatic growth and otolith accretion as a function of the chemical reaction rate is only one possible cause of decoupling; indirect effects such as changes in the metabolic costs associated with salinity and density-dependent behavioural processes could also be at work. However, irrespective of the cause, it seems clear that these decoupling effects are not independent of otolith growth, so it should be possible to differentiate between the effects at an individual level provided sample sizes are sufficient to estimate mean population trends accurately within the back-calculation submodel.

In general, decoupling at a cohort level is minor compared with seasonal decoupling, but further work is clearly needed because the underlying cause is unknown, so that it is not possible to determine whether it is appropriately assessed at a cohort level. Also, the apparent 5-year periodicity in cohort size is based on very small sample numbers, and the divergent decoupling trends between these unusual cohorts are less certain still. Environmental and even density-dependent effects with such precision seem un-

likely, and harmonic autocorrelation in the model or data are not possible, given that the periods are in prime numbers. A longer period of sampling would be helpful in establishing whether the apparent periodicity is coincidental and, if not, what the causes is that might underlie these fluctuations.

Bootstrap analysis

There are important differences in the assumptions underlying the models, which result in differences in the number of estimates provided by each method for a particular subsample. This is because fish are not sampled stratified by age, but by length, nor have they been bootstrapped by age. For example the yearly means model provides an estimate of length for a specific year, age and sex combination if the sample contains at least one individual for that combination. The direct length-at-age analysis can estimate this in the absence of a sample for that specific combination, provided at least one sample is available in each of the categories year, age, sex and cohort. The increment analysis obtains the year effect from the otolith record, so requires a sample only in the relevant categories of cohort, age and sex. Intuitively, then, the increment analysis is qualitatively the most efficient method in terms of being able to provide estimates of length-at-age.

Both the increment and direct analyses provide accurate estimates of the inter- and intra-cohort variation for ages 2–6. The latter also matches the observed values better at age 0 and to a lesser degree at age 1. The divergence of the increment analysis at those ages may be the result of model bias, but given the sampling gears used, it may also be due to size-specific selectivity, taking only the largest specimens of a cohort at the youngest ages, often attributed as the cause of Lee's phenomenon (Francis, 1990). The increment analysis is able to compensate for this overrepresentation of large fish when it attains information on initial increments from the fully selected cohort in later years, whereas the other methods cannot. The fact that it is the cohorts with the largest observed length at age 0 and 1 that fit the poorest is consistent with size-specific selectivity.

At age 6, both increment and direct length-at-age analyses indicate less variance in the mean cohort length compared with the yearly mean estimates attributing more of the observed variation to the standard deviation in the population. Seven-year old fish appear to be poorly estimated, more so than older or younger fish. The mean length estimate for these are based on an individual male much smaller than the average for age 7 and even age 6 males. Given the variability in length, these fish are likely to represent smaller examples of their cohort, rather than a bias in the analyses. At age 8 and 9, the predictions fit surprisingly well, but this is probably because sample numbers are so low that the flexibility in the GAMs can no longer differentiate between inter- and intra-cohort variation because the age effect is collinear with the cohort effect. This is also reflected in the decrease in the standard deviation estimates in the analysis using the whole dataset (Tables 4.3 and 4.4) and the standard error estimates (Figure 4.5) at ages 8 and 9.

Bootstrapping the increment analysis by year also proves that there is sufficient information retained in the otolith record to describe the differences in length of individual cohorts for ages 2–6 in the absence of data from a particular year (Figure 4.4). At older ages, the effect of individual fish heavily influences the estimates, and the estimates for

a year diverge for analyses with and without that year. At age 6, the jackknife estimates are still consistent but match observed values poorly, most likely because of the small sample numbers.

At ages 0 and 1, apart from the last year of the simulation, jackknife estimates are also consistent, but they differ proportionally from the observed values most likely because of size selectivity of the sampling gear used in the collection. This is also undoubtedly why the estimates diverge in the final year. In other years and for other ages, the size-selective bias has been reduced by the use of additional information on mean length-at-age from the smaller members of the cohort, because they have become fully selected at older ages. This divergence from the observed values at ages 0 and 1 should therefore not be interpreted as bias in the analysis, but rather as bias in the samples at these ages.

Quantitatively, the increase in information extracted is substantial in this case for the direct length-at-age, and more so for the increment analysis. However, the flexibility of GAMs in general makes them susceptible to outliers and multicollinearity (Hastie and Tibshirani, 1990; Chapters 2 and 5), particularly in the absence of a known error structure. In this case, there was little evidence of an increase in the bias of the increment analysis as a trade-off for the greater information density extracted compared with the direct length-at-age analysis. In fact, the former estimates provide less biased estimates of standard deviation, so the mean estimates must ultimately be more accurate as well as more efficient, justifying the increased model constraint over the degrees of freedom suggested by the AIC alone.

There is an additional labour cost in terms of measuring increment sizes, particularly for species where age determination may not require sectioning for age determination alone. This cost seems small though when compared with the cost of the assessment process as a whole, and indeed compared with the cost of managing stocks on the basis of biased assessments. The benefit of increment analysis is that it allows the construction of longer historical time-series of length-at-age where data are few or intermittent, greatly increasing the parsimony of modern stock assessment models burdened by estimating large numbers of parameters. However in situations where a well planned and executed sampling program has been in place for a considerable time the analysis is unlikely to yield significantly different results. It may be possible to reduce future sampling program costs if the additional cost in sample collection outweighs increases in otolith preparation and analysis expenditure.

Standard deviation estimates

For length-based assessment models, estimation of the variation in length-at-age is as important as the estimates of the mean. The residuals of both the direct length-at-age and the increment analyses show a small degree of positive skew but the effect is small, so given the large sample sizes (central limit theorem), the standard deviation estimates provide a convenient method to describe the population variance in lengths-at-age found. Both analyses indicate that variation in length increases with age, as expected given the cumulative effect of random variation of growth over time. The reduction in variance at the oldest ages, particularly in the IR, is interpreted here as an underestimate of the true population variance attributable to the very small sample numbers at the older ages.

Generally, the increment analysis estimates of standard deviation are slightly larger than those obtained from direct length-at-age analysis, but consistent at the overall sampling levels in each estuary, particularly for those ages well represented in the samples. Bootstrapping the methods confirmed that the direct length-at-age method tended to underestimate variance where samples were few, whereas precision in the increment analysis decreased at these small sample numbers. Both methods provide significantly better estimates of population variance than the yearly means method, which significantly underestimates variance at small sample sizes owing to overfit data as a result of insufficient constraints.

A significant portion of the variance is present at the youngest ages. Greater increases in variation in females than males at age may reflect larger differences in growth rates between individuals through greater asynchrony in maturation and different reproductive strategies between sexes (Chapter 3).

Biology of spotted seatrout:

Spotted seatrout females grow faster than males, consistent with the findings of others (Murphy and Taylor, 1994; DeVries et al., 1997, Nieland et al., 2002), but the current results also show asymptotic growth in both sexes. This is most obvious in CH and least obvious in the IR. Using the more appropriate error structure, accounting for intra-annual variation, and model-free spline estimation has allowed detection of this effect both in the direct length-at-age analysis and in the increment analysis. Although it has been possible to prove that such variation exists and that growth is asymptotic in both sexes, the consequence of these findings on assessments and subsequent management actions are unpredictable, but they do have the potential to improve management of the species substantially.

Florida spotted seatrout populations have an unusual seasonal pattern of growth, with most of the increase in length during the second half of the year. This is not an artefact of the analysis, size-selective migration or mortality, but a true biological effect at the level of the individual. One explanation may be that seatrout are serial spawners (Brown-Peterson et al., 1998) capable of frequent reproductive output spread over a long period (Roumillat and Brouwer, 2004; Chapter 4). The metabolic cost of such a reproductive strategy, particularly at a period of the year when temperature may be metabolically suboptimal, may leave little energy for somatic growth during the summer spawning season. Length frequency information from the fishery is therefore likely to be highly dependent on the time of year the data are collected and this fact should be considered in the assessment process along with choices of age-length keys and growth functional relationships in use in some of the models.

The linear contribution of otolith radius to the model describing fish length is larger than the contribution of the other variables put together, indicating that a large part of the information on somatic growth of a seatrout is retained in its otolith record. Yet, decoupling of otolith and somatic growth is substantial, seasonally, by age and by sex, as predicted by many previous investigators (Hare and Cowen, 1994; Sirois et al., 1998; Morita and Matsuishi, 2001; Schirripa, 2002). This suggests that for this species, all based methodologies, body- or scale-proportional, are likely to produce significant biases in the estimation of past lengths of an individual or for the population, if samples were not collected at random. Decoupling by cohort, although significant, is

small in comparison, and not independent of otolith accretion, so it might be possible to reconstruct individual growth histories based on more complex non-linear models for spotted seatrout.

Variation in fish size was sufficiently small to detect a relationship between the residuals from the size of the initial increment and the deviation from the mean predicted length-at-age from the increment analysis. The relationship with a positive slope suggests that for spotted seatrout, growth advantages gained early in life are generally maintained throughout life, in contrast to the findings of Živkov (1996), who found that compensatory growth mechanisms not linked to changes in the otolith growth rate tended to invalidate back-calculation as a means of reconstructing growth histories. The linearity of the relationship between the size of the first increment and the length residual suggests that it is not differences between the growth rate of individuals, but rather differences in age (differences in the time of hatching within a cohort), because of the protracted spawning period (Brown-Peterson et al., 1988; Nieland et al., 2002; Wuenschel et al., 2004; Chapter 3), also reflected in the recruitment patterns of juveniles (Chapter 2), that differentiate between small and large individuals. As Francis (1995) postulated, individuals do not start from the same conditions, so back-calculation methods based on a single starting point for the whole population are likely to produce biased results for small and large spotted seatrout. However, the level of variation is large, and its source cannot be traced back to either variation in growth rate of an individual, measurement error or process error (decoupling), with only a single measurement of the length of an individual.

Data examined here on length-at-age, along with evidence on the relative abundance of juveniles (Chapter 2) and reproductive dynamics (Chapter 3) indicate a number of population-specific trends in spotted seatrout. Genetic information suggests that the most proximate populations, CH and TB are genetically most distinct (Ward et al., 2007), and Iversen and Tabb (1962) suggested that movement between populations was minimal, through tagging experiments. All this points to distinct meta-populations unaccounted for in the current stock assessment methodology that may overestimate the resilience of the management unit to exploitation. Although in the long-term, management treating the stocks separately may not be practical, the sensitivity to the fully mixed population assumption does need to be investigated in light of these results.

Implications for management

The growth model developed provides new information for fisheries managers regarding the size distribution of individuals in a given year, and as such may provide an important link with the reproductive model, which requires estimates of size-at-age to determine reproductive output in an integrated size-based approach to stock assessment, as well as allowing for greater temporal resolution in the estimate of cohort strength than the current age-based model. The use of such information to conservation managers is more difficult to determine. Certainly, if persistence of the species is the only objective, the size of its individuals is unlikely to be of great significance beyond its effect on maturity and fecundity. However, the ability to compare growth in different populations or locations, when coupled with otolith chemistry techniques able to identify the origin of an individual (Comyns et al., 2008), may present important clues to the environmental impact on seatrout growth.

Unfortunately, the present model relies heavily on the assumption that individual seatrout within an estuary are exposed to similar environmental conditions, which is unlikely to be true given the variability of the estuarine environment and its effect on growth in seatrout (Smith et al., 2008). Nor can the model predict how future cohorts, not yet observed, will respond to changes in environmental conditions, because it uses “proxy” variables such as year and cohort to describe the effects of the environment on otolith growth and the relationship between otolith growth and somatic growth.

Although it is practical to do so for fisheries managers when no other information is available, for conservation managers, understanding the underlying processes is paramount to utilizing models such as the growth model and to a lesser degree the habitat model to their full potential.

In practice, relating cumulative effects to a number of environmental variables is difficult, because the functional forms of many of these relationships are unknown (Chapter 4). Temperature effects leave signatures in the stable isotope composition in the otoliths of fish, so certainly it would be possible to start examining temperature effects immediately. Other effects such as salinity and quantitative estimates of food consumption can be monitored using archival storage tags, or in experimental set-ups, where metabolic activity is more easily measured directly. Therefore, although the present increment analysis presents little opportunity for improving conservation advice, it does provide evidence that with further work it could be possible to provide conservation managers with the necessary understanding of the processes driving seatrout growth and the links to habitat quality and value that are associated with such results.

Table 4.1. Model parameterisation and results of each model developed. Negative residual deviances for the increment models are caused by arithmetic difficulties with 0-size increments and the log-link function. This is reflected in the larger dispersion parameter for the Gamma distribution estimated by S-Plus. This invalidates the use of the deviance residual, but not the analysis as a whole.

ANOVA Table for Length:						ANOVA table for Otolith Radii					
	Df	SS	MS	F	P		Df	SS	MS	F	P
Bay	2	3787435	1893718	555.39	0	Bay	2	18.16	9.08	227.52	0
Sex	1	6813897	6813897	1998.36	0	Sex	1	6.28	6.28	157.25	0
FactAge	9	43386599	4820733	1413.81	0	FactAge	9	1803.70	200.41	5021.65	0
Residuals	9700	33074471	3410			Residuals	9700	387.12	0.04		

Tukey's comparison for differences between populations					Tukey's comparison for differences between populations				
	Estimate	Std.Error	lower bound	upper bound		Estimate	Std.Error	lower bound	upper bound
CH-IR	-8.69	2.61	-14.80	-2.58 ****	CH-IR	0.07260	0.00892	0.05170	0.09350 ****
CH-TB	11.20	2.72	4.84	17.60 ****	CH-TB	0.07720	0.00930	0.05540	0.09900 ****
IR-TB	19.90	1.35	16.80	23.10 ****	IR-TB	0.00458	0.00461	-0.00621	0.01540

Table 4.1: ANOVA summary results for and pair-wise comparisons for length and otolith radius between populations

Table 4.2. Temporal, spatial and gender distribution of age samples indicating the imbalance in the sampling numbers between estuaries and sexes.

Model by estuary	Degrees of freedom		Sex	Radius	Day of the Age	Year	Cohort	Model total	Residual	Deviance		Dispersion coefficient for Gamma		
	Intercept	Bay								Total	Residual		% explained	
direct length-at-age analysis														
CH	1	--	1	--	spline 4	spline 4	6	14	29	522	23.34	5.44	76.69	0.011
IR	1	--	1	--	spline 4	spline 4	6	14	29	6264	371.00	109.36	70.47	0.017
TB	1	--	1	--	spline 4	spline 4	8	14	31	2834	132.19	29.27	77.86	0.010
Increment analysis: Increment submodel														
CH	1	--	1	--	spline 4	spline 4	15	--	24	1853	794.69	-94.81	--	0.094
IR	1	--	1	--	spline 4	spline 4	15	--	24	23425	9417.45	-814.92	--	0.106
TB	1	--	1	--	spline 4	spline 4	15	--	24	10130	3660.68	-3541.44	--	0.283
Increment analysis: back-calculation submodel														
CH	1	--	1	--	linear 1	spline 4	--	14	24	527	23.34	4.36	81.32	0.008
IR	1	--	1	--	linear 1	spline 4	--	14	24	6270	371.00	77.59	79.09	0.012
TB	1	--	1	--	linear 1	spline 4	--	14	24	2841	132.19	23.65	82.11	0.008

Table 4.2: Model parameterisation and results of each model developed. Negative residual deviances for the increment models are caused by arithmetic difficulties with 0-size increments and the loglink function. This is reflected in the larger dispersion parameter for the Gamma distribution estimated by S-Plus. This invalidates the use of the deviance residual, \hat{b} not the analysis as a whole.

Table 4.3. ANOVA summary results for and pair-wise comparisons for length and otolith radius between populations

Age	Charlotte Harbor Females										Total	Charlotte Harbor Males										Total									
	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001		1992	1993	1994	1995	1996	1997	1998	1999	2000	2001										
0	0	0	2	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
1	0	0	19	2	3	7	9	13	3	0	0	0	41	2	1	6	4	5	6	0	56	7	0	12	4	2	4	9	10	11	0
2	59	0	3	9	4	5	17	8	22	0	20	0	5	1	1	0	4	11	5	0	127	9	0	1	0	0	1	2	4	4	0
3	63	0	15	6	1	7	5	11	6	0	32	0	1	0	0	1	2	4	4	0	114	2	0	0	0	0	1	1	0	0	0
4	16	0	3	0	0	4	1	4	4	0	12	0	0	0	0	1	0	0	0	0	32	1	0	0	0	0	0	0	0	0	0
5	5	0	1	0	0	4	0	1	1	0	5	0	0	1	0	0	0	1	0	0	12	1	0	0	0	0	0	0	0	0	0
6	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	147	0	43	17	8	27	33	37	36	0	348	40	0	62	9	4	12	20	31	26	0										

Age	Indian River Females										Total	Indian River Males										Total									
	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001		1992	1993	1994	1995	1996	1997	1998	1999	2000	2001										
0	0	0	0	1	7	2	7	0	0	0	0	0	2	0	0	0	1	0	0	0	17	0	0	0	0	0	0	0	0	0	0
1	23	18	22	27	293	116	93	7	0	0	26	46	72	16	51	16	70	3	0	0	599	0	4	15	3	0	0	0	0	0	0
2	170	270	239	163	553	306	68	33	0	0	44	68	88	18	110	30	74	7	0	0	1802	32	36	32	25	48	37	0	0	0	0
3	138	329	180	226	369	257	12	32	0	0	17	15	16	7	197	51	12	1	0	0	1543	0	0	0	0	0	0	0	0	0	0
4	59	137	72	191	85	132	7	4	0	0	0	0	0	0	23	17	0	0	0	0	687	0	0	0	0	0	0	0	0	0	0
5	18	50	20	53	44	24	2	0	0	0	0	0	0	0	0	0	0	0	0	0	211	0	0	0	0	0	0	0	0	0	0
6	5	8	4	8	10	7	1	0	0	0	0	0	0	0	10	2	1	0	0	0	43	0	0	0	0	0	0	0	0	0	0
7	3	3	1	1	2	4	2	0	0	0	0	0	0	0	0	1	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0
8	2	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	418	815	539	670	1363	849	192	76	0	0	4922	130	175	228	77	439	155	158	11	0	0										

Age	Tampa Bay Females										Total	Tampa Bay Males										Total									
	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001		1992	1993	1994	1995	1996	1997	1998	1999	2000	2001										
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Chapter 4 Back-calculation

Table 4.4. Estimated mean length-at-age and standard deviation from the increment Analysis by sex, year and age for the three estuaries.

Table with columns for Sex (Female, Male), Estuary (Charlotte Harbor, Indian River, Tampa Bay), and Age (Age 0 to Age 9). Rows list years from 1985 to 2001, with a 'SD' row for standard deviation. Each cell contains mean length-at-age and standard deviation values.

Table 4.4. Estimated mean length-at-age and standard deviation from the increment Analysis by sex, year and age for the three estuaries.

Table 4.5. Estimated mean length-at-age and standard deviation from the length GAM Analysis by sex, year and age for the three estuaries.

		Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9	
Charlotte Harbor												
Females	1992	286.85	351.01	391.27	443.32	480.75	546.27	610.94	460.22			
	1993											
	1994	240.08	294.61	354.88	411.76	445.92	483.20	477.38	512.34			
	1995	261.10	300.52	360.18	421.21	489.07	506.18	522.87	511.82			
	1996	263.37	318.19	357.69	416.19	487.06	540.47	533.24	545.76			
	1997	259.04	303.53	358.15	390.87	455.12	509.02	538.44	526.35			
	1998	264.82	314.13	359.50	411.82	449.76	500.49	533.61	559.26			
	1999	289.62	327.77	379.73	421.89	483.64	504.80	535.49	565.67			
	2000	289.62	327.27	361.74	406.86	452.36	495.59	493.10	518.27			
	StDev	31.94	33.95	50.98	48.58	43.36	43.08					
	Males	1992	248.14	303.64	338.48	383.51	415.88	472.56	528.51	398.12		
1993												
1994		207.68	254.86	307.00	356.20	385.75	418.00	412.97	443.21			
1995		225.87	259.97	311.58	364.38	423.08	437.88	452.32	442.76			
1996		227.83	275.26	309.43	360.04	421.34	467.54	461.29	472.12			
1997		224.08	262.57	309.82	338.13	393.71	440.33	465.79	455.33			
1998		229.09	271.74	310.99	356.25	389.07	432.96	461.61	483.80			
1999		250.54	283.54	328.49	364.97	418.38	436.68	463.23	489.34			
2000		250.54	283.11	312.93	351.96	391.32	428.72	426.57	448.34			
StDev		23.59	32.10	33.79	32.60	49.18	53.20					
Indian River												
Females	1992	312.25	357.92	415.96	472.06	532.71	548.91	560.67	630.31	689.10		
	1993	288.64	368.48	416.60	471.15	518.81	574.18	584.95	592.58	664.24	725.58	
	1994	278.64	335.16	422.01	464.32	509.51	550.23	602.07	608.34	614.47	688.20	
	1995	266.50	334.38	396.72	486.12	518.96	558.48	596.30	647.13	651.96	657.98	
	1996	228.51	308.56	381.88	440.90	524.20	548.82	583.95	618.37	669.12	673.55	
	1997	217.02	273.93	364.83	439.39	492.23	573.94	594.11	626.95	661.97	715.70	
	1998	195.56	241.39	300.53	389.51	455.17	500.08	576.50	591.87	622.76	657.00	
	1999	195.56	264.34	321.83	389.92	490.35	561.97	610.43	697.95	714.45	751.12	
	StDev	47.12	48.86	60.41	65.38	66.87	66.79	72.22	19.22			
	Males	1992	267.95	307.14	356.94	405.08	457.12	471.02	481.11	540.87	591.32	
		1993	247.68	316.19	357.49	404.30	445.19	492.71	501.95	508.50	569.99	622.63
1994		239.10	287.60	362.13	398.44	437.21	472.16	516.64	522.02	527.28	590.55	
1995		228.68	286.94	340.43	417.14	445.32	479.24	511.69	555.31	559.45	564.62	
1996		196.09	264.78	327.69	378.34	449.82	470.94	501.09	530.63	574.18	577.98	
1997		186.22	235.06	313.06	377.05	422.38	492.50	509.81	537.99	568.04	614.15	
1998		167.81	207.14	257.88	334.24	390.59	429.12	494.70	507.89	534.39	563.78	
1999		167.81	226.83	276.17	334.59	420.78	482.23	523.82	598.92	613.08	644.54	
StDev		38.29	40.31	44.28	55.90	64.14	64.06	101.18	10.93	19.28		
Tampa Bay												
Females		1992	275.47	330.41	395.45	427.07	468.34	532.26	477.69	391.99	416.17	442.59
	1993	292.17	344.21	404.24	468.41	492.39	530.44	593.92	531.53	436.56	464.27	
	1994	272.48	327.46	377.74	429.49	484.41	500.22	530.91	592.78	530.98	436.84	
	1995	286.34	338.64	398.48	445.02	492.51	545.68	555.16	587.57	656.62	589.16	
	1996	251.04	305.95	354.29	403.61	438.75	477.00	520.68	528.24	559.57	626.38	
	1997	249.99	297.90	355.49	398.54	441.93	471.92	505.48	550.22	558.70	592.84	
	1998	258.00	320.91	374.43	432.58	472.05	514.20	540.98	577.82	629.52	640.30	
	1999	260.48	308.21	375.36	424.01	476.82	511.13	548.55	575.50	615.23	671.40	
	2000	242.88	298.05	345.30	407.14	447.66	494.53	522.28	558.94	586.91	628.49	
	2001	242.88	289.32	347.62	389.91	447.49	483.34	526.05	554.01	593.42	624.18	
	StDev	34.83	37.11	42.16	50.03	55.02	63.60	85.26				
Males	1992	240.87	288.90	345.78	373.42	409.51	465.40	417.69	342.75	363.90	387.00	
	1993	255.47	300.98	353.47	409.57	430.54	463.81	519.32	464.77	381.72	405.96	
	1994	238.26	286.33	330.30	375.54	423.56	437.39	464.23	518.32	464.29	381.97	
	1995	250.37	296.10	348.43	389.12	430.65	477.14	485.43	513.77	574.14	515.16	
	1996	219.51	267.52	309.79	352.91	383.64	417.08	455.28	461.89	489.28	547.70	
	1997	218.59	260.48	310.84	348.48	386.42	412.65	441.99	481.11	488.52	518.37	
	1998	225.60	280.60	327.40	378.24	412.76	449.62	473.03	505.24	550.45	559.88	
	1999	227.76	269.49	328.21	370.75	416.92	446.93	479.65	503.21	537.95	587.07	
	2000	212.37	260.61	301.93	356.00	391.43	432.41	456.68	488.73	513.19	549.55	
	2001	212.37	252.98	303.96	340.93	391.28	422.63	459.97	484.42	518.88	545.77	
	StDev	26.05	27.54	32.65	32.39	37.15	45.66	38.58				

Table 4.5: Estimated mean length-at-age and standard deviation from the length GAM Analysis by sex, year and age for the three estuaries.

Chapter 5: How robust are generalized additive models to changes in sampling design, and how sensitive are they to the underlying assumptions made for the purpose of management?

Introduction

Generalized additive models (GAMs) were first developed to explore the relationship between variables, when the functional form of the relationship, or knowledge of whether one existed at all, was unknown. The intent was not for them to be used per se, but the idea was that once the form of a relationship was known, to substitute the flexible, model-free spline function with an appropriate mathematical formula (Hastie and Tibshirani, 1990). Consequently, the GAM is also frequently placed in the “data mining tool” category, which somewhat belies its statistical heritage firmly based in regression theory, as emphasized by the fact that when using simple linear components and a Gaussian error structure, the results are identical to those from a linear regression analysis. At the complex end of GAMs, they can include factor variables, modelled as linear pseudo-variables, smoothing functions that make inference about the variability at a local level along a gradient, and they can accommodate a wide variety of error structures using the appropriate likelihood function. The resultant characteristics make them very flexible and applicable to a wide variety of situations, so it is not surprising that they have found their way into fisheries science (Swartzman et al., 1995; Maravelias et al., 2000; Loots et al., 2007; Wang et al., 2009), but in general their performance has not been reviewed in detail.

Fisheries science has produced some large long-term datasets for very specific purposes, but there is the feeling that some of these have been underutilized and that important additional information still remains to be discovered. This too was part of the motivation for starting this dissertation and I have used GAMs throughout, so it is only fitting that I take the opportunity now to re-evaluate, with hindsight, some of the choices I made early on with regards to the statistical approach taken in Chapter 2. This final chapter reviews the results with respect to new data, summarizes the lessons learned in more detail than was possible in the actual publication.

Chapter 2 describes a set of models that evaluate critical habitat for juvenile spotted seatrout in three Florida populations based on a 4-year time-series. Although a longer time-series of fisheries-independent data was available, the effects of gear and sampling design changes were uncertain, and this period was thought to comprise a reasonably consistent period with large annual sampling effort. In 2010, a much longer time-series became available, facilitating a re-evaluation of the model in terms of its ability to predict the distribution of seatrout in respect to the environmental covariables, but also to explore the robustness and the underlying model assumptions regarding its use as a predictor of recruitment in stock assessments.

Material and Methods

Sampling design changes

The sampling protocol and statistical methodology used are the same as that described in Chapter 2, but the survey design, and to a lesser degree the recording of some of the environmental variables has changed over time. A detailed timeline of the monitoring data for each estuary provided by the fisheries-independent monitoring program (Doug Adams, pers. com) is available from their website but a brief summary is given here by estuary, highlighting the most pertinent changes.

Indian River (IR)

Sampling effort increased proportionally by stratum from 1990 to 1995 from levels just below 20 samples per stratum to just under 50. Samples were collected biannually in spring and autumn. In 1996, sampling was altered to a monthly periodicity with a commensurate increase in effort to between 80 and 100 samples per stratum per year. The monthly sampling returned to seasonal sampling protocols, with little effort in the most northern strata, but with monthly sampling maintained in the southern region and in the Kennedy Space Center Wildlife Reserve. In addition a southern stratum, covering one of the major inlets to the lagoon, was included for monthly sampling. Sampling intensity was 48 samples per stratum per year. Prior to 2001 no freshwater river systems were sampled in the IR, but sampling levels in these tributary river systems increased from 72 samples per year (2001–2003) to about 350 samples per year, so that the IR monitoring program is now more freshwater-based than marine, reflecting the increased concern over freshwater run-off and pollution in the system (Sime, 2005).

Charlotte Harbour (CH)

From 1989 to 1994, 28 samples per year were collected in each of the inner bay strata in a biannual stratified random design, following which effort increased to around 1000 samples a year from 1995 to 1997, collected monthly. In 1998 effort returned to 1995 levels, after which it remained constant except in the upper bay, where it increased to 60 samples from 2004 on. Changes in the sampling design for the inner bay strata are therefore similar to those given for TB below, as are the sampling levels in the tributary systems. Several samples were also collected in the outer bay stratum from 1994 to 1997 in line with effort levels observed in the inner bay, but sampling ceased there from 1998 until the end of 2003.

Tampa Bay (TB)

From 1989 to 1994, nearly 30 stratified random samples were collected biannually per stratum within the bay, increasing to about 50 in 1995 and ~100 in 1996 and 1997, before dropping again to 1995 levels in 1998, after which the number remained constant until 2008. Sampling levels in the tributary river systems were low until 1995, when they rapidly increased to comparable levels to sampling in the bay in 1996 and 1997, but unlike the bay strata, sampling levels did not decline in these river systems since, so sampling effort has increased proportionally in the rivers.

Conservation

The effect of sampling design on accuracy of the estimated environmental preferences of seatrout

Two principal analyses were conducted. The first was to determine the effect of the data from tributary river systems in the analysis of statistical habitat suitability models. The approach here was to compare the models qualitatively with the original ones developed in Chapter 2, but using only data from 1996 to 1999 (with the original bottom type classification) to evaluate whether the additional data significantly altered the conclusions for conservation management. In addition, the results are discussed specifically in the context of the increased sampling of rivers in terms of the pertinent effects of salinity and depth between models developed using solely the bay strata with those using all data, and to make inferences across the different populations.

Fisheries management

Robustness of the year-effect to sampling design changes

The second evaluation aimed to investigate the effect of changes to the sampling design with respect to the year variable. The early part of the time-series of data was collected biannually, and the conclusions during the development of the original models were that this change was only partially reflected in the other covariables, so that the design change directly affected the assessment of cohort strength. As additional data are likely to define the effects of the covariables better, it is important to investigate whether the year-effect is robust to such changes in sampling design. Results from the whole time-series are compared with those from 1998 on and from the period used in the original models for the years 1996–1999, using the new bottom type classification throughout. The long-term index was compared with that currently used in the assessment, the mean abundance, and the estimated pattern of recruitment from the assessment.

Assumptions

The assumption of such an index is that abundance changes uniformly across all environmental gradients on the scale of the additive predictor. In other words, if abundance doubles from one year to the next at one temperature, it also changes proportionally at all other temperatures whether or not these conditions were observed. The breadth of the realized niche is assumed to be independent of abundance. This is contrary to the general ecological theory about competition and resource limitation, but may still be applicable, when either the realized niche is equal to the potential niche, or when individuals are restricted in their movements so that the ideal free distribution never arises and resources are not limiting in any part of the realized niche. For various reasons, the latter is assumed for juvenile seatrout, but an attempt is made to test for this.

If strong cohorts utilize the same realized niche (i.e. the same spatial area in a constant environment) as weak cohorts, then clearly the average abundance in a sample increases, but assuming sufficiently large samples, the probability of observing seatrout in random samples throughout the whole estuary will not change. In other words, it would be independent of the numbers of individuals in a cohort. If on the other hand the

probability increases with increasing cohort strength, it would suggest that additional environments in the potential niche are being exploited as resources become limiting. Unfortunately, such a direct comparison is only valid when the same environmental conditions are sampled each year, and that is not the case here because of the stratified random sampling design.

A relative estimate can be made if the estimate of cohort strength could be corrected for the environmental conditions sampled. This is not possible at an individual sample level, because of the random error term, but an annual estimate of the average habitat quality sampled can be derived from the difference between the observed mean abundance and that predicted for a cohort.

If sampling conditions were better in one year than the overall average conditions, the mean observed abundance would be higher than the model fit (because the latter accounts for the favourable sampling conditions) and the difference (mean – fit) is positive. Similarly in the years randomly oversampling favourable conditions, the probability of observing seatrout in samples should be greater, because a greater proportion of the suitable habitat has been sampled. In years where poor conditions were randomly selected, the difference (mean – fit) is negative and the probability of catching a seatrout lower.

Plotting the observed probability against the mean standardized estimates of the fit, the estimate of cohort strength and the quality of sampled habitat, the difference between observed mean and the model fit allows for a qualitative examination of the niche breadth independent of the environmental conditions sampled.

Results

Conservation

Original and updated model comparison

To determine the effects of using the whole time-series compared with the 4-year series used in Chapter 2, the new IR model using only bay data was compared, because in 1996-1999 no river data were collected in IR. For CH and TB models, the river data were included in the original model, so the complete dataset is used here although the relative proportion of the samples from the rivers has increased in both systems.

	Original	Update incl. rivers	Update bay only
CH	36.6% (1839)	37.0% (6499)	38.6% (4684)
IR	42.5% (1578)	48.2% (4905)	48.2% (3520)
TB	44.0% (2683)	43.3% (8362)	49.1% (4646)

Table 5.1. Percentage deviance explained and the residual degrees of freedom in parenthesis for the original model and the two update models for each estuary. Emboldened numbers indicate the most appropriate model comparison with the original model, given the changes to the survey designs in the different estuaries.

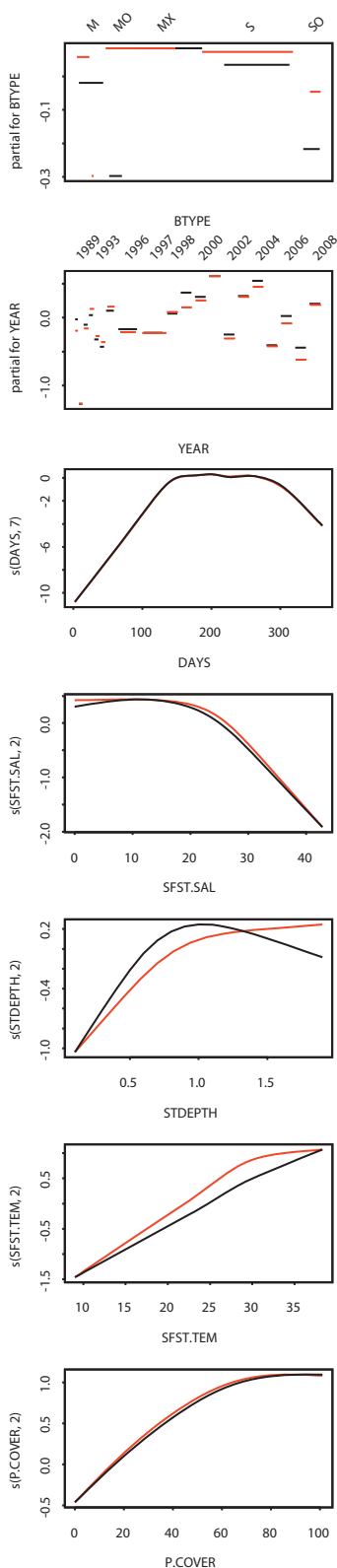


Figure 5.1. Comparison of updated habitat models based on GAMs using bay data only (red) and bay and river data (black) for the Indian River Lagoon. The model chosen for comparison with the original models (Figure 2.2) is the bay only (red) model as sampling of rivers had not commenced in 1999.

The overall percentage of the deviance explained by the models is shown in the table below. Over the main range of the data, where sample numbers are high, there is little difference in the prediction from the models as reflected by the comparison of the explained deviance estimates. Changes in the smoothed terms are mainly at the ends of the gradients where these have been extended by additional samples, which will effect estimates some distance towards the centre of the gradient.

In the IR the most obvious change is the temperature effect. In the original model (Figure 2.2) temperature reached an optimum at about 28°C whereas the updated model (Figure 5.1 red lines), although stabilising briefly at this level, now continues to rise, implying increased abundance up to the highest observed values of around 40°C, although data are sparse >35°C. Salinity implies a lower optimum salinity at around 15 psu, compared with previous values around 20 psu, but both models imply little difference in abundance over the range 10–20 psu. The effect of water depth now levels off at depths of >1 m, compared with the slow rise implied by the previous model.

The other smoothed terms show only minor changes from the original model. The day of the year variable implies that trends in abundance are relatively flat at their maximum between day 120 and 280 in both models, although the absolute maximum which used to occur in late spring now appears to have shifted to late summer. The percentage seagrass cover in the updated model implies slightly less of a decline in abundance at the highest densities of seagrass compared with the original model, but levels are still optimal at ~80% cover.

Factor variables imply some revisions, including differences in the ordering of bottom types, which may be due at least in part to the change in the way this variable is recorded. The main types in the data, sand and mud mix and sand, still yield the greatest abundances of seatrout. The year variable still retains the same ordering, with 1996 and 1997 being the poorer years and 1998 and 1999 the better ones, but the relative differences have changed with the distance between the earlier years and the later years increasing substantially.

All year ranges examined demonstrate a substantial increase in abundance of juveniles after 1997, the year that sampling in the northern regions of the IR was reduced to biannual sampling (Figure 5.2). This might suggest that the model was sensitive to these changes, although using data from just the southern regions over the whole time-series implies the same trend, with a reduced absolute difference between the abundances pre- and post-1998.

In CH, the most noticeable difference between the original and updated model is found in the contribution of depth. Optimal conditions are still observed at 1 m, but the magnitude of the effect has increased substantially over the observed range (Figures 2.4 and 5.3 black lines). The rate of decline at depths >1 m is still similar, but declines at the lower end of the gradient are now implied as being more severe than in the original model. The updated effect of temperature plateaus closer to 25°C, as opposed to 30°C in the original model, the seagrass effect rises more slowly but still levels off at around 80% cover, and salinity implies lesser abundance at lower salinity than before, but the difference is small.

Bottom type has been reordered as in the IR, but still sand, and sand mud mix are the preferred bottom types. The year effect was largely insensitive to the effects of the period used, suggesting that the model is well defined with respect to environmental covariables. The relative effect of year between the first two years and the last two years has increased and has resulted in a reordering of the index (Figure 5.4).

The most striking point about the comparison between the original and updated model in TB is the consistency (Figures 2.4 and 5.5). In the smoothed terms, there are some minor changes with regards to salinity, with abundances declining marginally less now at low salinity and percentage seagrass cover reaching its plateau nearer 80% as opposed to 60%. The order of the bottom type factors has changed as in the other estuaries. The effect of the additional data on annual fluctuations similar to CH displaces 1996 and 1997 downwards compared with 1998 and 1999. Originally, the year-effect was estimated to have the smallest effect of all the populations (Figures 2.2 – 2.4b), but it is estimated to be significantly larger over the same period now (Figure 5.6).

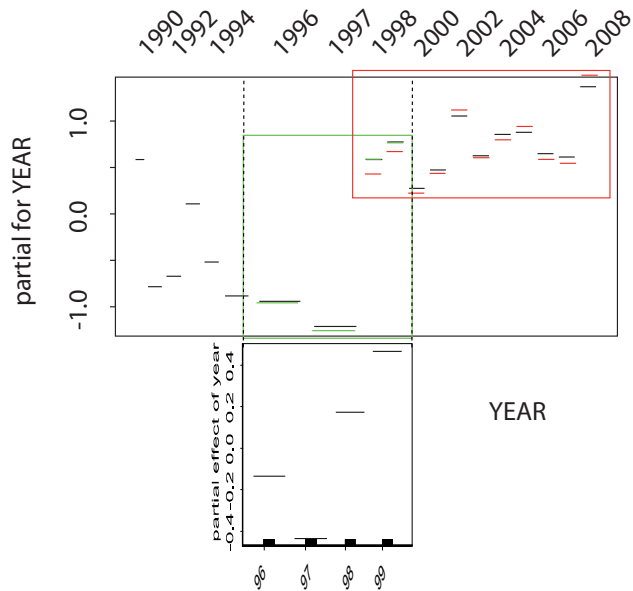


Figure 5.2. The effect of Indian River sampling design changes in the form of different periods of observations on the year effect for bay data only. In addition, the year effect of the original model, differing in the classification of bottom type is included for comparison.

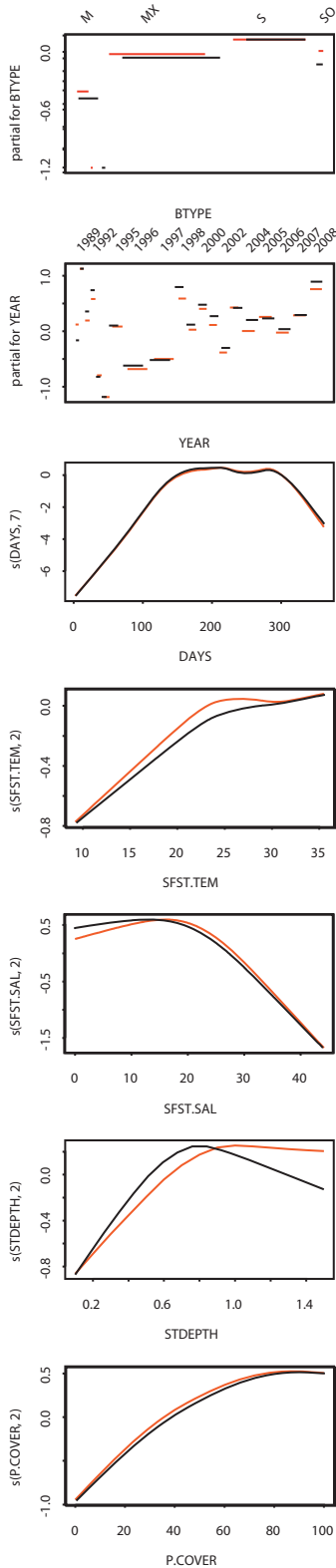


Figure 5.3. Comparison of updated habitat models based on GAMs using bay data only (red) and bay and river data (black) for Charlotte Harbor. The model chosen for comparison with the original models (Figure 2.4) is the bay and river (black) model as river data was included in the original models.

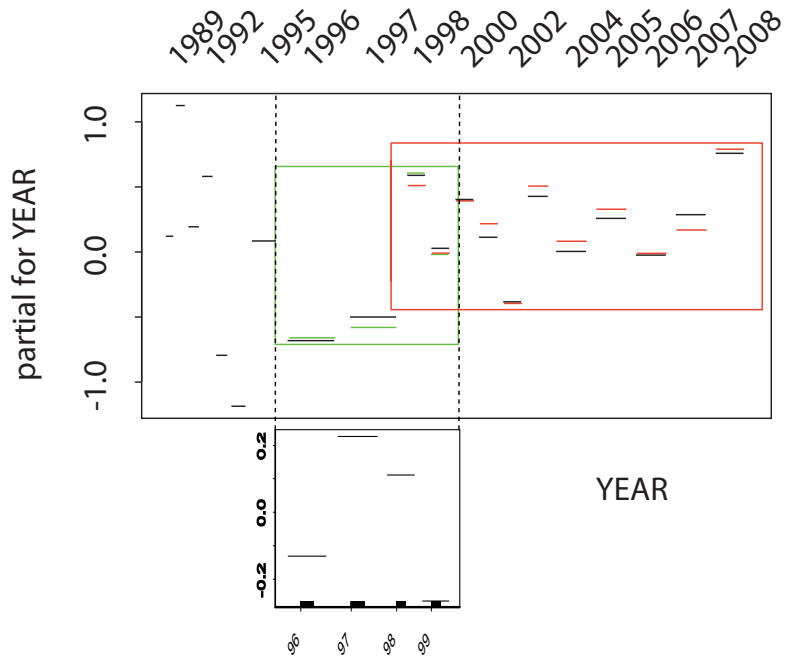


Figure 5.4. The effect of Charlotte Harbor sampling design changes in the form of different periods of observations on the year effect for bay data only. In addition, the year effect of the original model, differing in the classification of bottom type and inclusion of river data is included for comparison.

The effect of including river data in updated models

The effect of including river data in the TB models (Figure 5.3) over the whole time-series is surprisingly small. The largest differences observed are for the IR, which had the greatest proportional shift from bay to river sampling (Figure 5.1). At low salinity abundance declines more dramatically when the river data are included, and as depth increases above 1 m, abundances are estimated to decline in the absence of river data. In TB and CH, the effect is the same, although visibly less pronounced particularly for the salinity gradient (Figures 5.3 and 5.5).

The temperature effect is also affected by the inclusion of river data in the IR dataset. After increasing from low temperature, abundance stabilizes at between 25 and 30°, before rising again more sharply to a maximum of near 40° in both models, but the latter increase is steeper and more sustained in the bay-only model than when including river data. In TB the opposite is true; inclusion of river data lowers the predicted abundance at high temperatures, with little effect noticeable in CH.

Spline functions for bottom type, percentage seagrass cover, and day of the year are virtually unaffected in all estuaries, and factors such as bottom type and year are ordered equally in relation to each other, with slight variation in the relative distances.

Fisheries management

Robustness of the year-effect to sampling design changes

Given the additional uncertainty regarding seatrout distribution based on the inclusion of river data in conjunction with the disproportionate increase in sampling and the relatively small contribution that this environment is likely to have on seatrout recruitment, evaluation of robustness was based only on the bay data sources, so that the only original model consistent with this analysis is that for the IR, where river sampling did not commence until later.

The index of relative abundance was largely independent of the time-period examined in all populations (Figures 5.2, 5.4 and 5.6), but the importance of the effect in the model tended to increase with increasing numbers of years included, mainly because longer periods tended to include greater overall variability in recruitment, but also because the effects of the environmental covariables were more stable so that more of the variance could not be attributed to covariance among the other independent variables. This suggests that the longest index including the greatest variation in sampling conditions should also be the most robust, despite changes in the sampling design, and should be sufficiently robust to use in stock assessments as a measure of recruitment.

Assumptions

Examination of the niche breadth information indicates an increase in niche breadth with increasing cohort size for the IR, but an unexpected negative correlation with the sampled habitat quality indicator. The latter is heavily influenced by the years 1992–1997 (Figure 5.7a).

In CH, small increases in the probability of observing seatrout in samples in years of large cohort strength are implied by Figure 5.7b, although overall the fit is extremely poor and the 1991 cohort appears to have undue influence in the estimate of this gradient, as

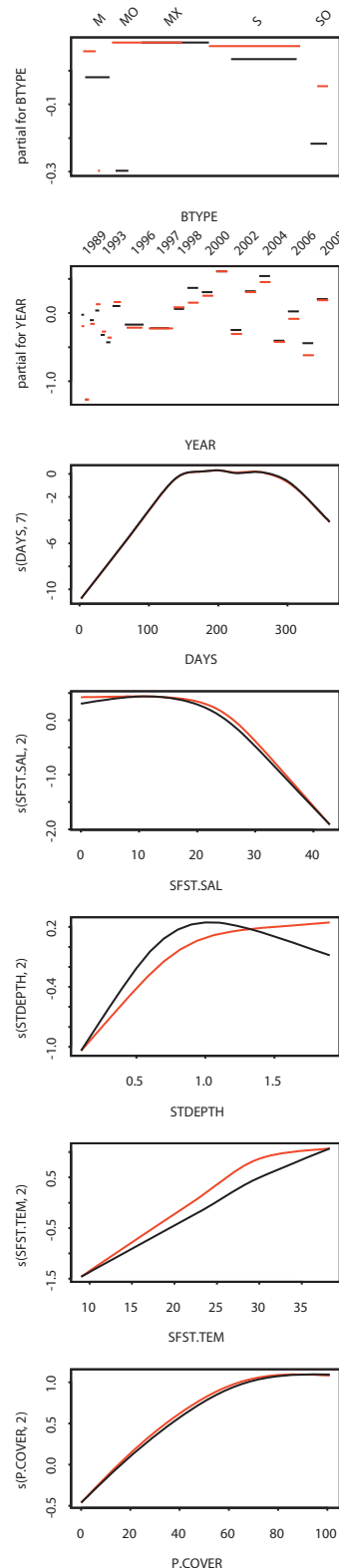


Figure 5.5. Comparison of updated habitat models based on GAMs using bay data only (red) and bay and river data (black) for Tampa Bay. The model chosen for comparison with the original models (Figure 2.3) is the bay and river (black) model as river data was included in the original models.

is the case for the habitat quality correction, the trend of which implies a faster increase in the probability than attributable to cohort strength alone.

The probability of observing seatrout in TB samples increases, both with cohort size and the quality of the conditions sampled at a similar rate, suggesting that there is no effective increase in the breadth of the sampling niche occupied by large or small cohorts (Figure 5.7c).

Comparison of the year-effect with other indices of recruitment

The IR index as calculated over the whole period estimates recruitment to have been generally poor and below the mean abundance estimates, with a substantial increase in abundance since 1997. This is in contrast to the index used in the assessment, which shows a decline in recruitment over the whole period, but it does match the general trend in the estimates of recruitment from the assessment, although the difference between high and low years is amplified. Tracking of individual cohorts between assessment and index is poor.

In CH, the index over the whole time-series suggests little long-term change in the abundance of juvenile seatrout. Strong cohorts in 1990 and 2008 and a succession of weaker ones from 1993 to 1997 are about the only contrast visible in the index, whereas the mean abundance estimates would suggest that there are a number of strong cohorts in the early period, after which the abundance in the samples generally declined. The survey index used in the assessment suggests slowly declining abundances, whereas the estimates of recruitment from the assessment indicate stable recruitment. There is no obvious cohort tracking between any of the indices.

For TB the index over the whole period is mostly consistent with the mean estimates where sampling has been comparable, but abundance in the samples for 1995–1997 was much higher than predicted by the model. The 1990 cohort was weak, with three recent cohorts (2001, 2003, 2004) being large. Aside from this there is relatively little variation in the estimates of cohort strength, consistent with the estimates of recruitment taken from the assessment.

Discussion

Overall, the models appear to be surprisingly resilient to changes in sampling designs. Small differences in model predictions between river and bay sampling are the result of covariance between the independent variables, mainly depth and salinity, and to a

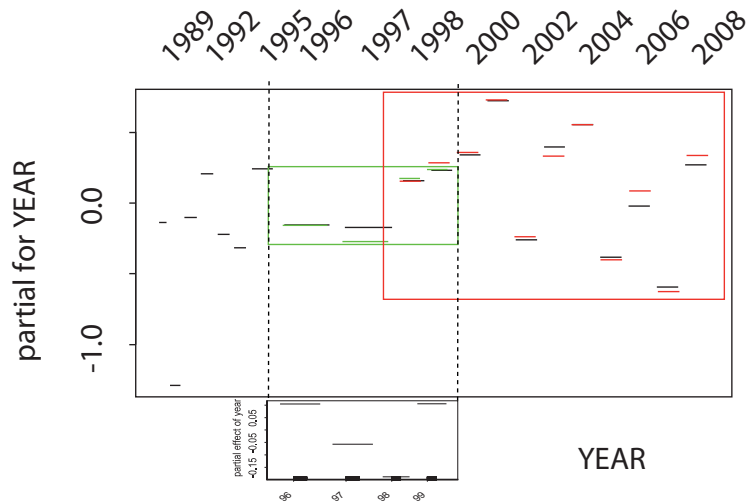


Figure 5.6. The effect of Tampa Bay sampling design changes in the form of different periods of observations on the year effect for bay data only. In addition, the year effect of the original model, differing in the classification of bottom type and inclusion of river data is included for comparison.

lesser extent temperature, possibly reflecting differences in the sampling methodology between these environments. As the relationship between abundance and environmental conditions is reasonably well defined, the index of relative abundance produced by the models is largely robust to the period of data used to develop the model, an important prerequisite to the use of the index as an estimate of cohort strength in an assessment.

Changes in the year-effect of the new models (1996–1999 using bay data only) compared with the original model (using bay and river data) were almost exclusively between 1997 and 1998, when there were significant changes in sampling design. In CH and TB, river sampling commenced then, and in the IR, sampling in the northern part of the system ceased. The impact was smallest in the IR with the order of the variables remaining the same, but in TB and CH the changes were more substantial. However, when considering the whole time-series, the effect of including river data on the year-effect is relatively small. Therefore it is the colinearity between year and sampled environmental conditions that drives the distribution of variance between the effects, highlighting the danger of using models based on inconsistent sampling designs over short periods (or small numbers of samples), but also suggesting that sampling levels and the range of conditions experienced over the full period are sufficient to attribute the variance components correctly. This is accomplished by reducing covariance in the independent variables to accommodate the significant changes in the sampling design observed in the dataset.

The analysis does highlight some dangers in the use of GAMs in providing management advice

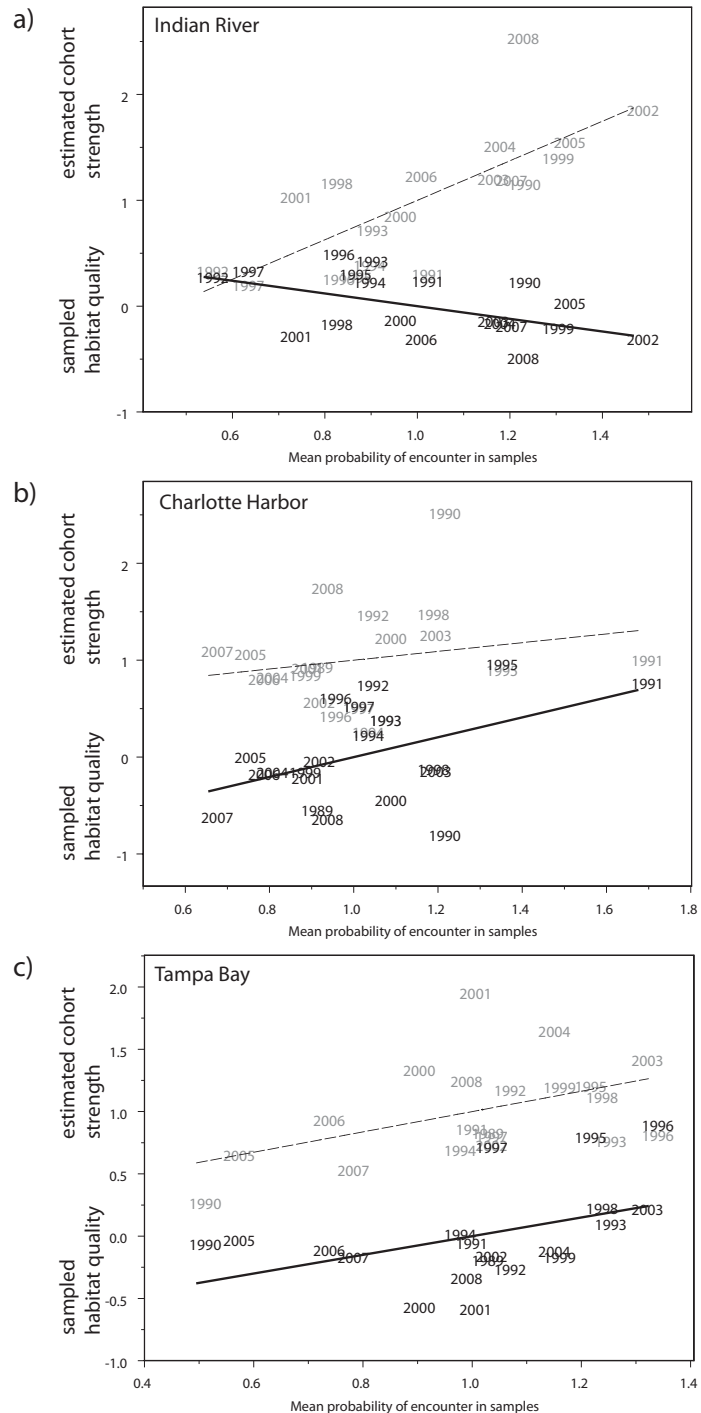


Figure 5.7. Relationship between the annual mean probability of capturing at least one seatrout and the sampled habitat quality (solid line: characterized as the difference between the mean abundance and the predicted abundance in a year), and the estimated cohort strength (dashed line) for a) Indian River, b) Charlotte Harbor, and c) Tampa Bay.

suggesting that careful consideration of the sampling design, of changes in that sampling design, and of the covariance of independent variables are essential when providing management advice. The important considerations for Florida seatrout management are considered separately from the conservation and sustainability aspect below, and are summarized as general considerations regarding the use of GAMs at the end of this chapter.

Conservation

Original and updated model comparison, and the effect of including river data in updated models

The statistical habitat-suitability models developed in this study are primarily designed to provide conservation managers with tools to determine habitat requirements of individual species and groups of species under threat, and to quantitatively prioritize their importance. For such tools to be effective, they have to be accurate not only in conveying the central tendencies, but also the variance or risk. GAMs can provide such quantitative estimates, but owing to their flexibility, are susceptible to bias caused by covariance in the independent variables and departures from the assumed error distribution.

Since the development of the original models described in Chapter 2, based on what was thought to be a reasonably consistent time-series, a much longer time-series of data has become available and provided the opportunity to examine the robustness of the models developed originally, and to ascertain their susceptibility to changes in sampling design of the monitoring data on which they are based. Answering these questions is important not only for seatrout conservation, but also to inform on the development of monitoring programs, the important characteristics of data sources, and some of the pitfalls to avoid in model development.

The models provided robust measures of the environmental space utilized by seatrout in each of the populations, and the updated models are even more consistent between populations than the original ones. For the entire time-series, this is largely true when comparing across models using only bay data, or across models using all data. When comparing models including and excluding river data, however, the covariance between salinity and depth, driven by the fact that deeper sites can be sampled by the gear in rivers, precludes the model from accurately attributing the variance in abundance at low salinity and large depth gradients, as postulated in Chapter 2. To a lesser extent, this is also true of the sampling design changes in the IR associated with the cessation of monthly sampling in the northern portion of the system.

This effect is severe when considering short subsets of the data where the sampling design has been inconsistent with regards to the inclusion of river data, although design changes from biannual to monthly sampling appear to have had less significant effects.

The described covariance has little effect on the overall deviance, or in predicting abundances at sites where the variables are equally correlated. Where it does present a problem is in extrapolating to areas not sampled, especially when sampling effort is not proportional to the area of the strata. Clearly, underpredicting the value to seatrout

of large areas of the deeper water in bays, on the basis of disproportionately larger numbers of samples collected in the spatially smaller rivers, will negatively bias estimates of the habitat value of an estuary as a whole as well as spatially within it.

If the collinearity is a gear effect only, then a re-evaluation of the survey design accounting for the differences in catchability can resolve the problem. If on the other hand the effect is attributable to differential behavioural strategies of seatrout in river and bay systems, then an interactive term in more complex models or separate models will be required to reflect the distribution accurately.

This conclusion highlights the dilemma faced by conservation managers when prioritizing limited funding under ever-changing political pressures. The move towards more riverine monitoring and the resultant decrease in bay sampling was driven by public concerns over water quality, and undoubtedly reduced the precision and accuracy of habitat models. From the perspective of seatrout conservation, however, this may not be of major consequence, because populations are generally less abundant in rivers and the rivers represent only a small part of the total area of the system. However, weighing up the relative merits of model choice for a species with high abundance in riverine areas and low abundance in bay areas will be much more difficult. Until the sources of the covariance can be determined, it would be best to exclude the river data from seatrout models, but to make it explicit that these models cannot be used to assess tributaries.

Fisheries management

The index of relative abundance is of interest to fisheries managers, both to assess recruitment as a direct measure of the state of the stock and as part of the stock assessment process, to provide estimates of stock productivity. The aim of such an index is to partition the sample variability caused by the stratified random sampling approach to monitoring from that attributable to the variability in recruitment abundance external to the assessment model.

From a survey design perspective, random sampling will always provide less biased estimates of abundance than other designs, such as disproportionate stratified random or fixed design, but usually this comes at the cost of significant decreases in precision when conditions are not homogenous across the sampling universe. Stratified random surveys, as implemented by the fisheries-independent monitoring program, are intended to reduce the variability by dividing the sampling universe into more homogenous subsets, or strata.

In general, natural systems are characterized by environmental gradients, rather than abrupt changes in conditions, so that further gains in precision can be achieved by accounting for gradients in conditions using estimates of the relationship between the response and measured environmental conditions, essentially a post-stratification process. Habitat models based on the GAMs developed in Chapter 2, and other forms of regression models describing abundance as a function of environmental covariables, provide such an index.

For the index to provide a robust measure of recruitment, it must fulfil three assumptions, orthogonality between the year-effect and the environmental covariables (it needs to be robust to changes in sampling design), realized niche breadth needs to be consistent

between years, and the variability in the average environmental conditions within a system across years have to be small in relation to its effect on abundance of seatrout. The following section sets out to evaluate whether such assumptions are reasonable for the populations examined here, and whether such indices will provide a useful index for use in the assessment process.

Robustness of the year-effect to sampling design changes

The model evaluation in the previous section suggested that the models for all three populations were unaffected with regards to the estimates of relative cohort strength irrespective of the period of data used to develop the model, provided sample numbers were large enough to cover the entirety of those gradients. The percentage explained was similar to those for the original model in CH and TB, with a >5% improvement in the IR model, indicating that the original models were not overfitted. However, all models explained less than half the deviance in the data overall, suggesting either that individual sample variability is high under identical conditions, or that important variables governing the distribution of seatrout are still missing from the models. Nevertheless the results do suggest that the year-effect is a robust measure of changes in relative abundance.

Assumptions

In all three populations, the probability of presence generally increases with increasing estimates of cohort strength, although the fit is poor particularly in CH. Sampling favourable conditions also expectedly increases the probability of observing seatrout in CH and TB, but implies a negative trend in the IR. Closer examination indicates that the years 1991–1997 are largely responsible for the negative trend. This corresponds to the period of sampling in the northern regions of the IR where lower salinities were encountered more frequently. It appears then that the differences in the environmental conditions encountered are not entirely accounted for in the model, and that consequently the difference in cohort abundance may be biased downwards for that period. However, using a model based on only the consistently sampled southern strata implies the same trends in cohort strength, so it is likely that the effect is mainly on the index of habitat quality sampled, rather than the index of abundance. Therefore, for neither the IR or the TB model, where capture probability increase at the same rate with cohort strength and habitat quality, is there any indication of broadening of the realized niche with increasing cohort size. In CH there is a suggestion of such broadening, but the fit is extremely poor and would likely only have influenced the large 1991 cohort.

Results then are consistent with the theory that seatrout are heavily exploited in Florida (Vanderkooy and Muller, 2003) and the juveniles are restricted by their size and affinity to seagrass patches, so the ideal free distribution, under which resource limitations would lead to broadening of the realized niche, is unlikely to be reached under current stock conditions. Consequently, the year index likely fulfils the assumption of a constant realized niche and should be sufficiently unbiased to use in the assessment process.

The abundance estimate described here has been corrected for random variability in sampling conditions and systematic changes in the sampling design, but it assumes that overall estuarine conditions are roughly equal over the years with regards to their effect on juvenile survival. Unfortunately, in the absence of independent data or suitably

detailed hydrodynamic models, it is not possible to distinguish interannual differences in the overall environmental conditions from those attributable to the random sampling design.

It is, however, safe to assume that such variation exists, particularly with regards to salinity. The sampling data certainly suggest that 1994 was a colder year in the more northern IR and TB estuaries, with the warmest years in the late 1990's and from 2004 to 2006 (Figure 5.8). Temperatures in CH followed similar trends, but the scale of variation was much less, with the dip in 1994 barely discernible. Salinities are most variable on an interannual basis in IR than on the Gulf coast, with low salinities observed from 1995 to 1997 and again in 2005 and 2006. Similar trends exist, but are less apparent, in CH and least so in TB. This variation is almost certainly linked to Florida-wide environmental fluctuations, rather than changes in sampling design.

Without having fine-scale spatial hydrodynamic models it is not possible to correct the index for such variation, but the range of observed mean temperature and salinity values is small compared with the length of the environmental gradients in the habitat models and is in parts of the environmental space where gradients are generally less steep, so the bias in the relative index, although underestimating variance in recruitment, should be relatively small.

Comparison of the year-effect with other indices of recruitment

Sampling design changes from biannual to monthly are likely fully accounted for in the index, whereas the addition of river data is only mostly accounted for and presents difficulties with regards to covariance, so should be excluded from an index until they are resolved. More dramatic changes in sampling design in terms of the loss of samples from the northern IR are more difficult to isolate, and it would probably be prudent to treat values of the index prior to 1997 with some caution. With caveats, it then becomes possible to use these indices of abundance based on bay data only as indicative of cohort strength over the period examined.

Comparison with estimates of recruitment from the assessments are complicated because the assessments are carried out by region, with the southwest region including both CH and TB and with the IR in the southeast region, but the area sampled only covering a relatively small proportion of the management unit.

In addition, the data used in habitat model construction are already used in the seatrout stock assessments (Murphy et al., 2006) in the form of general linear models (GLMs), so recruitment estimates are not entirely independent of the fisheries-independent dataset. However, the index used conflicts considerably with other sources of information used in the assessments and poorly fit the model. It suggests that abundance is declining in both the southeast and southwest management areas, contrasting with the more optimistic view of the indices produced here following the 1996 implementation of management measures to reduce exploitation of the resource.

One source of this discrepancy may be that GLMs, based on monotonic assumptions of the relationship between the environment and abundance, cannot replicate the often unimodal relationships with environmental conditions implied by the models developed in Chapter 2. The aim is to investigate if the increased flexibility of GAMs over GLMs

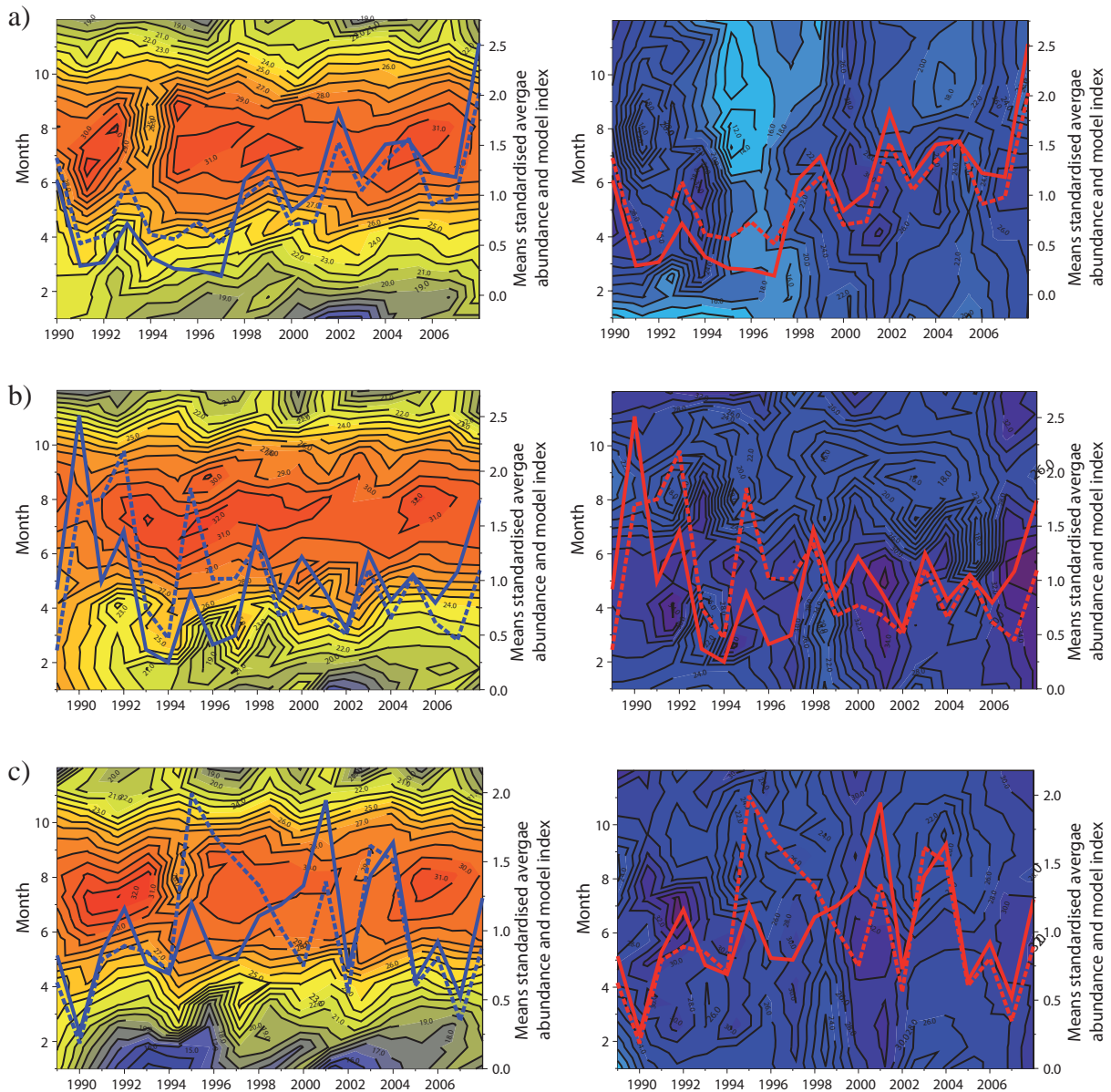


Figure 5.8. Temporally interpolated mean monthly sampling temperature (left) and salinity (right) each year overlaid with means standardised catch rates (dashed line) and predicted cohort strength (solid line) for a) Indian River, b) Charlotte Harbor, and c) Tampa Bay.

can provide more accurate information on recruitment abundance, or whether they underestimate the variance in recruitment by incorrectly attributing some of the variance to differences in the environmental conditions sampled.

Compared with overall mean estimates, the GAM index is only marginally less variable, suggesting that estimates of cohort strength variation are not unduly suppressed, and that the precision of estimates at any given point in time are likely to be significantly more precise, because a substantial proportion of the deviance has been explained. The fact that interannual variation in cohort strength covaries to a degree between the mean and the index over periods with consistent sampling design is expected and reassuring, because the stratification scheme is designed to account for at least some of the environmental variability.

Estimates of recruitment in the IR are estimated to have risen since 1997, with a peak in 2008 (Figure 5.9a). The assessment predicts similar trends in average recruitment, although the increase is less dramatic. Relative estimates of cohort strength again do not match the predicted values within this general trend. Mean observed abundances by the fisheries-independent monitoring program prior to 1998 are higher than the predicted values owing to changes in the sampling design, but since then the estimates track well, suggesting that the sampling variability in environmental conditions in a year are representative of the variability in the environmental conditions in the system as a whole.

The CH index estimates a large cohort in 1990 and some smaller ones from 1993 to 1997, but little in the way of long-term trends over the period, consistent with the assessment of seatrout for the southwest area, which indicated little in the way of trends in recruitment based largely on fisheries-dependent information (Figure 5.9b). However, relative cohort strength does not follow that derived from the assessment. As well as the failure of the index assumption regarding niche breadth, the use of age-length keys combined over years and the dominance of fish from other estuaries in the management unit could be responsible for this poor fit.

The TB model implies relatively little in the way of a long-term trend in recruitment. There is an indication that recruitment after 1997 improved temporarily, with large 2001, 2003, and 2004 cohorts, but it has declined since (Figure 5.9c). The period 1999–2005 is the only period where assessment-based recruitment estimates could be argued to match the index on a cohort-by-cohort basis. This is also the only period during which the

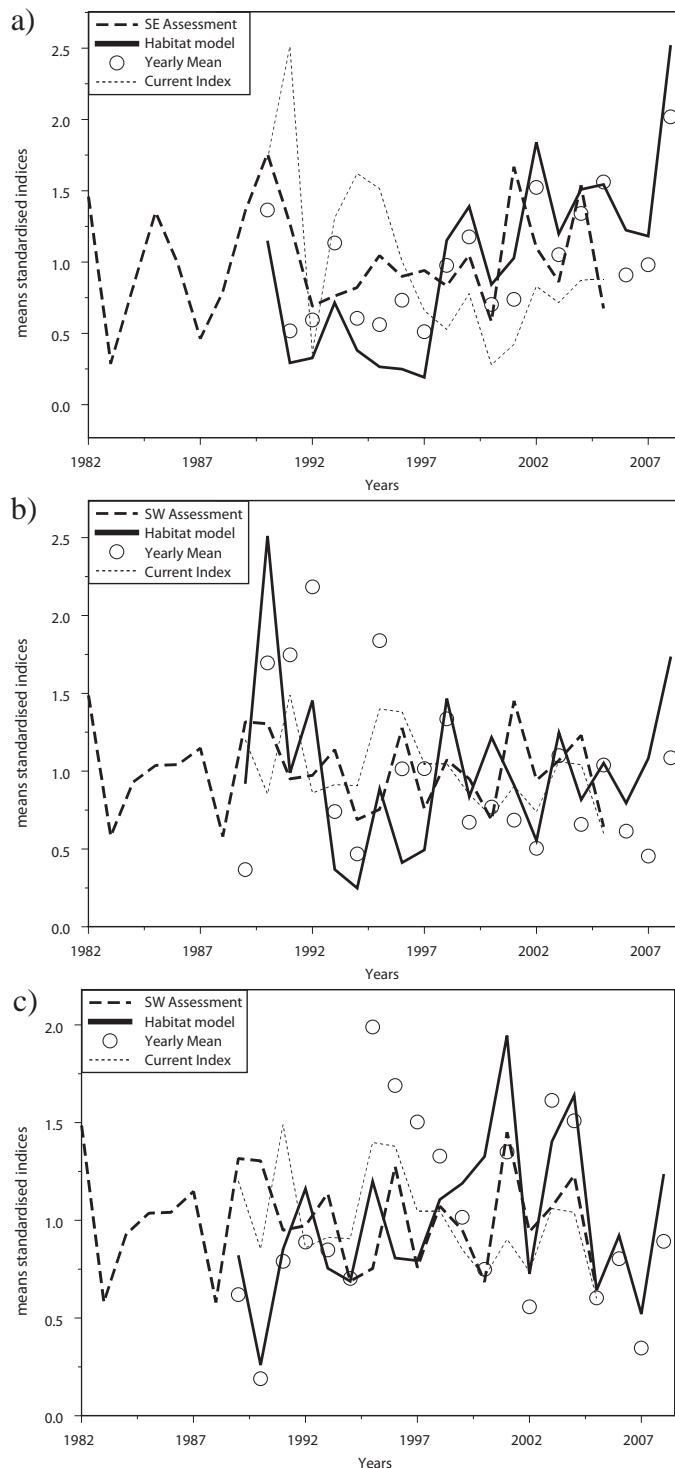


Figure 5.9. Comparison of the predicted estimates of cohort strength with the means standardised catch rates, observed catch rates (circles), the indices currently used in the assessment and the estimates of recruitment from the appropriate model (dashed line) for a) Indian River, b) Charlotte Harbor, and c) Tampa Bay.

assessment uses annual age-length keys for both sexes. TB represents only one of the populations assessed in the southwest management unit, and the contributions of other areas to catches is unknown, but TB is known to harbour one of the largest seatrout populations on the Gulf coast as a whole, so is almost certain to have a significant contribution to the overall population dynamics in the southwest management unit.

The evidence presented here suggests that the indices provided represent largely unbiased and suitably precise estimates of the abundance of pre-recruiting seatrout. Unfortunately, comparison with independent information from the fishery is not possible, because in Gulf coast estuaries, the long-term trend in abundance has been relatively stable with virtually all of the variation at an annual level over the assessed period. Hence, correlation with an assessment model that is unable to resolve interannual variation, cannot be expected to provide proof of the utility of the index. In contrast, in the IR, the recent trend since 1997 has been increasing in both the assessment and the index. Only a more detailed assessment model or a time-series with greater contrast in abundance estimates over the long term will be able to ascertain the true value of these models to fisheries managers.

Suggestions for a sound application of GAMs in management

GAMs, because of their flexibility, certainly have the potential to provide important additional information to natural resource managers from the data originally collected for alternative purposes.

Habitat models based on GAMs provide conservation managers with vital information on the distribution of juvenile seatrout in estuarine environments. Such models are superior to the currently developed HIS models (Rubec et al., 1999), because they better reflect the underlying biological processes and because they provide important evidence of the spatiotemporal variability in the use of estuarine regions by juvenile seatrout.

In addition, the value of the original habitat models has been expanded by the development of long-term time-series, which have been proved to be resilient to changes in sampling design and to comply with the underlying model assumptions so that they provide more robust information on cohort variability than currently available.

The important dependence of seatrout reproduction on temperature, female length and condition has highlighted the fact that environmental conditions potentially play as important a role in reproduction as the abundance of females, explaining why despite relatively stable stock conditions, recruitment varies considerably between years.

In addition, the potential of identifying spawning habitat through linking estuarine conditions with those required for reproduction is possible, though limited in its use owing to a lack of salinity information in the current model. The value of information such as this has been demonstrated qualitatively by providing a better understanding of the ecology of seatrout and quantitatively by allowing managers to assess the potential value of the impact of marine protected areas or habitat restoration efforts better prior to their implementation.

The additional information on historical patterns of growth resolved by the increment analysis using GAM models provides important additional information to the stock assessment process and has the potential to improve significantly the ability of the model to track individual cohorts more precisely than is currently possible.

The benefits of using GAMs demonstrated for a single species here will undoubtedly mean that the methodology will become increasingly important in the evaluation of large fisheries datasets and lead to further important discoveries in fisheries science and conservation. However, there is an unseen risk commensurate with improved model flexibility. In this study a large proportion of the time available has been spent evaluating models, as opposed to developing them. The methods used to evaluate the efficacy of the models range from cross-population comparisons, use of independent data of different type, bootstrapping and jackknifing, as well as the more classical evaluation of bias in residuals and model choice criteria. What is presented is a relatively small portion of the often fruitless avenues investigated in the quest to provide robust models suitable for use in management. The importance of such work is underscored in this chapter.

What follows is a summary of the pertinent lessons that were learned using generalized additive models (GAMs) in the form of a recipe to follow when using them, especially when used on data not collected to an appropriate sampling design, because of its intended use for other purposes.

Generalized additive models (GAMs): a synopsis of lessons learned

A model is only as good as the data used to develop it. There is no substitute for knowing how and with what possible biases the data were collected. The issue with historical datasets is that often the necessary metadata to evaluate the possible conflict with model assumptions is unavailable. In this respect, GAMs are no different from any other model, but because of their flexibility, determining the failure of assumptions from the results of a GAM is much more difficult than for a simpler model such as a linear one.

Statistical measures of the goodness of fit are generally useful only as rough guides, but are rarely suitable as a justification of model choice in complex multidimensional datasets with undefined error structures. Fitting GAMs assuming different error structures to the same dataset and using the AIC as the criterion for selecting model complexity frequently results in deviance residuals that more or less match the assumed error structure, yet one dataset clearly cannot have two error structures.

Using the central limit theorem, just because the dataset is large and the expected trends from the analysis do not appear to differ much when changing the likelihood function, is a sound option only when all parts of all gradients are equally covered with suitably large sample sizes. Although one gradient may have suitably even sample coverage, the results are still not valid, if some of those samples are able to hide large residuals in the other parts of the model space.

GAMs are regression models, so as linear models they assume that the independent variable is known without error and can be manipulated at will and in isolation of all other independent variables. Most datasets in fisheries science are observational, so statistically they can at best be described as covarying in that they are rarely known without error and certainly not easily manipulated in the environment. Even under these conditions, GAMs can provide useful information, but situations where independent variables covary and not necessarily linearly need to be investigated very carefully. Changes in a survey design readily lead to such inadvertent colinearities and misinterpretation of results.

The approach taken here with regards to evaluating the models has always been to reduce model complexity significantly beyond the level suggested by the AIC to very simple relationships with individual independent variables. There is enough complexity added by the number of variables to evaluate. If the results are unexpected in terms of the relationship, think of processes that might cause this form of the relationship and then develop methods by which it is possible to test for them within the data. If they are similar to what might reasonable be expected from the literature or experience, check anyway.

Once all these checks and balances have been carried out and a scientifically plausible model has been developed, it is still wrong, as in fact are all models that simplify reality. This in no way detracts from the utility of the model to managers, but it is worth checking with some form of independent data. There are a number of approaches for doing this, such as bootstrapping, predicting results for other independent datasets, or

finding a method to check the underlying process. This saves later embarrassment, and facilitates the communication of model accuracy and caveats much better than standard error estimates based on violated assumptions in a statistical model.

In conclusion, I firmly believe that all GAMs I have seen published in the fisheries literature (including my own) fail at least one of the model assumptions. In such cases a true statistician is unable to help a mere biologist, so knowing the data, the processes under consideration and how the model treats the failure of the assumption through experience is more important than detailed statistical knowledge. Carried out responsibly, the process is sure to reveal many scientifically interesting results, information that could not be provided to managers that need them the most any other way without going back in time and collecting data in a more appropriate sampling design. Carried out irresponsibly and haphazardly thrown at any data, GAMs have the potential to set back science and management significantly, not to mention the potential detriment to the natural environment.

References

- Alshuth, S., and Gilmore, R.G., Jr. 1993. Egg identification, early larval development and ecology of the spotted seatrout, *Cynoscion nebulosus* C. (Pisces: Sciaenidae). ICES Document CM 1993/G: 28.
- Alshuth, S., and Gilmore, R.G., Jr. 1994. Salinity and temperature tolerance limits for larval spotted seatrout, *Cynoscion nebulosus* C. (Pisces: Sciaenidae). ICES Document CM 1994/L: 17.
- Bigelow, K.A., Boggs, C.H., and He, X., 1999. Environmental effects on swordfish and blueshark catch rates in the US North Pacific longline fishery. *Fish. Oceanogr.* 8: 178-198.
- Beaumarige, D. S., 1969. Returns for the 1965 Schlitz Tagging Program including a cumulative analysis of previous results. Florida Department of Natural Resources Marine Research Laboratory Technical Series, 59. 38pp.
- Benaka, L., editor. 1999. Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society Symposium 22, Bethesda, Maryland.
- Bolle, L.J., Rijnsdorp, A.D., van Neer, W., Millner R.S., Leeuwen, P.I., Ervynnek, A., Ayers, R., and Ongenaes E., 2004. Growth changes in plaice, cod, haddock and saithe in the North Sea: a comparison of (post-)medieval and present-day growth rates based on otolith measurements. *J. Sea Res.* 51: 313-328.
- Botsford, L.W., Kaplan, D.M. and Hastings, A., 2004. Sustainability and yield in marine reserve policy. p75-86 In J.B. Shipley editor. Aquatic protected areas as a fisheries management tool. American Fisheries Society Symposium 42. Bethesda, Maryland.
- Brevian, G., Fontoura, N.F., and Haimoviv, M, 2006. Statistical model of variable allometric growth: otolith growth in *Micropogonias furnieri* (Actinoperygii, Sciaenidae). *J. Fish Biol.* 68: 196-208.
- Brothers, E.B. 1995. Estimation of Growth, Overview II. In Recent developments in fish otolith research eds. Secor, D.H., Dean, J.M. and Campana, S.E., University of South Carolina Press, Columbia, SC, US
- Brown, S.K., Buja, K.R., Jury, S.H., and Monaco, M.E., 2000. Habitat suitability index models for eight fish and invertebrate species in Casco and Sheepscot Bays, Maine. *N. Am. J. Fish. Mgmt* 20: 408-435.
- Brown-Petersen, N., and Thomas, P., 1988. Differing reproductive life histories between temperate and subtropical groups of *Cynoscion nebulosus*. *University of Texas Cont. Mar. Sci.*, 30: 71-78.
- Brown-Petersen, N., Thomas, P., and Arnold, C. E., 1988. Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in south Texas. *Fish. Bull. US* 86: 373-388.

References

- Bye, V.J., 1990. Temperate marine teleosts. In *Reproductive seasonality in teleosts: environmental influences*, pp 125-143. Ed. by A.D. Munroe, T.J. Lam, and A.P. Scott. CRC Press, Boca Raton, FL. 254 pp.
- Campana, S.E., 1990. How reliable are growth back-calculations based on otoliths? *Can. J. Fish. Aquat. Sci.* 47: 2219-2227.
- Campana, S.E., 2005. Otolith science entering the 21st century. *Mar. Freshwater. Res.* 56: 485-496.
- Capo, T.R., Wisner, B.B., Serafy, J.E., and Boyd, A.E., 1997. Short communication: Extended spawning of captive spotted seatrout (*Cynoscion nebulosus*) under photo-thermal regulations. *Proceedings Aquaculture Europe 97, Les-trois-ilets, Martinique, May 4-9, 1997.*
- Chauvelon, P., and Bach, P., 1993. Modelling the otolith shape as an ellipse: an attempt for back-calculation purposes. *ICES J. Mar. Sci.* 50: 121-128.
- Chester, A.J., and Thayer, G.W., 1990. Distribution of spotted seatrout (*Cynoscion nebulosus*) and gray snapper (*Lutjanus griseus*) juveniles in seagrass habitats of western Florida Bay. *Bull. Mar. Sci.* 46: 345-357.
- Colura, R.L., Maciorowski, A.F., and Henderson-Arapalo, A., 1988. Gonadal maturation, fecundity and strip spawning of female spotted seatrout. *Proceedings of the Annual Conference of the Southeast Association of Fish and Wildlife Agencies*, 48: 80-88.
- Comyns, B.H., Rakocinski, C.F., Peteron, M.S., and Shiller, A.M., 2008. Otolith chemistry of juvenile spotted seatrout *Cynoscion nebulosus* reflects natal regions of coastal Mississippi, USA. *Mar. Ecol. Prog. Ser.* 371: 243-252.
- Crabtree, R.E., Adams, D.H., 1998. Study V: Spawning frequency and fecundity of spotted seatrout, *Cynoscion nebulosus*, in the Indian River Lagoon, Florida. In: *Investigations into nearshore and estuarine gamefish abundance, ecology, and life history in Florida. Five-year technical report Sportfish restoration (Project F-59).* Fish and Wildlife Research Institute, St. Petersburg.
- Crocos, P.J., and van der Velde, T.D., 1995. Seasonal, spatial and interannual variability in the reproductive dynamics of the grooved tiger prawn *Penaeus semisulcatus* in Albatross Bay, Gulf of Carpentaria, Australia: the concept of effective spawning. *Mar. Biol.* 122: 557-570.
- DaCosta, S.L., Reichard, R.P., and Bhogal, V.K., 1987. Indian River Lagoon circulation and flushing study. Report to Florida Sea Grant College (R/IRL-3) and Florida Department of Environmental Regulation (CM 118). 177 pp.
- Darnell, R.M., 1958. Food habits of fishes and larger invertebrates of lake Ponchartrain, Louisiana, an estuarine community. *Publ. Inst. Mar. Sci* 5: 353-416.
- DeVries, D.A., Bedde, C.D., Palmer, C.L., and Bortone, S.A., 1997. Age, growth, maturity, and size composition of spotted seatrout, *Cynoscion nebulosus*, in the Panhandle Region of Florida. Final Report. Florida Department of Environmental Protection, Marine Resources Grants MR019 and MR024, Tallahassee, FL.

- Efron, B., and Tibshirani, R.J., 1993. An introduction to the bootstrap. Monographs on statistics and applied probability 57. Chapman and Hall /CRC Press, Boca Raton, FL, USA.
- Escot, C., and Granado-Lorencio, C., 1999. Comparison of four methods of back-calculating growth using otoliths of a European barble, *Barbus sclateri* (Gunther) (Pisces : Cyprinidae). *Mar. Freshwat. Res.* 50: 83-88.
- Finstad, A.G., 2003. Growth backcalculations based on otoliths incorporating an age effect: adding an interaction term. *J. Fish Biol.* 62: 1222-1225.
- Fournier, D., and Archibald, C.P., 1982. A general theory for analyzing catch at age data. *Can. J. Fish. Aquat. Sci.* 39: 1195-1207.
- Fournier, D.A., Sibert, J.R., Majkowski, J., and Hampton, J., 1990. MULTIFAN: a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tuna (*Thunnus maccoyi*). *Can. J. Fish. Aquat. Sci.* 47: 301-317.
- Fournier, D.A., Hampton, J., and Sibert, J.R., 1998. MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore, *Thunnus alalunga*. *Can. J. Fish. Aquat. Sci.* 55: 2105-2116.
- Francis, R.I.C.C., 1990. Back-calculation of fish length: a critical review. *J. Fish Biol.* 36: 883-902.
- Francis, R.I.C.C., 1995. The analysis of otolith data – a mathematician's perspective (what precisely is your model?) In *Recent developments in fish otolith research* eds. Secor, D.H., Dean, J.M. and Campana, S.E., University of South Carolina Press, Columbia, SC, US
- Gagliano, M., and McCormick, M.I., 2004. Feeding history influences otolith shape in tropical fish. *Mar. Ecol. Prog. Ser.* 278: 291-296.
- Geary, R.C., and Leser C.E.V., 1968. Significance tests in multiple regression. *Am. Stat.* 22: 20-21.
- Gilmore, R.G., 1977. Fishes of the Indian River Lagoon and adjacent waters, Florida. *Bull. Fla St. Mus. Bio. Sci.* 22: 101-147.
- Gilmore, R.G. 1995. Environmental and biogeographic factors influencing ichthyofaunal diversity in the Indian River Lagoon. *Bull. Mar. Sci.*, 57: 153-170.
- Gray, J.D., King, T.L., and Coulra, R.L. 1991. Effects of temperature and hypersalinity on hatching success of spotted seatrout eggs. *Prog. Fish Cult.* 53: 81-84.
- Halpin, P.M., 2000. Habitat use by an intertidal salt-marsh fish: trade-offs between predation and growth. *Mar. Ecol. Prog. Ser.* 198: 203-214.
- Hamilton, D., 1987. Sometimes $R^2 > r^2_{yx1} + r^2_{yx2}$. *Am. Stat.* 42: 90-91.
- Hare, J.A., and Cowen, R.K., 1995. Effect of age, growth rate, and ontogeny on the otolith size – fish size relationship in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in fish early life history stages. *Can. J. Fish. Aquat. Sci.* 52: 1909-1922.

References

- Hastie, T.J., and Tibshirani, R.J., 1990. Generalized additive models. Monographs on statistics and applied probability 43. Chapman & Hall /CRC Press, Boca Raton, FL, USA.
- Hein, S., and Shepard, J., 1979. Spawning of spotted seatrout in a Louisiana estuarine ecosystem. Proc. A. Conf. Southeast Ass. Fish Wildl. Agencies 33: 451-465.
- Hein, S., Dugas, C., and Shepard, J. 1980. Total length-standard and length-weight regressions for spotted seatrout *Cynoscion nebulosus*; red drum, *Sciaenops ocellata*; and black drum, *Pogonias cromis*, in south-central Louisiana. Louisiana Fish and Wildlife Marine Research Laboratory Tech. Bull. 31: 41-48.
- Helser, T.E., Condrey, R.E., and Geaghan, J.P., 1993. Spotted seatrout distribution in four coastal Louisiana estuaries. Trans. Am. Fish. Soc. 122: 99-111.
- Hilborn, R., and Mangel, M., 1997. The ecological detective, confronting models with data. Princeton University Press, Princeton, NJ.
- Hilborn, R., and Walters, C.J., 1992. Quantitative fisheries stock assessment, choice, dynamics and uncertainty. Kluwer Academic, Boston, MA. 570 pp.
- Hindell, J.S., Jenkins, G.P., and Keough, M.J., 2000. Variability in the abundance of fishes associated with seagrass habitats in relation to diets of predatory fishes. Mar. Biol. 136: 725-737.
- Hogarth W.T., Lent, R. and Brock, R.J., 2004. Area-based management and sustainable fisheries under purview of the National Marine Fisheries Service (NOAA Fisheries). In J.B. Shipley editor. Aquatic protected areas as a fisheries management tool. American Fisheries Society Symposium 42. Bethesda, MD.
- Holt, G.J., Holt, S.A. and Arnold, C.R., 1985. Diel periodicity of spawning in sciaenids. Mar. Ecol. Prog. Ser. 27: 1-7.
- Hüssy, K., and Mosegaard, H., 2004. Atlantic cod (*Gadus morhua*) growth and otolith accretion characteristics modelled in a bioenergetics context. Can. J. Fish. Aquat. Sci. 61: 1021-1031.
- Hutchings, J.A., 1997. Life history responses to environmental variability in early life. In Early life history and recruitment in fish populations. Ed. R.C. Chambers and E.A. Trippel. Chapman & Hall, London. 596 pp.
- Ihde, T.F., Chittenden, M.E. Jr., 2003. Validation of presumed annual marks on sectioned otoliths of spotted seatrout, *Cynoscion nebulosus*, in the Chesapeake Bay region. Bull. Mar. Sci. 72: 77-87.
- Iles, T.C., and Beverton, R.J.H., 2000. The concentration hypothesis: the statistical evidence. ICES J. Mar. Sci. 57: 216-227.
- Iversen, E.S., and Tabb, D.C., 1962. Subpopulations based on growth and tagging studies of spotted seatrout *Cynoscion nebulosus*, in Florida. Copeia, 1962: 544-548.

- Janke, T.E., 1971. Abundance of young sciaenid fishes in Everglades National Park, Florida, in relation to season and other variables. University of Miami Sea Grant Program, Seagrant Technical Bulletin, 11. 128 pp.
- Johnson, D. R., Funicelli, N. A., and Bohnsack, J. A., 1999. Effectiveness of an existing no-take fish sanctuary within the Kennedy Space Center, Florida. *N. Am. J. Fish. Mgmt* 19:436–453.
- Klumb, R.A., Bozak, A., and Frie, R.V., 2001. Validation of three back-calculation models by using multiple oxytetracycline marks formed in the otoliths and scales of bluegill x green sunfish hybrids. *Can. J. Fish. Aquat. Sci.* 58: 352-364.
- Kupschus, S., 2003. Development and evaluation of statistical habitat suitability models; an example based on juvenile spotted seatrout (*Cynoscion nebulosus*). *Mar. Ecol. Prog. Ser.* 265: 197–212.
- Kupschus, S., 2004. A temperature-dependent reproductive model for spotted seatrout (*Cynoscion nebulosus*) explaining spatio-temporal variations in reproduction and young-of-the-year recruitment in Florida estuaries. *ICES J. Mar. Sci.* 61: 3-11.
- Kupschus, S., and Tremain, D., 2001. Associations between fish assemblages and environmental factors in nearshore habitats of a subtropical estuary. *J. Fish Biol.* 58: 1383-1403.
- Llansó, R.J., Bell, S.S., and Vose, F.E. 1998. Food habits of red drum and spotted seatrout in a restored mangrove impoundment. *Estuaries*, 21: 294-306.
- Loots, C., Koubbi, P., and Duhamel, G., 2007. Habitat modelling of *Electrona antarctica* (Myctophidae, Pisces) in Kerguelen by generalized additive models and geographic information systems. *Polar Biol.* 30: 951-959.
- Lowerre-Barbieri, S.K., 2004. Research on the reproduction of spotted seatrout in Florida waters. Wallop-Breaux Five-Year Completion Report, Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St Petersburg, FL.
- Lowerre-Barbieri, S.K., Chittenden, M.E. Jr., and Jones, C.M., 1994. A comparison of validated otolith method to age weakfish, *Cynoscion regalis*, with the traditional scale method. *Fish. Bull. US* 92: 555-568.
- Lowerre-Barbieri, S. K., Chittenden, M. E., and Barbieri, L.R., 1996. The multiple spawning pattern of weakfish in the Chesapeake Bay and Middle Atlantic Bight. *J. Fish Biol.* 48: 1139–1163.
- Lowerre-Barbieri, S.K., Lowerre, J.M., and Barbieri, L.R., 1998. Multiple spawning and the dynamics of fish populations: inferences from an individual-based simulation model. *Can. J. Fish. Aquat. Sci.* 55: 2244-2254.
- Lowerre-Barbieri, S.K., Barbieri, L.R., and Alberts, J.J., 1999. Reproductive parameters needed to evaluate recruitment overfishing of spotted seatrout in the Southeastern US. Final Report. Saltonstall-Kennedy Grant Program, 15USC. 713e-c.

References

- Luczkovich, J.J., Pullinger, R.C., Johnson, S.E., and Sprague, M.W., 2008. Identifying Sciaenid critical spawning habitats by the use of passive Acoustics. *Trans. Amer. Fish. Soc.* 137: 576-605.
- Maceina, M.J., Hata, D.N., Linton, T.L., and Landry, A.M., Jr., 1987. Age and growth analysis of spotted seatrout from Galveston Bay, Texas. *Trans. Am. Fish. Soc.* 116: 54-59.
- Maravelias, C.D., Reid, D.G. and Swartzman, G., 2000. Modelling spatio-temporal effects of environment on Atlantic herring, *Clupea harengus*. *Environ. Biol. Fish.* 58: 157-172.
- Maunder, M.N., and Watters, G.M., 2003. A-SCALA: An Age-Structured Statistical Catch-at-Length Analysis for Assessing Tuna Stocks in the Eastern Pacific Ocean. *Inter-Amer. Trop. Tuna Comm., Bull.* 22(5) 433-582.
- McCullagh, P., and Nelder, J.A., 1989. *Generalized Linear Models* (2nd ed.) Chapman and Hall, London.
- McMichael, R.H., and Peters, K.M., 1989 Early life history of spotted seatrout, *Cynoscion nebulosus*(Piscies: Scieaenidae), in Tampa Bay, Florida. *Estuaries*, 16: 703-717.
- Methot, R. D., 1990. Synthesis model: an adaptable framework for analysis of diverse stock assessment data. In *Proceedings of the Symposium on Application of Stock Assessment Techniques to Gadids*, pp. 259–277. INPFC Bulletin, 50.
- Mok, H. K., and R. G. Gilmore. 1983. Analysis of sound production in estuarine fish aggregations of *Pogonias cromis*, *Bairdiella chrysoura*, and *Cynoscion nebulosus* (Sciaenidae). *Bulletin of the Institute of Zoology, Academia Sinica* 22:157–186.
- Moody, W.D., 1950. A study of the natural history of the spotted trout, *Cynoscion nebulosus*, in the Cedar Key, Florida, area. *Q. J. Fla Acad. Sci.* 12: 147-171.
- Moffet, A.W., 1961. Movement and growth of spotted seatrout (*Cynoscion nebulosus*) in West Florida. *Fla. Board Conserv. Mar. Res. Lab. Tech. Ser.* 36. 33 pp.
- Morita, K., and Matsuishi, T., 2001. A new model of growth back-calculation on incorporating age effect based on otoliths. *Can. J. Fish. Aquat. Sci.* 58: 1805-1811.
- Murphy, M.D., 2003. A stock assessment of spotted seatrout *Cynoscion nebulosus* in Florida: status of the stocks through 2001. Florida Fish and Wildlife Conservation Commission Fish and Wildlife Research Institute In-House Report Series 2003-012.
- Murphy, M.D., Guenther, C.B., and Mahmoudi, B., 2006. An assessment of the status of spotted seatrout in Florida waters through 2005. Florida Fish and Wildlife Conservation Commission Fish and Wildlife Research Institute In-House Report Series 2006-XXX.
- Murphy, M.D. and Taylor, R.G., 1994. Age, growth and mortality of spotted seatrout in Florida waters. *Trans. Am. Fish. Soc.* 123: 482-497.

- Nelson, G.A.,1998. Abundance, growth, and mortality of young-of-the-year pinfish, *Lagodon rhomboides*, in three estuaries along the gulf coast of Florida. *Fish. Bull. US* 96: 315-328.
- Nelson, G.A., 2002. Age, growth, mortality, and distribution of pinfish (*Lagodon rhomboides*) in Tampa Bay and adjacent Gulf of Mexico waters. *Fish. Bull. US* 100: 582-592.
- Nelson, G.A., and Leffler, D., 2001. Abundance, spatial distribution, and mortality of young-of-the-year spotted seatrout (*Cynoscion nebulosus*) along the Gulf coast of Florida. *Gulf Mex. Sci.* 19: 30-42.
- Neter, J., Kutner, M.H., Nachtsheim, C.J., and Wasserman, W., 1996. Applied linear statistics, fourth edition. WCB/McGraw-Hill, Boston, MA.
- Nieland, D.L., Thomas, R.G., and Wilson, C. A., 2002. Age, growth and reproduction of spotted seatrout in Barataria Bay Louisiana. *Trans. Am. Fish. Soc.* 131: 245-259.
- Orth, R.J., and Heck, K.L., van Montfrans, J., 1984. Faunal communities in seagrass beds: a review of the influences of plant structure and prey characteristics on predator-prey relationships. *Estuaries*, 7: 339-350.
- Ostermeier, D.M., 1999. The role of institutions in ecosystem management. In *Ecosystem management for sustainability*. Ed. J.D. Peine, CRC Press, Boca Raton, FL. 500 pp.
- Paterson, A.W., and Whitfield, A.K. 2000. Do shallow-water habitats function as refugia for juvenile fishes? *Estuar. Coast. Shelf. Sci.* 51: 359-364.
- Peebles EB, Tolley SG 1988. Distribution and mortality of larval spotted seatrout, *Cynoscion nebulosus*: a comparison between two adjacent estuarine areas of southwest Florida. *Bull. Mar. Sci.* 42: 397-410.
- Peebles, E.B., Flannery, M.S., Matheson, R.E., and Rast, J.P., 1991. Fish nursery utilization of the Little Manatee River estuary: relationships to physicochemical gradients and the distribution of food resources. In: *Proceedings, Tampa Bay Area Scientific Information Symposium 2*. 528 pp.
- Porch, C.E., Powell, A.B., and Settle, L. 2004. Power analysis for detecting trends in juvenile spotted seatrout abundance in Florida Bay. ,Miami, FL. NOAA/National Marine Fisheries Service/Southeast Fisheries Science Center ,(NOAA Technical Memorandum NMFS-SEFSC ,526)
- Powell, A.B., 2003.Larval abundance, distribution, and spawning habits of spotted seatrout (*Cynoscion nebulosus*) in Florida Bay, Everglades National Park, Florida. *Fish. Bull.* 101: 704-711.
- Powell, A.B., Cheshire, R.T., Laban, E.H., Colvocoresses, J, O'Donnell, P., and Davidian, M., 2004. Growth, mortality, and hatchdate distributions of larval and juvenile spotted seatrout (*Cynoscion nebulosus*) in Florida Bay, Everglades National Park. *Fish. Bull.* 102: 142-155.

References

- Quintero-Hunter, I, Grier, H., and Muscato, M., 1991. Enhancement of histological detail using mantanil yellowe as counterstain in periodic acid/Schiff's hematoxylin staining of glycol methacrolate tissue sections. *Biotech. Histochem.* 66: 169-172.
- Reyier, E.A., Shenker, J.M., and Christian, D., 2008. Role of an estuarine fisheries reserve in the production and export of ichthyoplankton. *Mar. Ecol. Prog. Ser.* 359: 249-260.
- Roberts, C. M., Bohnsack, J. A., Gell, F., Hawkins, J. P., and Goodridge, R., 2001. Effects of marine reserves on adjacent fisheries. *Science* 294:1920–1923.
- Rosenberg, A., Bigford, T.E., Leathery, S., Hill, R.L., and Bickers, K., 2000. Ecosystem approaches to fishery management through essential fish habitat. *Bull. Mar. Sci.* 66: 535-542.
- Roumillat, W.A., Brouwer, M.C., 2004. Reproductive dynamics of female spotted seatrout (*Cynoscion nebulosus*) in South Carolina. *Fish. Bull. US* 102: 473-487.
- Rubec, P.J., Bexley, J.C., Norris, H., Coyne, M.S., Monaco, M.E., Smith, S.G., and Ault, J.S., 1999. Suitability modeling to delineate habitat essential to sustainable fisheries. *Am. Fish. Soc. Symp.* 22: 108-133.
- Ruiz, G.M., Hines, A.H., and Posey, M.H., 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 99: 1-16.
- Rutherford, E.S., Thomas, W.S., and Tilmant, J.T. 1989. Early life history of spotted seatrout (*Cynoscion nebulosus*) and gray snapper (*Lutjanus griseus*) in Florida Bay, Everglades national park, Florida. *Bull. Mar. Sci.* 44: 49-64.
- Santiago, J., and Eltink, A., 1988. Distribution and abundance of anchovy eggs in the Bay of Biscay in 1987 in comparison with 1983 and 1986. *ICES Document CM* 1988/H: 9. 23 pp.
- Saucier, M.H., and Baltz, D.M..1992. Hydrophone identification of spawning sites of spotted seatrout *Cynoscion nebulosus* (Osteichthys: Sciaenidae) near Charleston, South Carolina. *Northeast Gulf Sci.*, 12: 141-145.
- Saucier, M.H., and Baltz, D.M., 1993. Spawning site selection by spotted seatrout, *Cynoscion nebulosus*, and black drum, *Pogonias cromis*, in Louisiana. *Environ. Biol. Fish.* 36: 257-272.
- Schaalje, G.B., Shaw, J.L., and Belk, M.C., 2002. Using nonlinear hierarchical models for analysing annulus-based size-at-age data. *Can. J. Fish. Aquat. Sci.* 59: 1524-1532.
- Schirripa, M.J., 2002. An evaluation of back-calculation methodology using simulated otolith data. *Fish. Bull. US* 100: 789-799.
- Schirripa, M.J., and Trexler, J.C., 2000. Effects of mortality and gear selectivity on the fish otolith radius-total length relation. *Fish. Res.* 46: 83-89.

- Secor, D. H., and Dean, J. M., 1992. Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis*. *Can. J. Fish. Aquat. Sci.* 49: 1439-1454.
- Secor, D. H., 2000. Spawning in the nick of time? Effect of adult demographics on spawning behaviour and recruitment in Chesapeake Bay striped bass. *ICES J. Mar. Sci.* 57: 403-411.
- Shafer, D. J., 2000. Evaluation of periodic and aperiodic otolith structure and somatic-otolith scaling for use in retrospective life history analysis of a tropical marine goby, *Bathygobius coalitus*. *Mar. Ecol. Prog. Ser.* 199: 217-229.
- Sheridan, P., 2003. Recovery of floral and faunal communities after placement of dredged material on seagrass in Laguna Madre, Texas. *Estuar. Coast. Shelf Sci.* 59: 441-458.
- Sime, P., 2005. St. Lucie estuary and Indian River lagoon conceptual ecological model. *Wetlands* 25: 898-907.
- Sinclair, A. F., Swain, D. P., and Hansom J. M., 2002. Disentangling the effects of size-selective mortality, density, and temperature on length-at-age. *Can J. Fish. Aquat. Sci.* 59: 372-382.
- Sirois, P., Lecomte, F., and Dodson, J. J., 1998. An otolith-based back-calculation method to account for time-varying growth rate in rainbow smelt (*Osmerus mordax*) larvae. *Can. J. Fish. Aquat. Sci.* 55: 2662-2671.
- Smedstad, O. M., and Holm, J. C., 1996. Validation of back-calculation formulae for cod otoliths. *J. Fish Biol.* 49: 973-985.
- Smith, N.P., 1987. An introduction to the tides of Florida's Indian River Lagoon. I. Water levels. *Fla. Sci.* 50: 49-61.
- Smith, N.G., Jones, C.M., and Van Montfrans, J., 2008. Spatial and temporal variability of juvenile spotted seatrout *Cynoscion nebulosus* growth in Chesapeake Bay. *J. Fish. Biol.* 73: 597-607.
- Stewart, K.W., 1961. Contributions to the biology of the spotted seatrout (*Cynoscion nebulosus*) in the Everglades National Park, Florida. Masters thesis. University of Miami, Coral Gables, Florida.
- Storer, J.A., 1992. Marine resource management international experience and aspects. *Am. Fish. Soc. Symp.* 13: 39-45.
- Swartzman, G., Silverman, E., and Willimason, N. 1995. Relating trends in walleye pollock (*Theragra chalcogramma*) abundance in the Bering Sea to environmental factors. *Can. J. Fish. Aquat. Sci.* 52: 369-380.
- Swartzman, G., Stuetzle, W., Kulman, K., and Powojowski, M., 1994. Relating the distribution of pollock schools in the Bering Sea to environmental factors. *ICES J. Mar. Sci.* 51: 481-492.

References

- Tabb, D.C., 1958. Differences in the estuarine ecology of Florida waters and their effect on populations of spotted weakfish, *Cynoscion nebulosus* (Cuvier and Valenciennes). Transcripts of the 23rd North American Wildlife Conference, pp. 392-401.
- Tabb, D.C., 1961. A contribution to the biology of the spotted seatrout *Cynoscion nebulosus* (Cuvier), of east-central Florida. Fla Board Conserv. Mar. Res. Lab. Tech. Ser. 35. 22 pp.
- Tabb, D.C., 1966. The estuary as a habitat for spotted seatrout, (*Cynoscion nebulosus*). Am. Fish. Soc. Spec. Publ. 3: 59-67.
- Taniguchi, A.K., 1981. Survival and growth of larval spotted seatrout (*Cynoscion nebulosus*) in relation to temperature, prey abundance and stocking densities. Rapp. P-v. Réunion. Cons. Int. l'Explor. Mer 178: 507-508.
- Tasker M., and Knapman, P., 1999. Marine environmental management and fisheries. In Alternative management systems for fisheries, Ed. D.Symes. Fishing News Book, Blackwell Science Ltd, Oxford. 242 pp.
- Taylor, M.H., 1990. Estuarine and intertidal teleosts In Reproductive seasonality in teleosts: environmental influences, p. 109-125. Ed. by A.D. Munroe, T.J. Lam, and A.P. Scott. CRC Press, Boca Raton, FL. 254 pp.
- Tremain, D.M., Harnden, C.W., and Adams, D.H., 2004. Multidirectional movements of sportfish species between an estuarine no-take zone and surrounding waters of the Indian River Lagoon, Florida. Fish. Bull. 102: 533-544.
- Tucker, J.W., and Faulkner, B.E. 1987. Voluntary spawning patterns of captive spotted seatrout. Northeast. Gulf Sci. 9: 59-63.
- Vanderkooy, S.J. and Muller, R.G., 2003. Management of spotted seatrout and fishery participants in the U.S. pp. 227-245. In Biology of the spotted seatrout Ed. By S.A. Bortone, CRC Press, Boca Raton, FL.
- van der Veer, H.W., Berghahn, R., Miller, J.M., and Rijnsdorp, A.D., 2000. Recruitment in flatfish, with special emphasis on North Atlantic species: progress made by the Flatfish Symposia. ICES J. Mar. Sci. 57: 202-215.
- Venables, W.N., and Ripley, B.D., 1999. Modern applied statistics with S-PLUS. (3rd edn), Springer, New York.
- Vetter, R.D., 1977. Respiratory metabolism of, and nicheseparation between two co-occurring congeneric species, *Cynsocio* *nebulosus* and *Cynoscion arenarius*, in a south Texas estuary. MS Thesis, University of Texas at Austin.
- Vetter, R.D., 1982. Seasonal metabolic compensation in sympatric seatrout: adaptation to the estuary.
- Vigliola, L., Harmelin-Vivien, M., and Meekan, M.G., 2000. Comparison of techniques of back-calculation of growth and settlement marks from the otoliths of three species of *Diplodus* from the Mediterranean Sea. Can. J. Fish. Aquat. Sci. 57: 1291-1299.

- Waggy, G.L., Brown-Peterson, N.J. and Peterson, M.S. 2006. Evaluation of the reproductive life history of the sciaenidae in the Gulf of Mexico and Caribbean Sea: "Greater" versus "Lesser". *Proc. Gulf Caribb. Fish. Inst.* 57: 263-282.
- Wang, S., Morishima, G., Sharma, R., and Gilbertson, L., 2009. The use of generalized additive models for forecasting the abundance of Queets River coho salmon. *N. Am.. J. Fish. Mgmt* 29:423–433.
- Walters C.J., and Martell J.D., 2004. *Fisheries Ecology and management*. Princeton University Press, Princeton, NJ, 399 pp.
- Walters, S., Lowerre-Barbieri, S.K., Bickford, J., and Mann, D., 2009. Using a passive acoustic survey to indentify spotted seatrout spawning sites and associated habitat in Tampa Bay, Florida. *Trans. Am.. Fish. Soc.* 138: 88-98.
- Ward, R., Bowers, K. Hensley, R. Mobley, B. and Belouski, E., 2007. Genetic variability in spotted seatrout (*Cynoscion nebulosus*) determined with microsatellite DNA markers. *Fish. Bull. US* 105: 197-206.
- Wieland, K., and Jarre-Teichmann, A., and Horbowa, K., 2000. Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. *ICES J. Mar. Sci.* 52: 452-464.
- Wohlschlag, D.E., and Wakeman, J.M., 1978. Salinity stresses, metabolic responses and distribution of the coastal spotted seatrout, *Cynoscion nebulosus*. *Contr. Mar. Sci.* 21: 171-185.
- Wuenschel, M.J., Werner, R.G. and Hoss, D.E. 2004. Effect of body size, temperature and salinity on routing metabolism of larval and juvenile spotted seatrout. *J. Fish Biol.* 64: 1088-1102.
- Xiao, Y., 1996. How does somatic growth rate affect otolith size in fishes? *Can. J. Fish. Aquat. Sci.* 53: 1675-1682.
- Yankee, D.H., Peine, J.D., Tuberville, J.D. and Gowan, D.W., 1999. Ecosystem stabilization and restoration: the Clinch-Powell River basin initiative. In *Ecosystem management for sustainability*. Ed. J.D. Peine, CRC Press, Boca Raton, FL. 500 pp.
- Yeo, G.-K., 1984. A note of caution on using statistical software. *The Statistician*, 33: 181-184.
- Živkov, O., 1996. Critique of proportional hypothesis and methods for back-calculation of fish growth. *Envir. Biol. Fish* 46: 309-320.

Wissenschaftlicher Werdegang für Sven Kupschus

Persönliche Daten:

Name: Sven Richard Kupschus
 Geburts Datum: 8th February 1970
 Alter: 40
 Geburtsort: Dayton, OHIO, USA
 Eltern: Dr. Hedda Kupschus MD und Dr. Peter H Kupschus
 Nationalität: Deutsch Amerikanisch

Arbeits Adresse: Cefas, Lowestoft Laboratory, Pakefield Road, Lowestoft, NR33 0HT, England
 e-mail sven.kupschus@ceafs.co.uk
 Tel +44 1502 524454

Schulung und Qualifikationen:

1992-1994 Masters (MSc) in Fisheries Biology and Management at the University College of North Wales, Bangor (Bangor University), mit Abschluß:
 pass with distinction = first class degree

Forschungsprojekt: The Ecology of Juvenile Sea Bass (*Dicentrarchus labrax*). An attempt to establish the importance of the Conwy as a nursery ground based on evidence from the Alaw and Foryd estuaries. I learnt a lot about the ecology of sea bass, complex statistical analysis of mark recapture and growth data, communication skills with government bodies such as the Ministry of Agriculture Fisheries & Food (MAFF), the National Rivers Authority (NRA) and the Nature Conservancy Council for Wales (CCW).

1988-1991 Joint Honours Bachelors (BSc) in Marine Biology / Biochemistry an der University College of North Wales Bangor (Bangor University), mit Abschluß:
 upper second class degree

Nebenfächer Biology, Earth Sciences and Statistics.

Forschungsprojekt: Varying Methods of Protein Determination and their Consequences on other assimilatory Parameters in Fish nutritional Studies (submitted 14th Jan 1991), developed my laboratory skills, biochemical assay techniques and fish husbandry abilities.

1982-1988 European Baccalaureate an der European School Culham, England

1980-1981 Gymnasium Zitadelle der Stadt Jülich, Jülich, NRW, Germany

1976-1980 Gemeinschaftsgrundschule Jülich Nord, Jülich, NRW, Germany

Vollzeitbeschäftigung:

Nov05–Present Senior Scientific Officer: Fisheries Research Scientist employed by the Centre for Environment, Fisheries & Aquatic Sciences (CEFAS).

Sep02–Oct 05 Higher Scientific Officer. Fisheries Research Scientist employed by the Centre for Environment, Fisheries & Aquatic Sciences (CEFAS).

Feb 01-Aug 02 Assistant Research Scientist employed by the Florida Marine Research Institute (FWC) Fisheries-Independent Monitoring Program.

Jul 99-Feb 01 Research Staff employed by the Florida Marine Research Institute (FWC) Stock Assessment Group on a three year federal Sportfish Restoration research grant .

May 96-Jun 99 Research Staff employed by the Florida Marine Research Institute (FWC) Fisheries-Independent Monitoring

