Proposed South Atlantic Council ABC Control Rule

Report of the SAFMC SSC September 2009 *Revised August 2010, April 2011*

Background

The SAMFC SSC first discussed acceptable biological catch (ABC) control rules in June 2008 in response to publication of a proposed rule addressing National Standards 1 (NS1) guidelines for the Magnuson-Stevens Reauthorization (MSRA). An issue paper outlining various alternative approaches to establishing ABC was provided to the Council in September 2008. The Council supported further developing a control rule approach which specified ABC as a function of yield at maximum sustainable yield (MSY) and assessment uncertainty. The Council further specified that ABC should be set at a level providing a 25% chance of overfishing, with a range of values corresponding to 10 to 50% chance of overfishing. The Council intends to specify ABC control rules in its comprehensive annual catch limit (ACL) amendment.

Although the approach suggested in September 2008 provides guidance for assessed stocks for which the probability of overfishing can be provided in terms of yield, it does not address those stocks that lack assessments. Therefore, the SSC requested a special meeting for March 2009 devoted solely to developing an ABC control rule that could be applied to all managed stocks. During that meeting, the SSC developed the control rule reflected in this document after much deliberation and discussion.

First, the group decided on general characteristics and components of the rule and developed a framework of dimensions and tiers. Dimensions reflect the critical characteristics to evaluate, including data and assessment information availability and life history traits. Tiers are objective levels within dimensions that reflect the range of information available. Each tier is assigned a score which contributes to the overall adjustment factor.

Once the general approach was established, a number of example stocks were put through the framework to ensure that it included adequate tiers to accommodate a variety of circumstances and appropriate dimensions to adequately address uncertainty. This exercise led to considerable further discussion that better defined the concepts and resulted in some tiers being combined to keep the rule as parsimonious as possible. The following sections of this document describe the tiers and summarize critical discussions that occurred during development.

An important caveat must be stated upfront. The approach described here is applicable when the OFL can be stated in weight and some measure of statistical uncertainty about the OFL can be estimated. Future discussions and development will focus on ways to apply this methodology in a consistent manner to stocks for which the OFL or its statistical uncertainty cannot be estimated.

Control Rule Concept

The SSC agreed that the ABC control rule should provide an objective means of determining the buffer, or amount of separation, between the overfishing level (typically MSY) and the ABC. The desired rule should evaluate multiple characteristics, accommodate varying data levels and assessment information, and incorporate productivity and susceptibility measures. Finally, the control rule should provide objective adjustments to the probability of overfishing according to key risk factors, with actual ABCs expressed as yield in mass obtained through a probability density distribution or a "P*" analysis.

Discussion of the general concept and approach led to creation of a system of dimensions composed of multiple tiers that are scored to provide a value that can be used to select the appropriate probability of overfishing for each stock. Each stock evaluated receives a single "adjustment factor", which is the sum of tier scores across dimensions and which ultimately determines the amount of buffer or separation between OFL and ABC. Adjustment factors are subtracted from the "base probability of overfishing" to provide the "critical probability". The base probability of overfishing is the value used to determine OFL. The critical probability is a probability of overfishing that is used to determine ABC in the same manner that the base probability is used to determine MSY and OFL. Through this process, tier scores equate to an adjustment in the probability of overfishing occurring, and do not represent, or necessarily correspond to, a specific poundage or percentage of the OFL. Recommended ABC values are

derived from probability density functions that provide the probability of overfishing occurring for any particular yield.

Control Rule Characteristics

The SSC began deliberations by developing a list of desirable characteristics and principles for ABC control rules. These included:

- Incorporate a tiered system based on data and assessment information availability
- Include objective criteria with numerical scoring that can be applied to all stocks
- Incorporate stock status
- Reflect the degree to which uncertainty is characterized
- Acknowledge the cumulative nature of uncertainty
- Provide a means to incorporate vulnerability and life history traits, ideally through inclusion of productivity-susceptibility analyses (PSA) scores
- Provide flexibility to accommodate a wide range of biological characteristics, assessment methods and information, data availability, and assessment age
- Provide an objective means of incorporating potential changes in data and assessment information availability over time

Control Rule Dimensions

The SSC incorporated these general characteristics and principles into a series of tiers and dimensions that form the foundation of the control rule. Four dimensions are included in the proposed control rule framework: assessment information, characterization of uncertainty, stock status, and productivity/susceptibility of the stock. Each dimension contains multiple levels or tiers that can be evaluated for each stock to determine a numerical score for the dimension. The four dimensions and their tiers are described in detail in the following section and summarized in Table 1. Application to particular stocks is illustrated in Table 2.

Dimension 1. Assessment Information

The assessment information dimension reflects available data and assessment outputs. The five tiers within this dimension range from a full quantitative assessment which provides biomass, exploitation, and MSY-based reference points to the bottom tier for those stocks which lack reliable catch records.

The age or degree of reliability of an assessment can be incorporated when determining the scoring for an individual stock. For example, a stock having a pre-SEDAR assessment may be ranked at a lower tier despite that assessment having the required outputs for a higher tier, because the reliability of an output value cannot be determined or the method by which an output was obtained is not clearly documented. Estimates from an assessment may be considered unreliable or inapplicable when considered at a later date (e.g. assumed equilibrium conditions may have changed). Similarly, an age-aggregated assessment approach may provide an estimate of MSY, but in some instances such estimates may be considered less reliable than estimates from an age-structured approach. The intent is that tier rankings are based on the data and outputs considered reliable at the time the ranking is made. Scores for these tiers increase as the level of available information declines.

Assessment Information Tiers Scoring

- 1. Quantitative assessment provides estimates of exploitation and biomass; includes MSY-derived benchmarks. (0)
- 2. Quantitative assessment provides estimates of either exploitation or biomass, but not MSY benchmarks; requires proxy reference points. (-2.5)
- 3. Quantitative assessment that provides relative measures of exploitation or biomass; absolute measures of status are unavailable; references may be based on proxy. (-5)
- 4. Reliable catch history available (-7.5)
- 5. Scarce or unreliable catch records (-10)

Dimension 2. Characterization of Uncertainty

This dimension is considered critical because it specifically addresses language in the MSRA stating that ABC should be reduced from OFL to account for assessment uncertainty. Because accounting for uncertainty tends to be a cumulative process, an incomplete or partial accounting of know uncertainties will tend to underestimate the underlying uncertainty in the results. Tiers for this dimension reflect how well uncertainty is characterized, not the actual magnitude of the uncertainty. The magnitude is incorporated through the assessment and is reflected in the distribution of yield estimates. Adjustment scores for this tier increase as the degree and completeness of uncertainty characterizations decrease..

Uncertainty Tiers, Examples, and Scoring

1. Complete. This tier is for assessments providing a complete statistical (e.g. Bayesian re-sampling approach) treatment of major uncertainties, incorporating both observed data and environmental variability, which are carried forward into reference point

calculations and stock projections. A key determinant of this level is that uncertainty in both assessment inputs and environmental conditions are included. (0)

Example: No currently assessed stocks meet this level.

2. High. This tier represents those assessments that include re-sampling (e.g. Bootstrap or Monte Carlo techniques) of important or critical inputs such as natural mortality, landings, discard rates, age and growth parameters. Such re-sampling is also carried forward and combined with recruitment uncertainty for projections and reference point calculations, including reference point distributions. The key determinant for this level is that reference point estimates distributions reflect more than just uncertainty in future recruitment. (-2.5)

Example: SEDAR 4, South Atlantic snowy grouper and tilefish.

3. Medium: This tier represents assessments in which key uncertainties are addressed via statistical techniques and sensitivities, but the full uncertainties are not carried forward into the projections and reference point calculations. Projections may, however, reflect uncertainty in recruitment and population abundance. Although outputs include distributions of F, F_{MSY} as in the 'High' category above, in this category fewer uncertainties are addressed in developing such distributions. One example for this level is a distribution of F_{MSY} which only reflects uncertainty in recruitment. (-5)

Examples: SEDAR 15, South Atlantic red snapper and greater amberjack; SEDAR 17, South Atlantic Spanish mackerel and vermilion snapper

4. Low. This tier represents those assessments lacking any statistical treatment of uncertainty. Sensitivity runs or explorations of multiple assessment models may be available. The key determinant for this level is that distributions for reference points are lacking. (-7.5)

Example: SEDAR 2, South Atlantic black sea bass

5. None. This tier represents assessments that only provide single point estimates, with no sensitivities or other evaluation of uncertainties. (-10)

Example: None.

Dimension 3. Stock Status

Stock status is included among the dimensions so that an additional adjustment to ABC can be added for stocks that are overfished or overfishing. Five tiers are included, ranging from a high biomass and low exploitation level where no additional buffer is applied to the situation

where either is unknown and the highest buffering is applied. With the exception of distinguishing between the top two tiers which both reflect stocks that are neither overfished nor experiencing overfishing, application of these tiers is straightforward and based directly on the final status determinations, independent of the sensitivity or uncertainty in that final determination. Scores for these tiers increase for decreasing and unknown stock status.

Stock Status Tiers and Scoring.

- 1. Neither overfished nor overfishing, and stock is at high biomass and low exploitation relative to benchmark values. (0)
- 2. Neither overfished nor overfishing, but stock may be in close proximity to benchmark values (-2.5)
- 3. Stock is either overfished or overfishing (-5)
- 4. Stock is both overfished and overfishing (-7.5)
- 5. Either status criterion is unknown. (-10)

Dimension 4. Productivity and Susceptibility Considerations

The final dimension addresses biological characteristics of the stock. This includes productivity, which reflects a population's reproductive potential, and susceptibility to overfishing, which reflects a stocks propensity to be harvested by various fishing gears. Efforts to quantify these characteristics, generally termed "PSA analyses", typically incorporate a variety of life history characteristics in a framework that distills many metrics into a single risk score. The two primary approaches currently available, one from NMFS and the other from MRAG, follow similar procedures, but incorporate slight differences in how characteristics are scored and how missing information is addressed. For example, the MRAG formulation incorporates a scoring value for parameter for which values are unknown into the overall score, whereas the NMFS formulation omits from scoring those parameters where the values are unknown.

After presentations on both approaches and considerable discussion on their differences, the SSC decided to incorporate the MRAG formulation of PSA into the SAFMC ABC control rule. The SSC believed this approach to be preferable based on the broad suite of attributes considered in the scoring and the inclusion of unknowns in the scoring. In general, it is believed that including unknowns in the scoring will provide stronger encouragement to address the

unknown parameters since doing so will in many cases tend to moderate the buffer contributed by the PSA value. Further, because unknown information contributes to overall uncertainty, accounting for potential unknowns in the scoring is consistent with the underlying control rule framework.

PSA Tiers and Scoring

- 1. Low Risk. High productivity, low vulnerability and susceptibility, score $<2.64^{1}$ (0)
- 2. Moderate Risk. Moderate productivity, vulnerability, susceptibility, score 2.64-3.18¹ (-5)
- High Risk. Low productivity, high vulnerability and susceptibility, score >3.18¹ (-10)
 ¹Scores as described in Hobday *et al.*, 2007

Determining Total Adjustment and Final ABC Recommendations

The uncertainty buffer, or difference between OFL and ABC, is expressed in terms of a reduction in the "probability of overfishing", or "P*". The adjustment score provided by the tiers and dimensions represents the amount by which P* is reduced to obtain the critical value for P*. Therefore, the key product of the control rule is the sum the scores for all the dimensions because that is the ABC adjustment factor that is used to calculate the critical value for P* from the base P*. The scoring of tiers within dimensions is designed to provide a maximum P* adjustment of 40% and a minimum of 0%. When applied to the base MSY specified at the 50% level, this range of possible adjustment results in a range of critical values for P* from 10% to 50%. These critical values are then used to determine the actual ABC using projection tables that provide the level of annual yield that corresponds to a particular P*.

The ABC adjustment factor is obtained by summing the scores across dimensions once the data are evaluated and tier assignments are made within each dimension. The scoring system is designed so that low values are assigned for the 'best' circumstances and the values increase as circumstances worsen. Considering dimension 1 for example, a stock which has an assessment providing estimates of biomass, exploitation, and MSY-based reference points would have a score of 0, while a stock which is unassessed and has unreliable catch records would receive a score of 10. Each stock will be categorized by tiers before the score is tallied so that categorizations are made independent of the final outcome. The critical P* is expressed as a probability of overfishing and is derived by subtracting the ABC adjustment factor from 50%. For example, if the adjustment factor (sum of the dimension scores) is 20, the critical value for P* will be 30% (50%-20), and the ABC recommendation will be based on a 30% probability of overfishing occurring in the year for which the recommendation is made. Note that, due to varying shapes in the distribution of estimated yield, it is unlikely that the observed difference between MSY and ABC will equal the difference between the P* that defines MSY and the critical P*, and it is also unlikely the two stocks receiving identical critical P* values will reflect equal differences between ABC and OFL when such differences are compared in weight units.

Setting ABC equal to OFL implies a P* equal to 50%, where 50% represents the chance of overfishing occurring. Reducing P* will reduce ABC and provide a reduction in the probability of overfishing occurring. The relationship between the amount of reduction in P* and the resulting reduction in ABC is determined by the shape of the distribution of yield about the management parameters. For a given reduction in P*, broad distributions (suggesting higher uncertainty) will result in larger reductions in ABC whereas narrower distributions (suggesting lower uncertainty) will result in smaller reductions in ABC.

Using the ABC control rule described here, the range of P* that is considered acceptable is from 50% to 10%. This range was derived after considering Council guidance directing the SSC to consider ABCs based on probabilities of overfishing between 10% and 40%, general guidance under the MSA that management actions must have at least a 50% chance of success, and the common practice of specifying MSY based on the midpoint of a distribution of possible outcomes. The top tier in each dimension does not reduce P*, so the ABC recommendation for a stock receiving the top score across all dimensions would be the same as the OFL recommendation and there would be no buffer applied between ABC and OFL. While this may be perceived as potentially risk-prone, and inconsistent with some interpretations of the language describing ABC with regard to OFL, the only situation in which this would occur in this framework is for a stock with a complete assessment including full, probability-based uncertainty evaluations that is at low exploitation and high biomass, and is considered highly productive with low vulnerability and susceptibility. It should be noted that none of the stocks

examined so far meet these criteria, and those stocks that have not been examined lack stock assessments and therefore they too will fail to meet these criteria.

The SSC considered whether each dimension should be equally scored and contribute the same relative weight to the final adjustment factor. After discussing various weighting schemes and approaches, the SSC determined that there was insufficient justification at this time to weight any particular dimension greater than another as all are considered important to objectively evaluating overall uncertainty. However, the SSC also recognizes that this could change and the ABC could be modified in the future if evidence develops that suggests one dimension should be more influential than the others.

The SSC is cognizant that ABCs, and the degree of separation between ABC and OFL, will be compared across stocks when recommendations are reviewed. The SSC also recognizes the importance of being consistent when evaluating the level of information for a wide range of stocks. In discussing ways of promoting consistency when multiple stocks must be evaluated, the SSC decided that tier assignments should be made within a single dimension for all stocks under consideration, as opposed to evaluating single stocks across all dimensions. This will help ensure that the data level for each stock is evaluated relative to and consistent with other stocks being considered. It is anticipated that approaching the process in this order will help avoid situations where stocks with similar conditions receive different tier ratings.

Overfished Stocks and Rebuilding Plan Selection

The adjustment factor can also be used to derive a probability of rebuilding success for selecting rebuilding schedules. The probability of rebuilding success is determined by subtracting the P* critical value from 100%, such that stocks with high P* values could be managed using a rebuilding schedule that approaches the 50% level commonly used now, and those with the lowest P* values will require rebuilding schedules with higher probability of success, up to a maximum of 90%.

The adjustment factor for stocks achieving the lowest scores across all dimension would be 0, resulting in a P* of 50% which would lead to recommendation of a rebuilding schedule with a 50% (100-50) probability of success by the end of the rebuilding period (Tmax), consistent with most current rebuilding schedules. The adjustment factor for stocks receiving the

highest scores across all dimensions would be 40%, resulting in a critical P* of 10% (50 baseline -40 for buffer adjustment) and compelling a recommendation for rebuilding projections based on 90% probability of success by the end of the rebuilding period.

Values for the rebuilding success probability are provided for all stocks in Table 2 for illustration of the concept, although in application only stocks with status 'overfished' would require this parameter. Because the decisions required to develop the rebuilding plan are the same ones required to develop ABC, this framework allows estimation of both the rebuilding schedules and the final yield for a rebuilt stock from a single set of decisions. The only change required once a stock reaches the rebuilt status would be to calculate an updated adjustment factor reflecting the change in stock status from 'overfished' to 'not overfished and not overfishing'. Any such changes can be evaluated efficiently and quickly, and the system is essentially self-adjusting to critical events such as a change in stock status because the criteria and scorings are all determined in advance.

Using red porgy as an example, the total buffer adjustment factor of 15 results in a critical P* of 35% (50% baseline – buffer adjustment of 15) and a rebuilding probability of success of 65% (100% baseline – P* of 35). However, once the stock is rebuilt and the stock is neither overfished nor is overfishing occurring, scoring within the status dimension changes from tier 3 (adjustment value of 5) to tier 2 (adjustment value of 2.5) and the overall adjustment factor decreases by 2.5 to 12.5. The expected critical P* for the rebuilt stock becomes 37.5 and the expected ABC for the rebuilt stock can be determined from the probability distribution table of MSY at equilibrium or rebuilt conditions. In management terms, the resultant recommendations for red porgy would be to select a rebuilding plan with at least a 65% chance of achieving SSB>SSB_{MSY} within the allotted rebuilding time period, followed by a recommendation to manage not to exceed a 37.5% chance of overfishing occurring once the stock is rebuilt.

Depletion Threshold

The NS1 guidelines state that an 'ABC control rule...may establish a stock abundance level below which fishing would not be allowed.' Currently the Pacific Fishery Management Council uses a 10% threshold. Specifically, if biomass is estimated below 10% of the virgin condition, then directed fishing is not allowed. The SAFMC SSC supports the concept of a depletion threshold and elimination of directed fishing when SSB falls below the threshold, and

recommends that the threshold be established at 10% of unfished conditions. The SSC will recommend that directed fishing not be allowed if there is a reliable indication that current biomass is at or below 10% of the unfished biomass or, in cases where biomass estimates are considered unreliable, if SPR is at or below 10%.

Future Control Rule Modifications

The SSC began working on this ABC control rule in June 2008, following approval of the MSRA but before finalization of revised National Standard Guidelines and before finalization of implementation guidelines. The Final Rule on establishing ACL's became available during the period that the SSC discussed the control rule and helped direct this final version. Although the SSC believes the rule described herein is consistent with the language of the MSRA and ACL Final Rule, and that Council guidance as to the overall acceptable level of risk and base P* that determines MSY and OFL is considered and incorporated, the Committee recognizes that this rule may require modification in the future as final guidance on MSRA implementation becomes available. The Committee also recognizes that this document provides scientific advice to the Council, which will ultimately adopt the Control Rule and in so doing may make modifications.

Experience in applying the rule and future scientific advances may also trigger changes in the control rule. Although the SSC attempted to consider the full range of situations and scenarios expected across stocks managed by the South Atlantic Council, it is acknowledged that situations may arise that cause difficulties in actual application and interpretation the rule and hinder the resultant ABC recommendations. Changes in the dimensions, tiers, and scoring approach may be needed in the future as the rule is tested through application to the many stocks managed by the Council. Further development in methods of analyzing and expressing probabilities of overfishing could also lead to changes in how ABC is determined from the adjustment factor provided by the control rule. Finally, the eight SSCs of the eight Fishery Management Councils are all working along a similar path to develop ABC control rules. These SSCs include many of the top fisheries scientists in the Country and it is expected that many good ideas will emerge from this collective effort. Such ideas will be shared amongst all SSCs through the annual National SSC Meetings initiated in 2008, and the SAFMC SSC intends to take full advantage of the insights, shared experiences, and potential improvements to ABC control rules offered by such national collaboration.

Table 1. Hierarchy of dimensions and tiers within dimensions used to characterize uncertainty associated with stock assessments in the South Atlantic. Parenthetical values indicate (1) the maximum adjustment value for a dimension; and (2) the adjustment values for each tier within a dimension.

- I. Assessment Information (10%)
 - 1. Quantitative assessment provides estimates of exploitation and biomass; includes MSY-derived benchmarks. (0%)
 - 2. Reliable measures of exploitation or biomass; no MSY benchmarks, proxy reference points. (2.5%)
 - 3. Relative measures of exploitation or biomass, absolute measures of status unavailable. Proxy reference points. (5%)
 - 4. Reliable catch history. (7.5%)
 - 5. Scarce or unreliable catch records. (10%)
- II. Uncertainty Characterization (10%)
 - 1. **Complete**. Key Determinant uncertainty in both assessment inputs and environmental conditions are included. (0%)
 - 2. **High**. Key Determinant reflects more than just uncertainty in future recruitment. (2.5%)
 - 3. **Medium**. Uncertainties are addressed via statistical techniques and sensitivities, but full uncertainty is not carried forward in projections. (5%)
 - 4. Low. Distributions of Fmsy and MSY are lacking. (7.5%)
 - 5. None. Only single point estimates; no sensitivities or uncertainty evaluations. (10%)
- III. Stock Status (10%)
 - 1. Neither overfished nor overfishing. Stock is at high biomass and low exploitation relative to benchmark values. (0%)
 - 2. Neither overfished nor overfishing. Stock may be in close proximity to benchmark values. (2.5%)
 - 3. Stock is either overfished or overfishing. (5%)
 - 4. Stock is both overfished and overfishing. (7.5%)
 - 5. Either status criterion is unknown. (10%)
- IV. Productivity and Susceptibility Risk Analysis (10%)
 - 1. Low risk. High productivity, low vulnerability, low susceptibility. (0%)
 - 2. Medium risk. Moderate productivity, moderate vulnerability, moderate susceptibility. (5%)
 - 3. High risk. Low productivity, high vulnerability, high susceptibility. (10%)

		Dimension			Adjustment	Critical	P(Successful	
Stock		I	П	Ш	IV	Factor (total score)	P*	Rebuild)
	Tier Within					(1010) 00010)		
Golden Lilefish	Dimension	1	2	3	3		32.5	67.5
	Score	0.0	2.5	5.0	10.0	17.5		
Spour Crouper	Tier Within	4	2	4	2			
Showy Grouper	Score		∠ 2.5	4	3 10 0	20.0	30.0	70.0
	Tion Within	0.0	2.5	7.5	10.0	20.0		
Gag Grouper	Dimension	1	3	3	3		30.0	70.0
c	Score	0.0	5.0	5.0	10.0	20.0		
	Tier Within							
Red Snapper	Dimension	2	3	4	2		30.0	70.0
	Score	2.5	5.0	7.5	5.0	20.0		
	Tier Within							
Vermilion Snapper	Dimension	2	3	5	2		27.5	72.5
	Score	2.5	5.0	10.0	5.0	22.5		
Black Soa Bass	Tier Within	1	2	2	2		05.0	05.0
DIACK SEA DASS	Penalty	0.0	50	50	2 5 0	15.0	35.0	65.0
	Tier Within	0.0	0.0	0.0	0.0	10.0		
Red Porgy	Dimension	1	3	3	2		35.0	65.0
	Score	0.0	5.0	5.0	5.0	15.0		
	Tier Within							
Yellowtail Snapper	Dimension	1	3	2	2		37.5	62.5
	Score	0.0	5.0	2.5	5.0	12.5		
	Tier Within							
Hogfish	Dimension	4	5	5	3		12.5	88.5
	Score	7.5	10.0	10.0	10.0	37.5		
	Tier Within							
Goliath Grouper	Dimension	4	5	5	3		12.5	88.5
	Score	7.5	10.0	10.0	10.0	37.5		
Mutton Snapper	Tier Within	1	з	2	З		20 E	67 E
Matton Shapper	Score	0.0	5.0	2.5	10.0	17.5	32.5	c.10
	Tier Within	0.0	010	2.0				
Greater Amberjack	Dimension	1	3	2	2		37.5	62.5
	Score	0.0	5.0	2.5	5.0	12.5		
	Tier Within							
King Mackerel	Dimension	3	3	2	3		27.5	72.5
	Score	5.0	5.0	2.5	10.0	22.5		
Spaniah Maakaral	Tier Within	0	0	F	0		05.0	75 0
Spanish Mackerel	Score	ა 50	ა 50	ວ 10 0	∠ 50	25.0	25.0	75.0
	00016	5.0	5.0	10.0	0.0	20.0		

Table 2. Example of tier assignments, scores, adjustment factors, and critical probability values as applied to assessed stocks in the South Atlantic.

NOTE: This table provides initial application examples based on information available as of March 2009, and do not constitute actual *P** or *ABC* recommendations of the SSC.

<u>Addenda</u>

Recommended Tiered Approach to Deriving OFL and ABC Values for Fisheries

August 2010

The SSC discussed control rules for unassessed stocks over several meetings in 2010. An initial approach was put forth in April and reviewed by the Council in June. The Council raised some concerns with the April proposal and provided guidance to the SSC along with a request for further consideration. In August 2010 the SSC discussed the Council's guidance and considered progress on this topic made in other regions, along with initial guidance provided through the National SSC workshop ad hoc workgroup on unassessed stocks control rules. These deliberations led to the rule described here.

<u>**Tier 1**</u> – Assessed stocks.- Whenever possible, ABC recommendations should conform to an ABC control rule that is based on the probability of overfishing(i.e., P* approach)

- Addressed with current control rule

-Provides pdf of OFL.

-Approach will be consistent.

Note: This tier is addressed in the preceding section

<u>**Tier 2</u>** - Depletion based stock reduction analysis (DBSRA) – (Dick and MacCall).</u>

-If the information necessary to implement the Council's approved ABC control rule is not available (e.g., MSY reference points, projected stock size, distribution of OFL, etc.), then the basis of the ABC should be explicit about what aspects of the derivation were based on expert judgment.

-Requires full history of landings and other life history info for the stock

- Gives a pdf of OFL. Could apply P* or other risk/p level to derive ABC

<u>**Tier 3**</u> - depletion-corrected average catch (DCAC) (MacCall 2009). If components of the ABC control rule cannot be provided, a provisional ABC should be based on alternative approaches, but deviation from the control rule should be justified..

-Requires less data than 2nd tier

- Provides provisional ABC directly – OFL unknown

<u>Tier 4</u>- Catch only.

-Difficult to prescribe.

-Requires judgment and careful consideration of all available sources, which may vary greatly between stocks falling in this tier

<u>Addenda</u>

Decision tree approach for addressing Level 4 stocks

<u>April 2011</u>

The SSC further modified Tier 4 of the Control Rule, providing better guidance for deriving ABC. A decision tree approach is applied to Tier 4 stocks to determine the appropriate ABC value. OFL is evaluated on a case by case basis, considering available information.

- 1. Are current catches likely to impact the stock? NO: Recommend move stock to ecosystem species category YES: Go to #2
- 2. Is it expected that increased catch (beyond current range, considering observed variability) will lead to decline or other stock concerns?

NO: ABC = 3rd highest point in the 99-08 time series. YES: Go to #3

3. Is the stock part of a directed fishery or is it primarily bycatch with other species?

DIRECTED: ABC = Median 99-08

BYCATCH/INCIDNETAL: Go to #4.

4. Bycatch, Incidental Catches.

Evaluate the situation and information.

The SSC's intent is to evaluate the situation and provide guidance to Council on possible catch levels, risk, and actions to consider for bycatch and directed components.

If the species is bycatch in a fishery targeting other species, issues that should be considered include: trends in that fishery, the current regulations, and the effort outlook.

If the directed fishery is increasing, and bycatch of the stock of concern is also increasing, the Council may need to find a means to reduce interactions or bycatch mortality. If that is not feasible, the Council will need to impact the directed fishery.

<u>Addenda</u>

Incorporate ORCS approach for unassessed stocks

November 2011

The SSC reviewed the "ORCS" report (Berkson et al 2011) in November 2011 and recommended that the ORCS Working Group approach be added as an additional evaluation approach for Tier 4 stocks. It was also noted that the general tier approach in this control rule is consistent with that recommended in the report. The following tables are taken from the ORCS report and summarize the approach for unassessed stocks.

Overall ORCS Working Group Recommendatiosns:

- Apply DB-SRA to a stock, if possible. The main limitation here is the availability of a complete time series of historical catch, which is often not available.
- If it is not possible to apply DB-SRA, apply DCAC to a stock. DCAC's main limitation is that it is only appropriate for stocks with moderate to low natural mortality rates (≤ 0.20 yr⁻¹).
- If DB-SRA and DCAC are not possible, apply the ORCS Working Group's Approach. The main limitation with this approach is that a number of critical decisions are required before it can be made operational. Some would also view this as an advantage, as it provides flexibility in its establishment.
- Finally, in some cases none of the above methods are practical for setting ABCs for an
 individual stock, as specific ORCS stocks may not have the capability to be effectively
 managed or monitored. In these cases, it may be best to use a stock complex approach.
 There are many limitations of applying a stock complex approach as described above,
 and the ORCS Working Group cautions against overusing or misusing this approach, as it
 may result in converse of precautionary management, exactly what MSA was designed to
 avoid.

Berkson, J., et al, 2011. Calculating Acceptable Biological Catch for Stocks that have Reliable Catch Data Only (Only Reliable Catch Stocks -- ORCS). NOAA/NMFS Tech. Mem. NMFS-SEFSC-616.

Table 4. Table of attributes for assigning stock status for historical catch-only assessments.

Overall scores are obtained by an unweighted average of the attributes for which scoring is possible, although alternative weighting schemes could also be considered. An initial assignment to a stock status category is: mean scores>2.5—heavily exploited; stocks with mean scores 1.5-2.5--moderately exploited; and stocks with mean scores<1.5--lightly exploited. When the attribute does not apply or is unknown it can be left unscored.

		Stock status	
Attribute	Lightly exploited (1)	Moderately exploited (2)	Heavily exploited (3)
Overall fishery exploitation	All known stocks are either moderately or	Most stocks are moderately exploited. No	Many stocks are overfished
based on assessed stocks	lightly exploited. No overfished stocks	more than a few overfished stocks	
Presence of natural or	Less than 50% of habitat is accessible to fishing	50%-75% of habitat is accessible to fishing	>75% of habitat is
managed refugia			accessible to fishing
Schooling, aggregation, or	Low susceptibility to capture (specific behaviors	Average susceptibility to capture (specific	High susceptibility to
other behavior responses	depend on gear type)	behaviors depend on gear type)	capture (specific behaviors
affecting capture			depend on gear type)
Morphological characteristics	Low susceptibility to capture (specific	Average susceptibility to capture (specific	High susceptibility to
affecting capture	characteristics depend on gear type)	characteristics depend on gear type)	capture (specific
			characteristics depend on
			gear type)
Bycatch or actively targeted	No targeted fishery	Occasionally targeted, but occurs in a mix	Actively targeted
by the fishery		with other species in catches	
Natural mortality compared	Natural mortality higher or approximately equal	Natural mortality equal to dominant species	Natural mortality less than
to dominant species in the	to dominant species $(M \ge \overline{M})$	$(M \approx \overline{M})$	dominant species (
fishery			$M < \overline{M}$)
Rarity	Sporadic occurrence in catch	Not uncommon, mostly pure catches are	Frequent occurrence in
		possible with targeting	catch
Value or desirability	Low value (< \$1.00/lb, often not retained (<	Moderate value (\$1.00 - \$2.25), usually	Very valuable or desirable
	33% of the time)	retained (34-66% of the time)	(e.g., > \$2.25/lb), almost
			always retained (>66% of
			the time).
Trend in catches (use only	Catch trend increasing or stable (assign score of	Catch trend increasing or stable (assign	Decreasing catches
when effort is stable)	1.5)	score of 1.5)	

Stock category									
Lightly exploited (B > B _{65%})	$\begin{array}{l} Moderately \ exploited \\ (B \sim B_{MSY}) \end{array}$	Heavily exploited (B < B _{20%})							
2.0 x catch statistic	1.0 x catch statistic	0.50 x catch statistic							

Table 6. Example ABC options for catch-only stocks using the ORCS Working Group Approach.

Risk level	Alternative A	Alternative B	Alternative C	Alternative D
Low risk (high productivity)	0.75 x OFL	0.75 x OFL	0.90 x OFL	0.90 x OFL
Moderate risk (moderate productivity)	0.75 x OFL	0.75 x OFL	0.75 x OFL	0.80 x OFL
High risk (low productivity)	0.75 x OFL	0.50 x OFL	0.50 x OFL	0.70 x OFL

SOUTH ATLANTIC FISHERY MANAGMENT COUNCIL SCIENTIFIC AND STATISTICAL COMMITTEE



Meeting Report ABC Control Rule Workshop

October 27 - 28, 2014 Crowne Plaza 4831 Tanger Outlet Boulevard North Charleston, SC 29418

Workshop Objectives

The objectives of this workshop were to consider how the current ABC control rule has performed and how continuing advances in assessments, particularly methods for datalimited stocks, can best be incorporated.

Time and Place

The workshop was held Oct. 27 through Oct. 28, in Charleston, SC.

Planning and Organization

The SSC requested that a workshop be held in October 2014, immediately prior to the SSC meeting, to consider revisions to the ABC control rule. A subcommittee was formed in October 2013 to develop a timeline and topic suggestions. Members include Steve Cadrin, Luiz Barbieri, and Marcel Reichert.

Documents:

Attachment 1. PstarPresentation_SSC_ABCwkshp_Oct2014: Presentation introducing TORs 1-3 and the information available.

Attachment 2. ABC_ContRule_Revise_1111: Current SA SSC ABC Control Rule.

Attachment 3. Pstar_Values: Contains all the P* values assigned by the SSC to date, including the assigned Tiers from each dimension and the frequency of occurrence of each Tier.

Attachment 4. SA_Stock_Info_2014: Contains information regarding stock status, fishing level recommendations, assessment information, sampling level, and level of landings for all South Atlantic stocks.

Attachment 5. Bentley&Stokes_2009a: Contrasting Paradigms for Fisheries Management Decision Making: How Well Do They Serve Data-Poor Fisheries?

Attachment 6. Bentley&Stokes_2009b: Moving Fisheries from Data-Poor to Data-Sufficient: Evaluating the Costs of Management versus the Benefits of Management.

Attachment 7. Carruthers_etal_2012: Evaluating methods that classify fisheries stock status using only fisheries catch data.

Attachment 8. Thorson_etal_2012b: Spawning biomass reference points for exploited marine fishes, incorporating taxonomic and body size information.

Attachment 9. Carruthers_etal_2013: Evaluating methods for setting catch limits in data-limited fisheries.

Attachment 10. Mangel_etal_2013: A perspective on steepness, reference points, and stock assessment.

Attachment 11. Wiedenmann_etal_2013: An Evaluation of Harvest Control Rules for Data-Poor Fisheries.

Attachment 12. Jun_2009_SSC_rpt_excerpt: An excerpt from the June 2009 SSC report that describes why the SSC chose the MRAG PSA analysis over the NMFS PSA analysis for use in the ABC Control Rule.

Attachment 13. MRAG_EWGPSA_SAresults: Annual catch limits report from the Lenfest expert working group and the results for the South Atlantic stocks of the MRAG PSA analysis.

Attachment 14. NMFS_PSA: Report of the NMFS PSA work group.

Attachment 15. MRAG_PSA_GULFResults: Results for the Gulf of Mexico stocks of the MRAG PSA analysis.

Attachment 16. National_SSC_Report_5-10-11: Report of the October 2010 National SSC Workshop on ABC Control Rule Implementation and Peer Review Procedures.

Attachment 17. RPW2013_RiskPolicyReport: Fisheries Leadership and Sustainability Forum 2012 report on Risk Policy and Managing for Uncertainty across the Regional

Fishery Management Councils. Prepared in support of the NEFMC Risk Policy Workshop in March 2013.

Attachment 18. Gulf_ABC_Control_Rule: Current Gulf of Mexico SSC ABC Control Rule.

Attachment 19. MAFMC_ABC_Control_Rule_and_Risk_Policy: Current Mid-Atlantic SSC ABC Control Rule and Risk Policy.

Attachment 20. NEFMC-Control_Rules: Current New England SSC ABC Control Rule.

Attachment 21. Baseline_Conditions_NEFMC: Current New England stocks fishing level recommendations.

1. Introduction

The SSC ABC Control Rule Workshop meeting was called to order at 1:00 pm, as scheduled. The agenda was adopted without change. The SSC Chair reviewed the agenda and outlined meeting format and process.

2. Workshop Terms of Reference

- **TOR 1.** Evaluate the performance of the ABC control rule based on recent assessments, i.e., benchmark vs. subsequent update. What was the realized performance of the control rule for avoiding overfishing and achieving the expected yield when applied to different assessments?
- **TOR 2.** Evaluate the current ABC control rule, considering whether it achieves the original objective of scaling uncertainty catch level adjustments (i.e., buffers) relative to assessment uncertainty, and whether it provides adequate categories and resolution given the types of available assessment information now encountered.
- **TOR 3.** Evaluate the scoring criteria of each of the factors within control rule dimensions and consider whether criteria should be revised based on performance, as considered in TOR #1 and #2, or in light of new scientific information. For example, recently published analyses demonstrate that fixing steepness is equivalent to choosing a spawner-per-recruit proxy.
- **TOR 4.** Discuss revamping of the scoring system to be more Tier-specific, allowing more refinement of the dimensions used to provide the adjustment in ABC for each tier.
- **TOR 5.** Evaluate use and application of the PSA score. Consider whether to keep, remove, or modify the role of PSA scores in the control rule.
- **TOR 6.** Draft a report containing recommendations for potential modifications to the ABC Control Rule for presentation to the Council.

3. SSC Discussion and Recommendations

TOR 1. Evaluate the performance of the ABC control rule based on recent assessments, i.e., benchmark vs. subsequent update. What was the realized performance of the control rule for avoiding overfishing and achieving the expected yield when applied to different assessments?

The SSC thought it was difficult to address this TOR since few SAFMC-managed stocks have had benchmark assessments followed by a subsequent update. Further, none of the stocks that fit this criterion have had ABC values set according to this control rule (i.e., their ABC setting process preceded implementation of the control rule). Nevertheless, the Committee discussed some examples of stocks that although outside the ABC control rule framework had ABC recommendations that later were considered inadequate. For example, blueline tilefish was originally assigned an ABC value based on the decision tree approach (ABC control rule Level 5). A subsequent benchmark assessment determined that ABC to be too high. Conversely, wreckfish had a DCAC-based ABC (ABC control rule Level 3) much lower than the SCAA-derived ABC value obtained through a subsequent stock assessment.

Despite these issues, the SSC pointed out a dearth of objective, empirically-based information to properly evaluate the efficacy of the control rule. For example, should the Committee focus on evaluating differences in P* values across similar species/assessments or differences in buffers resulting from the combination of P* and uncertainty? Further, what metric should be used to evaluate these differences? Therefore, after much discussion the SSC felt that although the ABC control rule needs to be cleaned up there isn't enough evidence indicating the current rule is not working properly.

TOR 2. Evaluate the current ABC control rule, considering whether it achieves the original objective of scaling uncertainty catch level adjustments (i.e., buffers) relative to assessment uncertainty, and whether it provides adequate categories and resolution given the types of available assessment information now encountered.

During discussion of this TOR the SSC reinforced the idea that the basic ABC control rule performance cannot be properly evaluated at this time and, therefore, the Committee should not attempt to adjust or re-weigh control rule dimensions at this workshop. Nevertheless, the SSC discussed potential issues with the current control rule and explored possible scenarios for control rule adjustments. For example, the MAFMC increases the CV on the pdf of OFL because they don't feel their assessments truly capture uncertainty in all the input data (e.g., recreational landings, age-length keys, etc.). Suggested modifications included:

- Revamp the control rule to address 3 main categories of analysis:
 - **1.** Analytical assessments supporting P* (BAM, Production Model, etc.)
 - **2.** Analyses supported by other approaches (DBSRA, DCAC, etc.)
 - 3. Analyses applied to unassessed, data limited stocks (ORCS, Decision Tree, etc.)

- Use the main types of uncertainty characterization techniques currently associated with assessments to group stocks/assign tiers within the Uncertainty Dimension. For example:
 - Monte Carlo-based approaches: Tier 1
 - Simpler bootstrapping approaches: Tier 2
 - Just use of sensitivity analyses (no bootstrapping): Tier 3

Further, the Committee discussed the importance of evaluating what is included in the characterization of assessment uncertainty. For example, how many parameters are fixed vs. freely estimated? How often are CV's assigned or 'borrowed' rather than calculated or estimated as part of the assessment framework?

The SSC recognized that there is a general lack of understanding of the current use and formulation of the control rule by the Council and stakeholders. The Committee suggested running several SAFMC-managed species through other Councils' ABC control rules to see how they fall out in comparison to the current SAFMC approach (be sure to use several very different life history characteristics when choosing stocks for comparison).

TOR 3. Evaluate the scoring criteria of each of the factors within control rule dimensions and consider whether criteria should be revised based on performance, as considered in TOR #1 and #2, or in light of new scientific information. For example, recently published analyses demonstrate that fixing steepness is equivalent to choosing a spawner-per-recruit proxy.

The SSC recommended a revamping of the control rule's Levels 2 and 3 to be less prescriptive in the methodology to be used. Also, the Committee discussed whether 'overfished' should have more weight than 'overfishing' when evaluating stock status (Tier 3 in the control rule's Level 1). Some SSC members felt that the 'overfished' status is more important but that it is already addressed by rebuilding plans or specific language in NS1. Also, although the 'overfishing' status represents a range (i.e., the degree of overfishing the stock is under) the SSC already has the ability to take this into account when assigning values to that control rule dimension.

Regarding the issue of fixed steepness the SSC pointed out that it already takes that into account by assigning those assessments to Tier 2 under Dimension 1 to capture that, rather than Tier 1. However, the Committee suggested that language under this control rule tier should be revised to indicate this applies specifically to fixing steepness (the current language is not explicit about this issue).

The SSC also discussed the fact that in the current structure of tiers under Dimension 1, Tiers 4 and 5 would never be used since the analyses assigned to those tiers would not result in a P* analysis (i.e., no pdf of MSY can be generated).

By taking out some of the Tiers, the weightings must be redistributed.

By leaving it as is, it is biased because can never have a 10% or 7.5% penalty.

- Another approach is to have triggers, with each trigger pulled, decrement another amount (ex. h fixed, -2.5%; single M across ages, -2.5%; etc.)
- Also leave flexibility for unforeseen/misc. uncertainties
- **TOR 4.** Discuss revamping of the scoring system to be more Tier-specific, allowing more refinement of the dimensions used to provide the adjustment in ABC for each tier.
 - Single value in lowest tier for catch statistic seem very risk prone
 - Carruthers paper shows the higher the catch the higher the prob of overfishing
 - Also assumes a directed fishery, which is not the case for many Tier 4 and 5 stocks
 - Only use 3rd highest if, by expert judgment, the increase or continued landings at that level is not expected to result in overfishing
 - Also must remember ABC is a cap, not a target
 - Setting ABC as mean or median landings means half the landings over that time period resulted in overfishing and future catches are going to be held below that mean/median level
 - For data-poor stocks, drastic swings in landings (on commercial side) may be due to changes in market conditions, which is currently not considered in the Control Rule
 - Can modify Dimensions 1 and 2 to be Tier specific, since will have different types of info available within the different Levels

TOR 5. Evaluate use and application of the PSA score. Consider whether to keep, remove, or modify the role of PSA scores in the control rule.

- For assessed stocks, assessments usually incorporate the characteristics of the PSA analysis explicitly within the modeling framework
- May be informative for the data poor species
- In practice, most stocks used on fall within the high, possibly moderate, susceptibility category
- Double-counting depends on how it is used
 - Less prod species in model as higher M, etc.
 - Does not increase CV about OFL, but PSA in Control Rule does

- Susceptibility aspect is only place in Control Rule that brings in tech aspects of how fishery is prosecuted
- Sock status is also questioned because it is more related to risk rather than uncertainty
 - Other jurisdictions use status to help inform risk tolerance
- Since the SSC is providing advice to the Council, including the P*, then it is appropriate to include dimensions that deal with management risk/uncertainty as well as scientific uncertainty
- Dimensions 1 and 2 deal with scientific uncertainty, Dimensions 3 and 4 deal with management uncertainty/risk
- Draft a report containing recommendations for potential modifications to the ABC Control Rule for presentation to the Council.
 - Prob not ready for Council by Dec Council meeting
 - Draft report and recommendations will be developed by planning committee and Council staff, then distributed to the SSC as a whole for review
 - Draft revisions to the Control Rule to the SSC for the April meeting, if possible

Comments

- Can develop TORs to SSC asking to consider type of assessment/analysis appropriate for a particular species and available data
 - SEDAR currently provides for alternative assessment methodologies
 - Requires the AW to look at available data from DW and decide on most appropriate method to use
 - External assessment process has the proposal process
- SSC can give guidance to the Council on what is available and what can be done to help inform the Council's prioritization process
- Council being involved in choosing P* is one way of relaying level of risk and is Council's prerogative to be more involved in setting the level of risk

ABC CONTROL RULE SUBCOMMITTEE REPORT

Steve Cadrin, Subcommittee Chair



Background

- 2007 Reauthorized Magnuson-Stevens Act requires Annual Catch Limits by 2011 for federally managed stocks based Acceptable Biological Catch (ABC) recommendations from the SSC.
- 2010 South Atlantic Council adopts an ABC Control Rule based on probability of overfishing P*, in which P* is derived from tiers of assessment information, uncertainty, stock status and vulnerability.
- 2014 ABC Control Rule Workshop to consider how the current control rule has performed and how continuing advances in assessments, particularly methods for data-limited stocks, can best be incorporated.
- 2015 formed a sub-committee to develop a draft proposal to bring to the entire SSC for review.
 - Steve Cadrin (chair), John Boreman, Amy Schueller, Tracy Yandle, Eric Johnson, Carolyn Belcher, Fred Serchuk
 - Thanks to Luiz Barbieri and John Carmichael for their participation and Mike Errigo for compiling P* and SEDAR information

Progress on Evaluating ABC Control Rule Performance

- Subcommittee Conference Call (Jan 4 2016) and Work Plan
- Review of performance of ABC Control Rule
 - Review of P* derivations (Mike Errigo & John Boreman)
 - Attachment 29. P-star Scoring Summary
 - Attachment 30. P-star Values
 - Review of SEDAR Stock Assessment Estimates (Mike Errigo)
 - Attachment 31. SA Stock Info
 - Attachment 32. SEDAR Status Plots
 - Comparison of ABC and catch
 - Attachment 33. Landings vs ABC
- Expansion of evaluation to include socio-economic indicators
 - Attachment 34. MAFMC Fishery Performance Report
 - Attachment 35. NEFSC Fishery Performance Report

ABC Control Rule



- ABC is a percentile (P*) of the overfishing limit (OFL) distribution
- P*=50% for a a 'perfect' situation, with reductions for 'imperfections'

				Annual catch (as proportio
Tiers	Dimension I	Dimension II	Dimension III	Dimension IV
ners	Assessment Information	Uncertainty Characterization	Stock Status	PSA Risk Analysis
Tier 1	Quantitative assessment provides estimates of exploitation and biomass; includes MSY-derived benchmarks. (0)	Complete. Key Determinant – uncertainty in both assessment inputs and environmental conditions are included. (0)	Neither overfished nor overfishing. Stock is at high biomass and low exploitation relative to benchmark values. (0)	Low risk . High productivity, low vulnerability, low susceptibility. (0)
Tier 2	Reliable measures of exploitation or biomass; no MSY benchmarks, proxy reference points. (-2.5%)	High. Key Determinant – reflects more than just uncertainty in future recruitment. (-2.5%)	Neither overfished nor overfishing. Stock may be in close proximity to benchmark values. (- 2.5%)	Medium risk. Moderate productivity, moderate vulnerability, moderate susceptibility. (-5%)
Tier 3	Relative measures of exploitation or biomass, absolute measures of status unavailable. Proxy reference points. (-5%)	Medium. Uncertainties are addressed via statistical techniques and sensitivities, but full uncertainty is not carried forward in projections. (-5%)	Stock is either overfished or overfishing. (-5%)	High risk . Low productivity, high vulnerability, high susceptibility. (-10%)
Tier 4	Reliable catch history. (-7.5%)	Low. Distributions of Fmsy and MSY are lacking. (-7.5%)	Stock is both overfished and overfishing. (-7.5%)	NA
Tier 5	Scarce or unreliable catch records. (-10%)	None. Only single point estimates; no sensitivities or uncertainty evaluations. (-10%)	Either status criterion is unknown. (-10%)	NA

2014 ABC Control Rule Workshop

- **Term of Reference 1.** Evaluate the performance of the ABC control rule based on recent assessments, i.e., benchmark vs. subsequent update. What was the realized performance of the control rule for avoiding overfishing and achieving the expected yield when applied to different assessments?
- Few SAFMC-managed stocks have had benchmark assessments followed by a subsequent update, and none of the stocks that fit this criterion have had ABC values set according to this control rule (i.e., their ABC setting process preceded implementation of the control rule).

2014 ABC Workshop

- Some stocks had ABC recommendations that later were considered inadequate.
 - blueline tilefish was originally assigned an ABC value based on an assessment level 5, but the subsequent benchmark assessment determined that ABC to be too high.
 - Wreckfish had a DCAC-based ABC (level 3) that was much lower than the SCAAderived ABC value obtained through a subsequent stock assessment.



2014 ABC Control Rule Workshop

- The SSC identified a lack of information to properly evaluate the efficacy of the control rule.
 - evaluating differences in P* values across similar species/assessments
 - metrics to evaluate performance
- Although the ABC control rule can be improved, there isn't enough evidence indicating the current rule is not working properly.

2014 ABC Control Rule Workshop

- **Term of Reference 2.** Evaluate the current ABC control rule, considering whether it achieves the original objective of scaling uncertainty catch level adjustments (i.e., buffers) relative to assessment uncertainty, and whether it provides adequate categories and resolution given the types of available assessment information now encountered.
- ABC control rule performance cannot be properly evaluated at this time.
- The SSC recognized that there is a general lack of understanding of the current use and formulation of the control rule by the Council and stakeholders. The Committee suggested running several SAFMC-managed species through other Councils' ABC control rules to see how they fall out in comparison to the current SAFMC approach (be sure to use several very different life history characteristics when choosing stocks for comparison).

2014 ABC Control Rule Workshop

- Suggested modifications included:
 - Revise the control rule to address 3 main categories of assessments:
 - 1. Analytical assessments supporting P* (BAM, Production Model, etc.)
 - 2. Analyses supported by other approaches (DBSRA, DCAC, etc.)
 - 3. Analyses applied to unassessed, data limited stocks (ORCS, Decision Tree, etc.)
 - Use the main types of uncertainty characterization techniques currently associated with assessments to group stocks/assign tiers within the Uncertainty Dimension. For example:
 - 1. Monte Carlo-based approaches: Tier 1
 - 2. Simpler bootstrapping approaches: Tier 2
 - 3. Just use of sensitivity analyses (no bootstrapping): Tier 3
 - Characterization of uncertainty is also important (e.g., how many parameters are fixed vs. freely estimated? How often are CV's assigned or 'borrowed' rather than calculated or estimated as part of the assessment framework?)

2014 ABC Control Rule Workshop

• **Term of Reference 3.** Evaluate the scoring criteria of each of the factors within control rule dimensions and consider whether criteria should be revised based on performance, as considered in TOR #1 and #2, or in light of new scientific information. For example, recently published analyses demonstrate that fixing steepness is equivalent to choosing a spawner-per-recruit proxy.

• Recommendations:

- The control rule's Assessment Levels 2 and 3 should be less prescriptive about the methodology to be used.
- The SSC considered whether 'overfished' should have more weight than 'overfishing' when evaluating stock status.
- The SSC considers fixed steepness as a proxy reference point in assessment tier 2, but a more explicit criterion is needed.
- Assessment Tiers 4 and 5 present a problem in the control rule, because those assessments do not produce a distribution of OFL to determine ABC from P*.
- If tiers are revised, penalties may also need to be revised.

General Approach of ABC Control Rule Subcommittee

- The number of stocks with 'bookend' assessments between ABC implementation are still limited
- Reviewing the information available will help to refine the approach to evaluating performance and eventually refining the control rule to improve performance.
 - Review of P* derivations (Mike Errigo & John Boreman)
 - Attachment 29. P-star Scoring Summary
 - Attachment 30. P-star Values
 - Review of SEDAR Stock Assessment Estimates (Mike Errigo)
 - Attachment 31. SA Stock Info
 - Attachment 32. SEDAR Status Plots
 - Comparison of ABC and catch
 - Attachment 33. Landings vs ABC
- Expansion of evaluation to include socio-economic indicators
 - Attachment 34. MAFMC Fishery Performance Report
 - Attachment 35. NEFSC Fishery Performance Report
- Eventually evaluate performance with Management Strategy Evaluation





Review of P* Scoring

Review of P* Scoring

- P* scores within dimensions generally became less conservative (i.e., tended to shift to lower-numbered tiers) over time.
- This trend may reflect an expanding information base with more years of surveys.



Review of P* Scoring

• P* scores for stocks with multiple ABC reviews tended to improve over time.

Stock	1 st P*	2 nd P*	3 rd P*
Black Sea Bass:	35.0%	37.5%	40.0%
Gag:	30.0%	30.0%	
Golden Tilefish:	32.5%	35.0%	
Hogfish:	12.5%	27.5% (split into	2 stocks for 2 nd scoring)
King Mackerel:	27.5%	32.5%	
Mutton Snapper:	32.5%	30.0%	
Spanish Mackerel:	25.0%	40.0%	
Vermillion Snapper:	27.5%	40.0%	
Yellowtail Snapper:	37.5%	40.0%	

Attachments 29 & 30

Review of SEDAR Stock Assessment Information

• Recent SEDAR (post ACL) assessments of SA Snapper-Grouper complex (Cadrin 2016 for "Assessing and Managing Data-Limited Fish Stocks".

Stock	% Recreational	Assessment type	Assessment period	Source document
Red porgy	16-87%	Age-based	1972-2011	SEFSC 2012a
Vermilion snapper	17-100%	Age-based	1946-2011	SEFSC 2012b
Blueline tilefish	0-88%	Age-based	1974-2011	SEDAR 2013a
Snowy grouper	0-17%	Age-based	1974-2012	SEDAR 2013b
Hogfish	3-87%	Age-based	1986-2012	Cooper et al. 2014
Black sea bass	41-84%	Age-based	1978-2012	SEFSC 2013

Review of SEDAR Stock Assessment Information

• All SEDAR assessments of SA Council management units.

• Categorized as data-rich, unassessed, and 'catch-22' (unknown status) stocks.

540 (G	01		Status	Determination Cri	teria		Stock	Status	Fishing Level Recommendation (lbs ww. unless otherwise noted)					
FMP/Complex	STOCK	MFMT Definition	MFMT Value	MSST Definition	MSST Value	м	Overfishing?	Overfished?	OFL	ABC	Year	ABC Basis	ACL Definition	ACL
	Atlantic Spadefish	F _{30%SPR}	UNK	(1-M)*SSB _{30%SPR}	UNK	NA	UNK	UNK	UNK	812,478	2015	ORCS	ACL = ABC	812,478
	Bar Jack	F _{30%SPR}	UNK	(1-M)*SSB _{30%SPR}	UNK	NA	UNK	UNK	UNK	62,249	2015	ORCS	ACL = ABC	62,249
	Black Grouper	F _{30%SPR}	0.216	(1-M)*SSB _{MSY}	5.92 mp	0.15	No	No	294,949	262,594	2015	Tier 1	ACL = ABC	262,594
	Black Sea Bass	F _{MSY}	0.61	(1-M)*SSB _{MSY}	256E10 eggs	0.3	No	No	2,296,000	1,814,000	2015	Tier 1	ACL = Yield 75% F _{MSY}	1,756,450
	Blueline Tilefish	F _{MSY}	0.302	75%*SSB _{MSY}	184.95 mt	0.1	Yes	No	UNK	224,100	2016	Tier 1/Yield F _{MSY}	ACL = 78% ABC	174,798
	Gag	F _{MSY}	0.21	(1-M)*SSB _{MSY}	6.82 mp	0.15	Yes	No	782,000 gw	666,000 gw	2015	Tier 1	ACL = 95% ABC	632,700 gw
	Golden Tilefish	FMSY	0.185	75%*SSB _{MSY}	22.6 mt	0.07	No	No	1,242,000	715,000	2015	Tier 1	ACL = Yield 75% F _{MSY}	560,490 gw
	Goliath Grouper	F40%SPR	UNK	(1-M)*SSB _{40%SPR}	UNK	0.13	No	UNK	UNK	0	1990	Decision Tree	ACL = ABC	0
	Gray Triggerfish	F _{30%SPR}	UNK	(1-M)*SSB _{30%SPR}	UNK	0.3	No	UNK	UNK	717,000	2015	ORCS	ACL = ABC	717,000
	Greater Amberjack	F _{MSY}	0.424	(1-M)*SSB _{MSY}	3.21 mp	0.25	No	No	2,005,000	1,968,000	2015	Decision Tree	ACL = ABC	1,968,000
	FLK/EFL Hogfish	F _{MSY}	0.138	(1-M)*SSB _{MSY}	856.664 mt	0.13	Yes	Yes	48,026	38,367	2017	Tier 1	ACL = ABC	38,367
Snapper -	GA-NC Hogfish	F _{30%SPR}	UNK	(1-M)*SSB _{30%SPR}	UNK	0.13	UNK	UNK	UNK	28, 161	2017	ORCS	ACL = 95% ABC	26,753
Grouper	Mutton Snapper	F _{30%SPR}	0.34	(1-M)*SSB _{MSY}	12.35 mp	0.21	No	No	1,515,300 (GM+SA)	926,600	2012	Tier 1	ACL = ABC	926,600
	Nassau Grouper	F _{40%SPR}	UNK	(1-M)*SSB _{40%SPR}	UNK	0.18	No	UNK	UNK	0	1992	Decision Tree	ACL = ABC	0
	Red Grouper	F _{MSY}	0.221	75%*SSB _{MSY}	4.29 mp	0.2	No	No	865,000	780,000	2014	Tier 1	ACL = ABC	780,000
	Red Porgy	F _{MSY}	0.17	(1-M)*SSB _{MSY}	6.72 mp	0.225	No	Yes	400,000	354,000	2016	Tier 1	ACL = ABC	354,000
	Red Snapper	F _{MSY}	0.178	(1-M)*SSB _{MSY}	317,500 lbs	0.25	Yes	Yes	109,000 fish	114,000 fish	2015	Tier 1	ACL = Formula Am 24	0
	Scamp	F _{30%SPR}	UNK	(1-M)*SSB _{30%SPR}	UNK	0.15	No	UNK	UNK	335,744	2015	ORCS	$A^{\Gamma I} = \Delta R \Gamma$	335 744
	Snowy Grouper	F _{MSY}	0.05	75%*SSB _{MSY}	3.50 mp	0.12	Yes	Yes	129,503	102,960	2013	Tier 1	Attachi	ment 31
	استاد استاناست	E	LINUZ	(1_M)*CCR	LINIZ	0.13	Vee	LINIZ	LINUZ.	0	2010	Desision Trees		

Review of SEDAR Stock Assessment Information

Assessment Information						Sampling Levels (Avergaes from last 5 years) Average Landings Last 5 Years (Ib					ars (Ibs ww)	
	Last SEDAR	Next SEDAR	Non-SEDAR	Terminal Year of Data	Time Since Terminal	MARMAP/SEFIS /SEAMAP	Num of Indices	Avg # Dep Samples Per Yr	Avg # Age Samples Per Yr	Commercial	Recreational	Total
	NA	NA	NA	NA	NA	SM	1	99	0	25,449	272,360	297,810
	NA	NA	NA	NA	NA	NA	0	9	0	4,539	5,376	9,915
	SEDAR 19 (2010)	Benchmark (2016)	NA	2008	8	NA	0	130	94	56,473	34,052	90,525
	Update (2013)	NA	NA	2010	6	Chevron	1	6,754	2,283	441,070	595,960	1,037,031
	SEDAR 32 (2013)	Update (2017)	NA	2011	5	S-B LL	1	1,197	765	273,593	140,271	413,864
	Update (2014)	NA	NA	2012	4	Chevron, S-B LL	2	1,276	665	445,117	201,960	647,077
	SEDAR 25 (2011)	Update (2016)	NA	2010	6	L-B LL	1	1,285	1,095	557,038	13,125	570,163
	SEDAR 23 (2011, Rejected)	Benchmark (2016)	NA	2009	7	NA	0	0	0	0	1	1
]	NA	Benchmark (2016)	YPR (2011)	2009	7	Chevron	1	4,306	314	359,861	394,915	754,776
	SEDAR 15 (2008)	NA	NA	2006	10	S-B LL	1	862	117	976,649	719,224	1,695,873
	SEDAR 37 (2013)	NA	NA	2012	4	REEF, RVC	9	250	29	12,573	177,369	189,942
]	NA	NA	NA	NA	NA	NA	0	168	22	27,892	6,970	34,862
	Update (2015)	NA	NA	2013	3	NA	0	897	605	76,881	488,119	565,000
	NA	NA	NA	NA	NA	NA	0	0	0	0	0	0
	SEDAR 19 (2010)	Update (2017)	NA	2008	8	Chevron, S-B LL	2	152	108	202,196	92,879	295,075
1	Update (2012)	Benchmark (2016)	NA	2011	5	Chevron, S-B LL	2	413	126	167,253	77,122	244,375
	SEDAR 24 (2010)	Benchmark (2016)	NA	2009	7	Chevron	1	1,837	561	190,471	489,173	679,644
1	NA	Benchmark (2016)	Catch Curve (2001)	1999	17	Chevron, S-B LL	2	1,072	683	173,092	54,431	227,522
]	SEDAR 36 (2014)	NA	NA	2012	4	Chevron, S-B LL	2	869	306	91,120	59,701	150,821
	NA	NA	Catch Curve (2011)	2007	9	Chevron, S-B LL	2	3	2	1,239	Attachm	ont 31
1	Lindate (2012)	Undate (2015)	NIA	2011	Ę	Chavron	1	8 CJJ	2 77/	066 010	Audum	ient 51








8.0 **GA-NC Hogfish** Y/MSY 7.0 8 Status Relative to MSX Reference 7.0 8.0 9.0 9.0 9.0 1.0 SSB/SSBmsy F/Fmsy 0.0 1986 1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008 2010 2012

Review of SEDAR Stock Assessment Information













- The performance of 24 ABC recommendations for 11 stocks have been evaluated by subsequent stock assessments.
 - Avoiding Overfishing
 - 41% (7/17) resulted in overfishing
 - Some cases of overfishing are from excessive catch (>ACL, e.g., hogfish, blueline tilefish). Removing them
 improved the performance to 33% (5/15) which is generally consistent with the expected frequency of
 P*= 15% to 40%.
 - Rebuilding Stocks
 - ABCs allowed for growth of some overfished stocks (black sea bass, snowy grouper)
 - ... but not others (red porgy)
- These preliminary results are insufficient for a definitive evaluation
 - Such evaluations should be updated to accumulate a sufficient number of stocks and ABC recommendations.
 - Evaluations should be expanded to include more performance metrics (e.g., socioeconomics).

Actions?

- Consider and comment on the ABC Control Rule <u>performance information</u> presented by the sub-committee.
- Provide recommendations on control rule revisions, if appropriate and necessary.
 - Consider removing Stock Status from the ABC Control Rule since NMFS, not the SSC, determines status.
 - Provide guidance on next steps to be taken in considering revisions to the control rule.

MODIFICATIONS TO THE ABC CONTROL RULE

- The initial ABC Control Rule was developed in 2008:
 - **Dimensions**: address uncertainty parameters
 - **Tiers**: provide scores
- SSC has been discussing the components of risk and uncertainty associated with the CR
- Good time to review and revise, if needed

Why is this Important?

National Standard 1 (§ 600.335)

Councils must build into the reference points and control rules appropriate consideration of risk, taking into account uncertainties in estimating harvest, stock conditions, life history parameters, or the effects of environmental factors.



Does the SSC have a role to play?





Uncertainty is part of the equation...

Calculation of reference points depends on knowing (or assuming) the nature of reproduction, growth and natural mortality

The choice of the specific mathematical model has enormous consequences for management. However, there are rarely, if ever, sufficient data from nature to indicate which model is most appropriate.

Sydney Holt

Photo credit: Steve Cadrin

Breaking Down Uncertainty



- Easier to control
- Reducible, at a cost

- Inherent variability
- Very hard to control
- In principle, irreducible

How Are We Defining Risk?

Risk = Probability × Consequence



Target and Limit Reference Points



NS1: Target and Limit RP Framework

Overfishing Limit (OFL): Catch expected when fishing at MFMT (catch with a 50% probability of exceeding the true OFL as determined by the stock assessment)

Acceptable Biological Catch (ABC): Catch reduced below OFL to account for scientific uncertainty (catch with less than a 50% probability of exceeding the true OFL)

Annual Catch Limit (ACL): Catch that invokes accountability measures

Catch (Ibs)

Increasing

Annual Catch Target (ACT): Catch reduced below ACL to account for management uncertainty or achieve optimum yield

SSC ABC Control Rule

- Council

NS1 and the ACL Framework



Risk



ABC Control Rule in a Risk Analysis Framework



ABC Control Rule

 $NS1 \rightarrow Account$ for scientific uncertainty in estimating the true OFL

The determination of ABC should be based, when possible, on the probability that a catch equal to the stock's ABC would result in P* of overfishing. The probability of overfishing cannot exceed 50% and should be a lower value.



 \rightarrow Involves components of <u>RISK</u> and <u>UNCERTAINTY</u>

Unknown S-R relationship: MSY indeterminable



What SPR Level is a Good Proxy for MSY?

Depends heavily on life history parameters...

But using observations on other stocks and by doing many simulation analyses scientists have found that $\rm F_{MSY}$ is often in the range of $\rm F_{20\% SPR}$ and $\rm F_{40\% SPR}$

Therefore, in circumstances where F_{MSY} is poorly estimated, scientists will use, for example, $F_{30\% SPR}$ as a proxy for F_{MSY}

The choice of 30% or some other percentage depends upon the life history schedules for that species or stock

Joe Powers



Life-history traits determine a population's compensatory capacity



POSE Framework (Kindsvater *et al*. 2016) (Precocial–Opportunistic–Survivor–Episodic), which illustrates how a species' life-history traits determine a population's compensatory capacity

Next Steps

• Do we want to establish a Working Group to discuss the changes necessary in the scoring and assessment criteria and bring us a draft framework for evaluation?



REVIEW

Ten principles from evolutionary ecology essential for effective marine conservation

Holly K. Kindsvater^{1,2}, Marc Mangel^{2,3}, John D. Revnolds¹ & Nicholas K. Dulvy¹

¹Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada ²Center for Stock Assessment Research, University of California, Santa Cruz, California 95064

³Department of Biology, University of Bergen Bergen 5020, Norway

Keywords

Conservation, demography, extinction risk, fish, life-history theory, management, reference points, sustainability.

Correspondence

Holly K. Kindsvater, Department of Ecology, Evolution, and Natural Resources, Rutgers University, 14 College Farm Rd., New Brunswick, NJ 08901. Tel: 1(848) 932-9631; Fax: 1(732) 932-2587; E-mail: holly.kindsvater@gmail.com

Funding Information

HKK was supported by an NSF Postdoctoral Fellowship in Biology and Math (DBI-1305929). MM was funded by NSF grants OCE 11-30483 and DEB 14-51931. JDR and NKD were each supported by NSERC Discovery Grants.

Received: 26 October 2015; Revised: 14 January 2016; Accepted: 23 January 2016

Ecology and Evolution 2016; 6(7): 2125-2138

doi: 10.1002/ece3.2012

Introduction

Preventing extinction and maintaining healthy marine ecosystems are common goals of fishery managers and conservation biologists, yet there is little consensus as to which populations or species are at greatest risk of extinction, and which are candidates for sustainable management. For example, two recent meta-analyses of fish population dynamics suggest that species with fast growth and early maturity are likely to collapse from fishing pressure and environmental factors (Essington et al. 2015; Pinsky and Byler 2015). By contrast, conventional wisdom, synthesis and meta-analysis suggest that latematuring species with slow life histories have an elevated

Abstract

Sustainably managing marine species is crucial for the future health of the human population. Yet there are diverse perspectives concerning which species can be exploited sustainably, and how best to do so. Motivated by recent debates in the published literature over marine conservation challenges, we review ten principles connecting life-history traits, population growth rate, and density-dependent population regulation. We introduce a framework for categorizing life histories, POSE (Precocial-Opportunistic-Survivor-Episodic), which illustrates how a species' life-history traits determine a population's compensatory capacity. We show why considering the evolutionary context that has shaped life histories is crucial to sustainable management. We then review recent work that connects our framework to specific opportunities where the life-history traits of marine species can be used to improve current conservation practices.

> risk of overexploitation and extinction (Reynolds et al. 2005; Juan-Jordá et al. 2015). Other examples include the debate surrounding the importance of old females to future generations (Hixon et al. 2014; Shelton et al. 2015), and whether spatial closures or fisheries management is the most effective tool of conservation biologists (Edgar et al. 2014; MacNeil et al. 2015; Shiffman and Hammerschlag in press).

> Naturally the truth falls somewhere in the middle of each of these debates. Here, we show that understanding the evolutionary connection between individual lifehistory traits and population dynamics can relieve the tension over each of these topics. We review recent work that clarifies the ecological and evolutionary factors

© 2016 The Authors. Ecology and Evolution published by John Wiley & Sons Ltd.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

contributing to sustainability. We have organized our points into ten principles that bring together insights from evolutionary ecology, fisheries science, and conservation biology, and have included mathematical and empirical analyses to support them (Appendices S1–S3).

Density-dependent regulation is central to concepts of sustainability and management, because it determines population stability and fisheries yield. Thus, the central theme of our review is that selection on species' life-history traits is intertwined with the strength of density-dependent regulation of populations. We will show how density-dependent regulation can be quantified with life-history-based metrics that have been developed for use in fisheries. We present a framework, POSE, that explicitly connects characteristic life histories - Precocial, Opportunistic, Survivor, and Episodic - to their compensatory capacity. The compensatory capacity determines a population's ability to withstand various types of mortality, including fishing. Finally, we review recent work highlighting that there is no single solution for managing human activities to conserve and ensure sustainability of a population. Appropriate tools depend on a species' life history, the threat, and the set of conservation and management values.

Population Growth and Density Dependence can be Modeled in Several Ways

One of the universal "laws" in ecology is that population dynamics are determined by a few fundamental properties of species and their environment (Lawton 1999). The trajectory of a population depends on the per capita birth rate b and death rate d, such that without density dependence, population size N changes according to rN, where r = b - d (Table 1 row A). Any per capita change in population growth rate with increasing density is known as density dependence. It is revealed in the relationship between r and N, which is usually negative.

The simplest model of population growth rate with density dependence is the logistic model (Table 1, row C), in which r increases and then decreases linearly as population size N increases (Appendix S1). The increase in r near zero is a result of positive density dependence. In this model, negative density dependence in the per capita death rate is determined by predation (top-down regulation) or resource limitation (bottom-up regulation), or some combination of both (Munch et al. 2005). The per capita birth rate is potentially limited at high densities of adults if resources or space are limited for juveniles or adults. Accordingly, fisheries models of population dynamics assume that density dependence in the birth rate of new individuals captures the biology of both adult crowding and juvenile competition (Myers 2002). While

the focus of most fisheries models is a statistical description of patterns in data, we discuss the biological mechanisms that generate these patterns, keeping in mind that both density-independent and density-dependent mechanisms determine population growth rate and trajectory. These mechanisms are intertwined with species' biology, including physiology and life history (Hutchings 2000).

Carrying Capacity is Just One of Many Possible Steady States Determined by the Environment and Biology of a Species

The carrying capacity is the "ceiling" population size beyond which populations cannot be stable, represented in the logistic model by the parameter K (Table 1 Row C). The name "carrying capacity" implies the environment is like a jug that can carry a maximum quantity of water; once full, additional water will spill over the rim and be lost. However, it is not widely appreciated that in the logistic model K is actually a function of birth and death rates, as well as the mechanisms determining how these rates change with density (Appendix S1). This means that in the logistic family of models, including fisheries recruitment models and age-structured models, a change in life-history traits could change the maximum potential population size (Fig. 1), depending on the mechanism by which crowding affects birth rates or survival. Thus, while the concept of a population's "carrying capacity" has permeated the ecological literature, maximum abundance is not fixed. Instead, life-history traits (r = b - d) and physiology interact with the environment to determine population abundance (or biomass) at the steady state, or the equilibrium population size (Box 1). In nature, populations fluctuate around their steady state for many reasons, including natural variability (environmental stochasticity) as well as anthropogenic effects caused by fishing or habitat loss (Box 1). Recent metaanalyses of marine fishes have demonstrated that the lifehistory traits of a population or species determine its ability to cope with this environmental variability, as well as to compensate for increased death rates due to human activity (Bjørkvoll et al. 2012; Juan-Jordá et al. 2015). Therefore, understanding life history-environment interactions is integral to sustainability.

The Compensatory Capacity of Populations Relies on Density-Dependent Regulation

Density-dependent regulation of population dynamics depends on the life-history traits of a population or species (Coulson et al. 2008; Saether et al. 2013). If per cap-

Table	1.	Common	models and	metrics	used	to o	guantify	po	pulation	growth

	Model name	Equation	Criteria for persistence	Interpretation of units	Biological description
A	Discrete population growth	N(t + 1) = N(t) + rN(t) where $r = b - d$	b > d	<i>b</i> is the per capita production of progeny per time <i>t</i> ; <i>d</i> is the fraction of current individuals dying per time <i>t</i>	Population growth with nonoverlapping generations and no density dependence
В	Population growth	$\frac{\mathrm{d}N}{\mathrm{d}t} = N\mathrm{e}^{rt}$	$r \ge 0$	<i>r</i> is the intrinsic rate of population growth per time <i>t</i>	Continuous population growth without density dependence
С	Logistic population growth	$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(1 - \frac{N}{K}\right)$	<i>r</i> ≥ 0	r is the rate of population growth per time t; K is the number of individuals in the steady state population	Continuous population growth with density dependence
D	Stock-recruitment relationship	$\frac{\mathrm{d}N}{\mathrm{d}t} = \frac{\omega N}{1+\beta N} - MN$	$\alpha > M$ at low density; $\frac{\alpha}{M} > 1$ at high density	α is the per capita production of new individuals; β is 1/individuals; <i>M</i> is deaths per time <i>t</i>	Continuous population dynamics with density-dependent survival of juveniles (see Appendix S1)
E	Spawning Potential Ratio (SPR)	Age- and size-structured model with density dependence (Appendix S2)	Low SPR means fishing has eroded lifetime egg production (LEP)	Proportional change in offspring production at a given level of fishing mortality per time (F)	Index of recruitment per spawner in a fished stock vs. unfished population
F	Steepness in stock-recruitment relationship	$h = \frac{0.2(N_{F=0})}{N_{F=0}}$	$\alpha > M$ at low density; as α increases $h \rightarrow 1$	<i>h</i> is a proportional change in offspring production when a population is at 20% of its unfished level ($N_{F=0}$). This could also be in units of biomass	Arises from population dynamics with density dependence (see Appendix S1)
G	Life tables	$R_0 = \sum_a l(a)m(a)$	$R_0 \ge 1$	<i>R</i> ₀ is the lifetime production of daughters	Lifetime fitness in age-structured population; also known as spawners per spawner
H	Euler – Lotka equation	$1 = \sum_{a} e^{-ra} l(a) m(a)$	<i>r</i> ≥ 0	<i>r</i> is the instantaneous rate of age-structured population growth	<i>r</i> is the age-structured population growth rate; it is greatest at small population sizes; does not incorporate population density

ita births or juvenile survival rates increase at reduced population sizes, this increased production (r) can compensate for increased death rates of adults from fishing. Some species (including many fish) can also compensate by growing faster at lower densities (Gardmark et al. 2006; Lorenzen 2008). In fisheries, metrics known as reference points have been developed to quantify population or stock characteristics. These metrics indicate a population's vulnerability to overexploitation as well as its potential yield. As we will show, they can be used to determine the compensatory capacity of a population. For that reason, reference points are of use to both fisheries managers and conservation biologists.

Reference points relate some characteristic of a depleted population - such as biomass or egg production - to its baseline. In fisheries, this means that reference points are calculated for a given level of fishing effort and compared to the unfished population, resulting in a ratio. These reference metrics capture multiple changes that happen in

disturbed populations, including changes in age structure, individual growth, and natural mortality and reproductive rates, without requiring a lot of assumptions about when and what type of density dependence operates. But it is important to recognize that these metrics are rooted in species' life-history traits, including individual birth rates, death rates, and growth rates (Clark 1991; Goodwin et al. 2006; Thorson et al. 2012; Zhou et al. 2012; Mangel et al. 2013) and will vary predictably with species' biology. Calculating these metrics requires data on population abundance, including historical biomass, reproductive capacity, and estimates of natural mortality, as well as fishing effort (Mangel et al. 2013). Adaptive management based on reference points therefore requires regular stock assessments, something that will never happen for many of the world's exploited populations or species (Sadovy 2005).

Despite these data requirements, in some cases life-history trait data and the size distribution of the catch can be used to calculate the reference point known as the



Figure 1. Population growth rates and steady states in the logistic population growth model. **Main panel**: Changes in birth or death rates, as well as the effect of crowding on births or deaths, affect logistic population growth and the steady state population size (Appendix S1). Notice that the effect of crowding changes only the steady state (*K*); population growth at low population sizes is identical for both bold lines. **Inset**: the population dynamics through time for each population (line) represented in the main panel. This example is a continuous logistic model (Eq. S1.6).

Spawning Potential Ratio (SPR), which is the proporational egg production of a depleted population relative to its unfished egg production (Goodyear 1980; O'Farrell and Botsford 2005; Brooks and Powers 2007). For this reason, this metric has gained popularity as a metric of population sustainability for data-limited fisheries (Brooks et al. 2010; Hordyk et al. 2014; Nadon et al. 2015). For a given level of exploitation, the SPR is a quantitative index of the compensatory capacity of a population. We next review how considering the evolution of life-history traits can inform the compensatory capacity of populations when the data needed to calculate SPR are unavailable.

Life-History Traits are integral to a Population's Compensatory Capacity

It is helpful to broadly categorize species based on their life-history traits (Fig. 2) and compare their compensatory capacities. Age at maturation, body size, and offspring size and number evolve in response to selection from predation, resource availability, and environmental stochasticity (Bell 1980; Stearns 1992; Conover and Munch 2002; Walsh and Reznick 2009; Kindsvater and Otto 2014; Kindsvater et al. *in review*). Closely related species within the same family will be more similar to each other due to their shared evolutionary history.

In Figure 2, the vertical dimension (adult mortality rate) corresponds to the existing paradigm of a continuum between slow and fast life histories (i.e., slow life histories have low adult mortality, large body sizes, and low abundance; fast life histories have high mortality, small body sizes, and high abundance). We have extended this paradigm in the horizontal dimension (juvenile mortality rate) to explain the remaining variation in compensatory capacity. This framework builds on previous work examining the role of environmental variability in explaining life-history variation (Winemiller and Rose 1992; Winemiller 2005; Grime and Pierce 2012). It refines prior work addressing how life-history traits indicate species' risk of overexploitation or extinction (Adams 1980; Purvis et al. 2000; Reynolds 2003; Reynolds et al. 2005; Hutchings et al. 2012). We focus, however, on the relative mortality risk of adults and juveniles, because selection from environmental variability acts through the mortality risk experienced by individuals. Specifically, our framework organizes life histories into four strategies: Precocial, Opportunistic, Survivor, and Episodic (POSE).

In Figure 2, we use taxonomically distant species that represent extreme life histories, but these comparisons could also be made among species in the same lineage (Cortés 2000; Juan-Jordá et al. 2013). For each representative species, we used a size- and age-structured population dynamics model, parameterized with life-history data, to calculate the SPR for the same intensity of fishing, SPR_F. This provides an index of the compensatory capacity of each life history (Table 1 Row E; Appendix S2). The differences in SPR for the same level of fishing mortality F show how anthropogenic activity interacts differently with each life-history type; in an unperturbed population, the SPR will be 1, and in a depleted population, it will be near 0.

When adult mortality is high, selection favors earlier maturation, unless reproduction itself is the main driver of adult mortality (e.g., Kindsvater et al. in review). High background mortality or high reproductive costs tend to coevolve with small body size and short lifespans, resulting in rapid population growth rates. In Fig. 2, we consider how increasing background mortality (i.e., fishing) changes $SPR_{F = 0.2}$. This exercise shows that while both density-dependent and density-independent processes regulate the population dynamics of early-maturing species, compensatory capacity will be greatest in small species like anchovies or herring ("Opportunistic" species; in our example $SPR_{F = 0.2} = 0.78$) and seahorses ("Precocial" species; example $SPR_{F = 0.2} = 0.85$). It may be surprising that seahorses (which have parental care) are predicted to bounce back quickly from exploitation, despite their high per-offspring investment. This is because of their early age at maturity (less than a year). Opportunistic species like herring are highly productive, and their early age at maturity allows them to capitalize on favorable environments. This also makes them susceptible to decline when

Box 1. The steady state

The logistic model (Table 1 rows C and D) illustrates a very useful concept, the steady state, where population growth rate $\frac{dN}{dt} = 0$. Of course, populations in a steady state deviate from the average growth rate of 0, but they are expected to be stable over a long period of time despite these short-term fluctuations. This means that if perturbed, the population will eventually return to this state if the perturbation or disturbance ends. We use the term *steady state* in place of stable state or equilibrium because we want to emphasize that populations can be stable at many different sizes (see figure).

All that is necessary for a population to be in a steady state is that births equal deaths; in age-structured populations, the proportion of the population in each age class must be constant over time. The rate of return to a steady state will depend on species' life-history traits, particularly generation time (the average age of adults). Populations that have been perturbed from historical levels can still be stable indefinitely, even without recovering to their previous abundance or biomass, if an increase in per capita birth rates, or a decrease in natural mortality, compensates for increased mortality due to the perturbation. Once population growth can no longer keep up with increased mortality, the population (or species) will decline toward extinction. In the figure below, we use a model of an age-structured population with overlapping generations; the details of this model can be found in Appendix S2.

Box 1 Figure. Different levels of fishing intensity F are represented by each line. The figure shows that multiple steady states are possible, although as fishing mortality increases, the steady state abundance decreases. Notice that the relative effect of F on the steady state decreases as F increases because F is a coefficient in an exponential function (Table 1; Appendix S2).



environments are poor, explaining why fishing can magnify population collapses (Shelton and Mangel 2011; Essington et al. 2015).

Juvenile mortality of fish is frequently a function of chance processes, such as the encounter of predators, food, or suitable habitat during dispersal (Winemiller and Rose 1993; Mangel 2000). When juvenile survival increases rapidly with size, greater parental investment per offspring - including prolonged gestation or parental care - evolves, along with a concomitant reduction in fecundity. For example, larger offspring are advantageous when there is a size advantage in density-dependent competition (Perez and Munch 2010; Schrader and Travis 2012; Kindsvater and Otto 2014). In this case, if adult mortality is also low, selection favors increased investment per offspring, long lifespans, and large body sizes ("Survivor" species in Fig. 2). Survivor species - including large mammals and chondrichthyans such as sawfishes - tend to have slow growth and few, relatively large offspring. They can have obligate parental care, as in whales. Selection for these traits reduces the effects of crowding on population growth

rate (Travis et al. 2013). Therefore, the compensatory capacity of these species must be low (in Fig. 2, example $SPR_{F=0,2} = 0.39$ or less), and they are highly likely to be threatened (Dulvy et al. 2014). In Figure 2, we show the relative placement of several extreme Survivor species on the spectrum, to illustrate that even within Survivor species, compensatory capacity varies.

Low juvenile mortality and high adult mortality are associated with large offspring and early maturity ("Precocial" species in Fig. 2), which increase the compensatory capacity of populations of these species (example SPR_F = 0.2 = 0.85). These traits are found in species with parental care, such as seahorses. When size- or density-independent mortality of juveniles is high, selection is expected to favor large numbers of offspring instead of increased investment per offspring (Winemiller and Rose 1993). Indeed, fecundity might serve as a useful proxy for juvenile survival. Therefore, in environments where adult mortality is low, and juvenile mortality is high, species assemblages will have bet-hedging life histories ("Episodic" species in Fig. 2). Episodic species such as groupers, Pacific



rockfishes, or Atlantic Cod (*Gadus morhua*) typically have long lifespans, slow growth, and highly variable recruitment. Density-independent environmental processes, such as unfavorable climatic regimes, can overwhelm the potential for compensation in their population dynamics, and their compensatory capacity is relatively low (example SPR_F = 0.2 = 0.46).

With this framework in mind, we next review how lifehistory traits and the Spawning Potential Ratio are related to traditional metrics of population growth R_0 , and how they can be used to improve population management, even where time series of abundance are scarce.

Metrics of Individual Fitness are Useful Indicators of Population Productivity

Classic demographic models based on life-history trait data (age-specific birth and death rates, or life-table data) can be used to calculate the intrinsic population growth rate r and the per-generation per capita reproduction R_0 using the Euler–Lotka equation (Table 1 rows G, H; Appendix S1. A population with an R_0 near 1 is expected to only be replacing itself, while one with an $R_0 > 1$ will eventually grow to a new steady state. If R_0 is less than 1, further declines are expected because individuals are not replacing themselves. R_0 is very similar to the fishery index of spawners per spawner (sometimes called spawn-

Figure 2. Differential mortality of juveniles and adults selects for different life histories (POSE, Precocial-Opportunistic-Survivor-Episodic), resulting in differences in compensatory capacity, guantified here for a set level of fishing mortality (F = 0.2). Reproductive traits, body size, growth, age at maturity, and lifespan coevolve according to size-independent juvenile mortality and adult mortality. We illustrate the connection between life-history traits and compensatory capacity by calculating the Spawning Potential Ratio (SPR_{F = 0.2}) for a fished species in each quadrant (see Appendix S2; Precocial: Tiger Tail Seahorse Hippocampus comes; Opportunist: Atlantic Herring Clupea harengus; Episodic: Brown-marbled Grouper Epinephelus fuscoguttatus; Survivor: Smalltooth Sawfish Pristis pectinata; Extreme Survivor: North Pacific Spiny Dogfish Squalus suckleyi). Inset: Life histories with the lowest compensatory capacity, Extreme Survivors. This combination of life-history traits characterizes species of greatest conservation concern. Illustrations are not to scale

ers per recruit, where in this case "recruit" is a fish that has recently become vulnerable to a fishery based on its size).

The SPR is calculated with the same data that are used to calculate R_0 , although it is compared to a historical baseline value of R₀ (i.e., without anthropogenic disturbance), and the populations are assumed to be in a steady state, rather than declining or increasing. However, this equivalence means that in data-limited situations, demographic data used for R₀ can be used to calculate the compensatory capacity of a population, as long as population size structure, age or size at maturity, and age- or size-specific fecundity are known, and if there are historical reference data (Nadon et al. 2015). This may sound like a lot, but these values can be estimated by measuring individuals caught in a fishery, hunted, or otherwise removed. It is not essential to find data on abundance, recruitment, or anthropogenic mortality rates, which are much more difficult to measure.

Age-specific survival and fecundity rates can also inform which life stages are most important for population productivity, and hence management. Reproductive value (Box 2) is a useful metric for this concept. Reproductive value represents the fitness of a female of a given age or older (i.e., current and future fitness) in a steady state population (without sex change). The various metrics of reproductive value are closely related to the lifetime egg production of females (LEP; analogous results hold for livebearers). These metrics are per-generation estimates of population productivity (offspring produced per generation). In some cases, LEP can be easier to estimate than reproductive value, by making use of size-specific fecundity and population size structure (e.g., estimated from fisheries catch (O'Farrell and Botsford 2005; Nadon et al. 2015). Where historical information on the relationship between size, age, and fecundity is known, calculating the LEP (or R_0) of a mature female in the depleted population relative to historic female LEP (or R_0) is equivalent to calculating the SPR (Table 1 rows E, G), provided the depleted population is in a steady state. The greater the ratio the more sustainable the population, because compensatory density-dependent processes must be acting. Low LEP, relative to the historic LEP, would indicate the population has been depleted to a dangerous level (O'Farrell and Botsford 2005). This ratio allows us to judge the capacity of a species or population to withstand exploitation and recover to a target (its compensatory capacity), even if the level of depletion is unknown. It does not require any assumptions about the mechanisms of density-dependent regulation, but rather will provide an indirect metric of the role of density dependence in the population's dynamics.

Thus, life-history traits allow the calculation of useful proxies of fitness and compensatory capacity. But life-history traits alone can be used to categorize species' risk of overexploitation or potential to sustain fishing if the data needed to calculate lifetime egg production or other fitness metrics are unavailable. We next review general rules of thumb that come out of our POSE framework and our review of the connections between SPR, R_0 , and reproductive value.

High Fecundity and High-Quality Eggs are not Enough for Sustainability

That high fecundity makes fish populations resistant to overexploitation is a zombie idea, in that it has been thor-

Box 2. Reproductive value

Demographic models, including simple life-table models and the Euler–Lotka equation, can be used to calculate how reproductive value changes over a female's lifetime. Reproductive value is the contribution of each age class to future generations, discounted by the probability of survival to that age. It is closely related to R_0 , but relates these values to maternal age (or size). The relationship between reproductive value and age depends on growth, lifespan, maturation, and age-specific survival and fecundity.

Reproductive value is confusing because it has been defined and used in several ways (Appendix S3). An early definition was simply an individual's current and future fitness at a given age, discounted by the chance of surviving to that age (Eq S3.1, Fig. S3.1a). This represents the reproductive value of an individual, given that it survives. As not all individuals survive to all ages, it is more useful to rescale this quantity as the current and future contribution of each age class relative to the total offspring production of the steady state population (Eq S3.2). The two metrics are related, but the former is a property of a long-lived individual, the latter a property of a population.

This raises a second source of confusion about the units of reproductive value, which are often scaled for a specific purpose, for example, relative to the fitness of a juvenile. By definition, if the population is in a steady state, we know the female's contribution to future generations is one (female) offspring. This is always true unless a change in the environment changes the steady state. Thus, noticing how the units are scaled is less important than understanding how reproductive value changes with age, but scaling can be useful for comparisons among different populations or species, which have very different juvenile survival.

Calculating a female's contribution to reproductive value at each age – relative to the total production of a population – highlights which mature age classes are contributing the most to the productivity of a population (Eq. S3.3). We call this the "relative fitness" of each female. It is scaled so that lifetime fitness (the sum of fitness over all ages) is equivalent to 1. In the figure below, we plot the relative fitness at each age for four species with published estimates of mortality and reproductive rates (data and details in Appendix S3). Calculating the relative fitness of each age tells us the maternal age distribution of the juvenile population. In other words, what is the most probable age of a juvenile's mother? This information is very useful when considering how protecting different ages or life stages changes population growth rate (Fitzhugh et al. 2012). Note that for species with delayed maturity, low relative fitness as juveniles does not mean that these age classes are unimportant to population growth rate. In fact, juveniles are very important to population productivity if juvenile ages or stages have high expected future fitness relative to their current fitness. In stage-structured models, the relative importance of each life stage (in

terms of reproductive value) depends on the length of time the individual spends in it and its survival during that stage. Therefore, the importance of the juvenile stage for population productivity increases for species with late maturity, because they spend more time as juveniles. This explains why juvenile survival is more important to population growth rate in long-lived, late-maturing rays and sharks than in early-maturing species (Cortés 2002; Frisk et al. 2005).



Box 2 Figure. The relative fitness (the contribution of each age class to reproductive value) for four species with contrasting life histories. Mean age at maturity for each species is noted with a \star . Curves are generated from simulations based on published growth, mortality, and life-history parameters; each curve represents the expected fitness of each age class, scaled by total births in a steady state population. For each species, mean fecundity is known – from this, the relationship between fertility and age was assumed to be proportional to body size at age. Data and supplementary graphs are in Appendix S3.

oughly refuted but refuses to die (Sadovy 2001; Denney et al. 2002). Species with high fecundity may be unable to recover quickly from depleted levels, because their eggs have very low survival and their contribution to population recovery will be discounted by the time it takes to mature (Rothschild 1986). In other words, they have low reproductive value (Box 2). As a rule, changes in individual growth rates, age at maturation, and body size have a greater effect on the population dynamics of long-lived, late-maturing species than do egg number or egg quality (Heppell et al. 1999).

In some long-lived species, older females produce more, higher quality eggs that have higher survival in early life (Berkeley et al. 2004; Hixon et al. 2014). However, the net contribution of these eggs to population growth rate will be low in species with late maturation and low juvenile survival. Furthermore, environmental variability is an important driver of recruitment for longlived, highly fecund (Episodic) species. Egg quality differences due to population age and size structure do not necessarily contribute meaningfully to long-term population dynamics (Shelton et al. 2012, 2015; Le Bris et al. 2015).

The timing and importance of density-dependent and density-independent mortality will determine the importance of egg quality for population dynamics (Myers 2002; Munch et al. 2005). For example, it is possible that density-dependent mechanisms of mortality or growth operate well after effects of egg quality on larval survival and growth have been swamped by other sources of variability, and the long-term implications for population dynamics will be dominated by these factors. A good rule of thumb for management of long-lived species is to protect the age classes with the greatest potential contribution to lifetime fitness (MacArthur 1960). Usually, that means females that are just starting to breed (Heppell et al. 1999) but it also includes juvenile stages in species with high per capita survival during that stage, for example, late-maturing species like spiny dogfishes.

Large Biomass of a Population does not Protect it from Collapse

Populations of some species can reach very high densities in productive environments. Yet this does not mean that the population is able to withstand high fishing pressure. Recent attention has revived the question of sustainability of fisheries for herring, sardines, and other forage fish (Essington et al. 2015; Pinsky and Byler 2015; Szuwalski and Hilborn 2015). Forage fish populations have supported some of the most profitable fisheries in history and have also collapsed spectacularly and repeatedly (Essington et al. 2015; Pinsky and Byler 2015). These fish are typically considered to be Opportunistic species, as they experience highly variable environments. In our deterministic calculation of SPR in Appendix S2, we showed that these species do have potentially high rates of recovery if environmental conditions are favorable for their recruitment. Yet we emphasize that density-independent processes regulate their dynamics, so that population size and recruitment are poorly correlated, and their true compensatory capacity can be very low over short time scales. Poor environmental conditions and fishing can interact to destabilize their dynamics (Shelton and Mangel 2011). For this reason, forage fisheries can easily become overcapitalized, resulting in collapse.

Another example of species with very high biomass but low productivity are the spiny dogfishes (or Spurdog as they are known in Europe) ('Survivor' strategy Fig. 2). These cartilaginous fishes have extremely long gestation (nearly 2 years), low fecundity, and a long lifespan (up to 80 years in Pacific Spiny Dogfish *Squalus suckleyii*). Spiny dogfishes (*S. acanthias* and *S. suckleyi*) can reach very high levels of standing biomass because they have a low trophic level, feeding mainly on planktivorous fishes and invertebrates. This slow life history has led to repeated collapses of spiny dogfish fisheries, despite the fact that they are among the most abundant coastal sharks. In general, species with large standing biomass, low adult mortality, and slow growth are the slowest to recover from overexploitation (Jennings et al. 1998; Ralston 2003).

Long Lifespans Evolved for a Reason

Long lifespans and high fecundity evolve in response to selection for persistence in highly variable (stochastic) environments (Winemiller and Rose 1993). High variability can arise from processes operating on several scales, including high uncertainty in juvenile survival due to the vagaries of oceanic currents or decades of poor juvenile survival due to unfavorable climatic conditions (Warner and Chesson 1985; Longhurst 2002; Mangel 2003). For example, Sablefish (Anoplopoma fimbria) - which can live for more than 90 years - can have decades between successful recruitment events (King et al. 2001). When an unfavorable environmental regime can persist for a decade or more, only long-lived females will have the opportunity to experience a successful recruitment year (King et al. 2001). Hence, population stability of these Episodic fish depends on an occasionally successful cohort that lives a long time (McFarlane and Beamish 1992; Wright 2014).

This evolutionary perspective makes it clear that changes in age- and size-structure have important consequences for the stability of populations of Episodic species, as fishing will erode the buffer against infrequent recruitment provided by old individuals (Kuparinen and Hutchings 2012). Fishing itself also leads to plastic and evolutionary changes in population demography and life history, which can decrease the population's capacity for density-dependent compensation (Walsh et al. 2006; Swain 2010; Kuparinen and Hutchings 2012). The most important message for conservation practitioners is that truncating population age structure can be very risky for species with long natural lifespans.

Allee Effects are Hard to Detect but Should not be Ignored

Until now, we have focused largely on the role of negative density dependence limiting populations. But it is also possible for mechanisms of positive density dependence to affect population growth rates, particularly at low population sizes (Goodyear 1980; Hutchings 2015). In other words, population growth rate increases with density or number. This pattern is known as depensation or the Allee effect. Changes in population growth rate at low population sizes can arise for many reasons. For example, sessile species such as abalone or urchins can have low fertilization success at low densities. Overexploitation of one sex, as in a size-selective fishery on a sex-changing fish, can also lead to sperm limitation (Alonzo and Mangel 2004; Heppell et al. 2006). Aggregating species are at risk of depensation if reproductive success depends on density (Stoner and Ray-Culp 2000; Sadovy and Domeier 2005). Finally, predation can also lead to depensation if predator density is high enough that prey death rates increase at low prey density, or if prey are more vulnerable at low densities, which may be the case for species that cooperate for defense, such as schooling fish (Walters et al. 2000; Walters and Kitchell 2001; Dulvy et al. 2004).

The prevalence of depensation in marine populations has been widely debated (Keith and Hutchings 2012; Hilborn et al. 2014; Hutchings 2015). Detecting positive density dependence is very difficult, because the importance of stochastic processes to population dynamics increases at low population sizes. In other words, the dynamics of small populations are expected to be exceptionally noisy. For this reason, we recommend a conservative approach to estimating population recovery that leaves a buffer against low population size to prevent potential depensatory effects.

Spatial Planning (Marine Protected Areas) Should be Informed by Life Histories

When faced with population declines and few data, many conservation practitioners have turned to Marine Protected Areas (MPAs) as a management tool, often called "spatial planning". These areas may be designed to protect juvenile nursery habitat, or to protect species interactions with the intention of restoring ecosystem function. In some cases, MPAs are implemented with the hope they will export production to nearby areas open to exploitation (Hilborn 2004; Pelc et al. 2010). MPAs are most effective when all fishing is prohibited, enforcement is strong, and they are large, old, and isolated (Edgar et al. 2014). Even if these criteria are met, an MPA may not affect production in nearby areas, and so might not solve the problem of displaced fishing effort. Finally, while MPAs are appealing for their conceptual simplicity, designing and implementing an effective MPA is far from simple. Protected areas require continuous governance and financial investment and specifically need to account for the redistribution of displaced fishing effort, as well as the biology of the species they are designed to protect. For this reason, simple fisheries management tools (such as size limits or access limits) are essential complements to spatial protection measures.

Despite these limitations, for some species spatial protection is a highly effective method of conservation. That depends on the biology, including life history and behavior (Mangel 1998). Spatial protection is most appropriate for species that have limited home ranges, such as sessile invertebrates, or limited geographic ranges, including endemic species and species with low dispersal. Protecting habitat associated with specific life stages can be essential if natural mortality is low (e.g., sawfishes in mangroves; Morgan et al. 2015), or if reproductive individuals are clustered (e.g., during spawning aggregations or migrations (Sadovy and Domeier 2005). By the same token, MPAs are less likely to be appropriate management tools for migratory species or those with large home ranges. Finally, it is futile to protect metapopulation sinks if sources are not protected (Cooper and Mangel 1999; Burgess et al. 2014). Spatial protection will increase or maintain populations if it protects age or size classes (stages) in the locations that contribute the most to subsequent generations (e.g., those with high relative fitness; Box 2). This means that spatial management will be most effective if the individuals it protects are near maturity, if they have high survival during their time in that habitat, or if a large proportion of the population uses the area.

Conclusion

We have emphasized the connection between life-history traits and reference metrics for conservation and management, because the sustainability of a population depends on the species' life history as well as environmental and anthropogenic factors. Considering where a species' life history falls on the POSE spectrum can therefore be used to go beyond the usual cast of stock-assessed species to diagnose vulnerability to human exploitation of data-poor species.

We have used examples from fish and fisheries throughout this review to show that sustainable fisheries are possible even for species with extremely slow life histories (e.g., spiny dogfishes and Sablefish) and that understanding which species are likely to be sustainable can be inferred from considering the evolutionary context of their life-history traits. In general, Precocial or Opportunistic species with high or unpredictable natural adult mortality will have greater compensatory capacity and potentially the greatest sustainable yield (Fig. 2). The clearest examples of relative sustainability come from comparisons within phylogenetic groups. For example, the life-history traits of Yellowfin Tuna (Thunnus albacares) allow their populations to withstand greater fishing pressure than tuna species such as T. orientalis (Juan-Jordá et al. 2015; Box 2).

Yet there is more to sustainable management than getting the biology right. A depleted population must have a positive population growth rate to recover, but the appropriate metrics of recovery are not as clear. One benchmark is recovery to a set proportion of initial population size (Brooks et al. 2010). Recovery can also imply a return to a former demographic structure (Redford et al. 2011) or ecosystem role (Hughes et al. 2007). In some cases, this means human welfare and economic interests must be weighed against the possibility of local extinction (Allison et al. 2009) and the desire to return to a baseline ecosystem state (Levin and Lubchenco 2008; Mace 2014).

The principle underlying our narrative is that management accounting for life-history traits can lead to recovery, and eventually to resilient populations that are better able to withstand further environmental change. "Resilience" implies that a species will be able to recover from a perturbation, because of built-in redundancy or robustness (Holling 2001; Redford et al. 2011), which here we have called compensatory capacity. In marine ecosystems, resiliency means the ability to withstand fishing pressure and habitat loss, to maintain trophic structure, to resist invasion of non-natives, or to cope with climate change (Graham et al. 2011). However, it can also be the ability to recover from short-term disturbances such as an oil spill. Different definitions are appropriate, depending on the scale of the problem and the goal, but the connection to life-history traits is always present.

Acknowledgments

HKK was supported by an NSF Postdoctoral Fellowship in Biology and Math (DBI-1305929). MM was funded

by NSF grants OCE 11-30483 and DEB 14-51931. JDR and NKD were supported by NSERC Discovery Grants. NKD was supported by the Canada Research Chairs Program. HKK and NKD conceived of the idea. HKK, MM, JDR, and NKD discussed the ideas and wrote the manuscript.

Conflict of Interest

None declared.

References

- Adams, P. B. 1980. Life-history patterns in marine fishes and their consequences for fisheries management. Fish. Bull. 78:1–12.
- Allison, E. H., A. L. Perry, M.-C. Badjeck, W. N. Adger, K. Brown, D. Conway, et al. 2009. Vulnerability of national economies to the impacts of climate change on fisheries. Fish Fish. 10:173–196.
- Alonzo, S. H., and M. Mangel. 2004. The effects of sizeselective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. Fish. Bull. 102:1–13.
- Bell, G. 1980. The costs of reproduction and their consequences. Am. Nat. 116:45–76.
- Berkeley, S. A., C. Chapman, and S. M. Sogard. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology 85:1258–1264.
- Bjørkvoll, E., V. Grøton, S. Aanes, B. E. Saether, S. Engen, and R. Aanes. 2012. Stochastic population dynamics and life-history variation in marine fish species. Am. Nat. 180:372–387.
- Brooks, E. N., and J. E. Powers. 2007. Generalized compensation in stock-recruit functions: properties and implications for management. ICES J. Mar. Sci. 64:413–424.
- Brooks, E. N., J. E. Powers, and E. Cortés. 2010. Analytical reference points for age-structured models: application to data-poor fisheries. ICES J. Mar. Sci. 67:165–175.
- Burgess, S. C., K. J. Nikols, C. D. Griesemer, L. A. K. Barnett, A. G. Dedrick, E. V. Satterthwaite, et al. 2014. Beyond connectivity: how empirical methods can quantify population persistence to improve marine protected-area design. Ecol. Appl. 24:257–270.
- Clark, W. G. 1991. Groundfish exploitation rates based on life history parameters. Can. J. Fish Aquat. Sci. 48:734–750.
- Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary timescales. Science 297:94–96.
- Cooper, A. B., and M. Mangel. 1999. The dangers of ignoring metapopulation structure for the conservation of salmonids. Fish. Bull. 97:213–226.
- Cortés, E. 2000. Life history patterns and correlations in sharks. Rev. Fish. Sci. 8:299–344.
- Cortés, E. 2002. Incorporating uncertainty into demographic modeling. Conserv. Biol. 16:1048–1062.

Coulson, T., T. H. G. Ezard, F. Pelletier, G. Tavecchia, N. C. Stenseth, D.Z. Childs, et al. 2008. Estimating the functional form for the density dependence from life history data. Ecology 89:1661–1674.

Denney, N. H., S. Jennings, and J. D. Reynolds. 2002. Lifehistory correlates of maximum population growth rates in marine fishes. Proc. Biol. Sci. 269:2229–2237.

Dulvy, N. K., R. P. Freckleton, and N. V. C. Polunin. 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. Ecol. Lett. 7:410–416.

Dulvy, N. K., S. Fowler, J. A. Musick, R. D. Cavanagh, P. M. Kyne, L.R. Harrison, et al. 2014. Extinction risk and conservation of the world's sharks and rays. eLIFE 3:e00590. doi:10.7554/eLife.00590

- Edgar, G. J., R. D. Stuart-Smith, T. J. Willis, S. Kininmonth, S. C. Baker, S. Banks, et al. 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature 506:216–220.
- Essington, T. E., P. E. Moriarty, H. E. Froelich, E. E. Hodgson, L. E. Koehn, K. L. Oken, et al. 2015. Fishing amplifies forage fish population collapses. Proc. Natl Acad. Sci. USA 112:6648–6652.
- Fitzhugh, G. R., K. W. Shertzer, G. T. Kellison, and D. M. Wyanski. 2012. Review of size- and age-dependence in batch spawning: implications for stock assessment of fish species exhibiting indeterminate fecundity. Fish. Bull. 110:413–425.
- Frisk, M. G., T. Miller, and N. K. Dulvy. 2005. Life histories and vulnerability to exploitation of elasmobranchs: inferences from elasticity, perturbation, and phylogenetic analyses. J. Northwest Atl. Fish ScI. 35:27–45. doi:10.2960/ J.v35.m514.
- Gardmark, A., N. Jonzen, and M. Mangel. 2006. Densitydependent body growth reduces the potential of marine reserves to enhance yields. J. Appl. Ecol. 43:61–66.
- Goodwin, N. B., A. Grant, A. L. Perry, N. K. Dulvy, and J. D. Reynolds. 2006. Life history correlates of density-dependent recruitment in marine fishes. Can. J. Fish Aquat. Sci. 63:494–509.
- Goodyear, C. P. 1980. Compensation in fish populations. Pp. 253–280 in C. H. Hocutt and J. R. Stauffer, eds. Biological monitoring of fish. DC Heath, Lexington, KY.
- Graham, N. A. J., P. Chabanet, R. D. Evans, S. Jennings, Y. Letourneur, M. A. MacNeil, et al. 2011. Extinction vulnerability of coral reef fishes. Ecol. Lett. 14:341–348.
- Grime, J. P., and S. Pierce. 2012. The evolutionary strategies that shape ecosystems. John Wiley & Sons, Ltd, Chichester, UK.
- Heppell, S. S., L. B. Crowder, and T. R. Menzel. 1999. Life table analysis of long-lived marine species with implications for conservation and management. Pp. 137– 148 *in* J. A. Musick, ed. Life in the slow lane: ecology and conservation of long-lived marine animals. American

Fisheries Society Symposium 23. American Fisheries Society, Bethesda, MD.

Heppell, S. S., S. A. Heppell, F. C. Coleman, and C. C. Koenig. 2006. Models to compare management options for a protogynous fish. Ecol. Appl. 16:238–249.

Hilborn, R. 2004. When can marine reserves improve fisheries management? Ocean Coast. Manag. 47:197–205.

Hilborn, R., D. J. Hively, O. P. Jensen, and T. A. Branch. 2014. The dynamics of fish populations at low abundance and prospects for rebuilding and recovery. ICES J. Mar. Sci. 71:2141–2151.

Hixon, M. A., D. W. Johnson, and S. M. Sogard. 2014. BOFFFS: on the importance of conserving old-growth age structure in fishery populations. ICES J. Mar. Sci. 71:2171– 2185.

Holling, C. S. 2001. Understanding the complexity of economic, ecological, and social systems. Ecosystems 4:390–405.

Hordyk, A., K. Ono, K. Sainsbury, N. Loneragan, and J. Prince. 2014. Some explorations of the life history ratios to describe length composition, spawning-per-recruit, and the spawning potential ratio. ICES J. Mar. Sci. 72:204– 216.

Hughes, T. P., M. J. Rodrigues, D. R. Bellwood, D. Ceccarelli, O. Hoegh-Goldberg, L. McCook, et al. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr. Biol. 17:360–365.

Hutchings, J. A. 2000. Numerical assessment in the front seat, ecology and evolution in the back seat: time to change drivers in fisheries and aquatic sciences? Mar. Ecol. Prog. Ser. 208:299–302.

Hutchings, J. A. 2015. Thresholds for impaired species recovery. Proc. Biol. Sci. 282:20150654. doi:10.1098/ rspb.2015.0654.

Hutchings, J. A., R. A. Myers, V. García, L. O. Lucifora, and A. Kuparinen. 2012. Life-history correlates of extinction risk and recovery potential. Ecol. Appl. 22:1061–1067.

Jennings, S., J. D. Reynolds, and S. C. Mills. 1998. Life history correlates of responses to fisheries exploitation. Proc. Biol. Sci. 265:333–339.

Juan-Jordá, M. J., I. Mosqueira, J. Freire, and N. K. Dulvy. 2013. Life in 3-D: life history strategies in tunas, mackerels and bonitos. Rev. Fish Biol. Fisheries 23:135–155.

Juan-Jordá, M. J., I. Mosqueira, J. Freire, and N. K. Dulvy. 2015. Population declines of tuna and relatives depend on their speed of life. Proc. Biol. Sci. 282 (1811), 20150322.

Keith, D. M., and J. A. Hutchings. 2012. Population dynamics of marine fishes at low abundance. Can. J. Fish Aquat. Sci. 69:1150–1163.

Kindsvater, H. K., and S. P. Otto. 2014. The evolution of egg size across life-history stages. Am. Nat. 184:543–555.

Kindsvater, H. K., D. Braun, S. P. Otto, and J. D. Reynolds. in review. Costs of reproduction explain the correlated evolution of semelparity and egg size: theory and a test with salmon. King, J. R., G. A. McFarlane, and R. J. Beamish. 2001. Incorporating the dynamics of marine systems into the stock assessment and management of sablefish. Prog. Oceanogr. 49:619–639.

Kuparinen, A., and J. A. Hutchings. 2012. Consequences of fisheries-induced evolution for population productivity and recovery potential. Proc. Biol. Sci. 279:2571–2579.

Lawton, J. H. 1999. Are there general laws in ecology? Oikos 84:177–192.

Le Bris, A., A. J. Pershing, C. M. Hernandez, K. E. Mills, and G. D. Sherwood. 2015. Modelling the effects of variation in reproductive traits on fish population resilience. ICES J. Mar. Sci. 72:2590–2599.

Levin, S., and J. Lubchenco. 2008. Robustness, resilience, and ecosystem based management. Bioscience 58:27–32.

Longhurst, A. 2002. Murphy's law revisited: longevity as a factor in recruitment to fish populations. Fish. Res. 56:126–131.

Lorenzen, K. 2008. Fish population regulation beyond "stock and recruitment": the role of density-dependent growth in the recruited stock. Bull. Mar. Sci. 83:183–196.

MacArthur, R. H. 1960. On the relation between optimal predation and reproductive value. Proc. Natl Acad. Sci. USA 46:143–145.

Mace, G. M. 2014. Whose conservation? Science 345:1558– 1560.

MacNeil, M. A., N. A. J. Graham, J. E. Cinner, S. K. Wilson, I. D. Williams, J. Maina, et al. 2015. Recovery potential of the world's coral reef fishes. Nature 520:341–344. doi:10.1038/ nature14358.

Mangel, M. 1998. No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. Ecol. Lett. 1:87–90.

Mangel, M. 2000. Irreducible uncertainties, sustainable fisheries and marine reserves. Evol. Ecol. Res. 2:547–557.

Mangel, M. 2003. Environment and longevity: the demography of the growth rate. Popul. Dev. Rev. 29 (Supplement):57–70.

Mangel, M., A. D. MacCall, J. Brodziak, E. J. Dick, R. E. Forrest, R. Pourzand, et al. 2013. A perspective on steepness, reference points, and stock assessment. Can. J. Fish Aquat. Sci. 70:930–940.

McFarlane, G. A., and R. J. Beamish. 1992. Climatic influence linking copepod production with strong year classes in sablefish *Anoplopoma fimbria*. Can. J. Fish Aquat. Sci. 49:743–753.

Morgan, D. L., M. G. Allen, B. C. Ebner, J. M. Whitty, and S. J. Beatty. 2015. Discovery of a pupping site and nursery for critically endangered green sawfish *Pristis zijsron*. J. Fish Biol. 86:1658–1663.

Munch, S. B., M. L. Snover, G. M. Watters, and M. Mangel. 2005. A unified treatment of top-down and bottom-up control of reproduction in populations. Ecol. Lett. 8:691–695.

Myers, R. A. 2002. Recruitment: understanding density dependence in fish populations. Pp 123–148 *in* P. J. B. Hart

and J. D. Reynolds, eds. Handbook of fish biology and fisheries 1. Fish biology. Blackwell Science, Malden, MA.

Nadon, M. O., J. S. Ault, I. D. Williams, S. G. Smith, and G. T. DiNardo. 2015. Length-based assessment of coral reef fish populations in the main and northwestern Hawaiian islands. PLoS ONE 10:e0133960. doi:10.1371/journal.pone.0133960.

O'Farrell, M. R., and L. W. Botsford. 2005. Estimation of change in lifetime egg production from length frequency data. Can. J. Fish Aquat. Sci. 62:1626–1639.

Pelc, R. A., R. R. Warner, S. D. Gaines, and C. B. Paris. 2010. Detecting larval export from marine reserves. Proc. Natl Acad. Sci. USA 107:18266–18271.

Perez, K. O., and S. B. Munch. 2010. Extreme selection on size in the early lives of fish. Evolution 64:2450–2457.

Pinsky, M. L., and D. Byler. 2015. Fishing, fast growth and climate variability increase the risk of collapse. Proc. R. Soc. B 282:20151053. doi:10.1098/rspb.2015.1053.

Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. Proc. R. Soc. B 267:1947–1952.

Ralston, S. 2003. The groundfish crisis – What went wrong? Ecosyst. Obs. Monterey Bay Natl Mar. Sanct. NOAA 2002:19–20.

Redford, K. H., G. Amato, J. Baillie, P. Beldomenico, E. L. Bennett, N. Clum, et al. 2011. What does it mean to successfully conserve a (vertebrate) species? Bioscience 61:39–48.

Reynolds, J. D. 2003. Life histories and extinction risk. Pp. 195–217 in T. M. Blackburn and K. J. Gaston, eds. Macroecology. Blackwell Publishing, Oxford, U.K.

Reynolds, J. D., N. K. Dulvy, N. B. Goodwin, and J. A. Hutchings. 2005. Biology of extinction risk in marine fishes. Proc. R. Soc. B 272:2337–2344.

Rothschild, B. J. 1986. The dynamics of marine fish populations. Harvard Univ. Press, Cambridge, MA.

Sadovy, Y. 2001. The threat of fishing to highly fecund fishes. J. Fish Biol. 59:90–108.

Sadovy, Y. 2005. Trouble on the reef: the imperative for managing vulnerable and valuable fisheries. Fish Fish. 6:167– 185. doi:10.1111/j.1467-2979.2005.00186.x.

Sadovy, Y., and M. Domeier. 2005. Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs 24:254–262. doi:0.1007/s00338-005-0474-6.

Saether, B., T. Coulson, V. Grøtan, S. Engen, R. Altwegg, et al. 2013. How life history influences population dynamics in fluctuating environments. Am. Nat. 182:734–759.

Schrader, M., and J. Travis. 2012. Assessing the roles of population density and predation risk in the evolution of offspring size in populations of a placental fish. Ecol. Evol. 2:1480–1490. doi:10.1002/ece3.255.

Shelton, A. O., and M. Mangel. 2011. Fluctuations of fish populations and the magnifying effects of fishing. Proc. Natl Acad. Sci. USA 108:7075–7080.

Shelton, A. O., S. B. Munch, D. Keith, and M. Mangel. 2012. Maternal age, fecundity, egg quality, and recruitment: linking stock structure to recruitment using an age-structured Ricker model. Can. J. Fish Aquat. Sci. 69:1631–1641.

Shelton, A. O., J. A. Hutchings, R. S. Waples, D. M. Keith, H. R. Akçakaya, and N. K. Dulvy. 2015. Maternal age effects on Atlantic cod recruitment and implications for future population trajectories. ICES J. Mar. Sci. 72(6), 1769–1778.

Shiffman, D. S., and N. Hammerschlag. in press. Preferred conservation policies of shark researchers. Conserv. Biol. DOI: 10.1111/cobi.12668.

Stearns, S. C. 1992. The evolution of life histories. Oxford Univ. Press, Oxford.

Stoner, A. W., and M. Ray-Culp. 2000. Evidence for Allee effects in a marine gastropod: density-dependent mating and egg production. Mar. Ecol. Prog. Ser. 202:297–302.

Swain, D. P. 2010. Life-history evolution and elevated natural mortality in a population of Atlantic cod (*Gadus morhua*). Evol. Appl. 4:18–29.

Szuwalski, C. S., and R. Hilborn. 2015. Environment drives forage fish productivity. Proc. Natl Acad. Sci. USA 112: E3314–E3315.

Thorson, J. T., J. M. Cope, T. A. Branch, and O. P. Jensen. 2012. Spawning biomass reference points for exploited marine fishes, incorporating taxonomic and body size information. Can. J. Fish Aquat. Sci. 69:1556–1568.

Travis, J., J. Leips, and F. H. Rodd. 2013. Evolution in population parameters: density-dependent selection or density-dependent fitness? Am. Nat. 181:S9–S20.

Walsh, M. R., and D. N. Reznick. 2009. Phenotypic diversification across an environmental gradient: a role for predators and resource availability on the evolution of life histories. Evolution 63:3201–3213.

Walsh, M. R., S. B. Munch, S. Chiba, and D. O. Conover. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. Ecol. Lett. 9:142–148.

Walters, C. J., and J. F. Kitchell. 2001. Cultivation/ depensation effects on juvenile survival and recruitment: implications for the theory of fishing. Can. J. Fish Aquat. Sci. 58:39–50.

Walters, C. J., D. Pauly, V. Christensen, and J. F. Kitchell. 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. Ecosystems 3:70–83.

Warner, R. R., and P. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. Am. Nat. 125:769–787.

Winemiller, K. O. 2005. Life history strategies, population regulation, and implications for fisheries management. Can. J. Fish Aquat. Sci. 62:872–885.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of lifehistory diversification in North American fishes implications for population regulation. Can. J. Fish Aquat. Sci. 49:2196–2218.

Winemiller, K. O., and K. A. Rose. 1993. Why do most fish produce so many tiny offspring? Am. Nat. 142:585–603.

- Wright, P. J. 2014. Are there useful life history indicators of stock recovery rate in gadoids? ICES J. Mar. Sci. 71: 1393–1406.
- Zhou, S., S. Yin, J. T. Thorson, A. D. M. Smith, and M. Fuller. 2012. Linking fishing mortality reference points to life history traits: an empirical study Can. J. Fish. Aquat. Sci. 69:1292–1301.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Classic models of population dynamics in ecology and fisheries science.

Appendix S2. Calculation of reference points in an ageand size-structured population.

Table S2.1. Description of the age-structured model in the Box 1 Figure and Figure 2, including the biological

processes modeled, corresponding equations, and parameter interpretations.

Table S2.2. Life history parameters for the analyses in Fig. 2 (main text) and Eqs. S2.1–2.5.

Appendix S3. Calculating reproductive value.

 Table S3.1. Data used to calculate relative fitness of each age in Box 2.

Fig. S3.1. In (a) we plot V(a) over age using Eq. S3.1 and estimates of age-specific mortality, maturity and length.