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Natural Mortality: Theory, Estimation, and Application in Fishery Stock Assessment Models

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Natural Mortality: Theory, Estimation, and Application in Fishery Stock Assessment Models

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Executive Summary

The natural mortality rate, *M*, is one of the key parameters in stock assessments based on age- or size-structured population dynamics models. However, it is a notoriously difficult parameter to estimate owing to confounding among population parameters as well as because *M* is likely to vary by sex, age, size, and time. A range of approaches for estimating *M* have been proposed. These include methods that estimate *M* based on theoretical life-history relationships among biological parameters, empirical relationships among *M* and other biological parameters, methods based on tagging and catch-at-age data, and estimation within stock assessment methods. The 14–17 June 2021 workshop, **Natural Mortality: Theory, Estimation, and Application in Fishery Stock Assessment Models**, brought together scientists from a range of disciplines to understand the properties of natural mortality, evaluate different methods for how *M* can be estimated for use in fisheries stock assessments, explore the estimates of *M* for specific case studies, and evaluate the consequences of errors when estimating *M*. The workshop discussed tentative best practices for estimating *M* for stock assessment purposes.

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1 Introduction

The Center for the Advancement of Population Assessment Methodology (CAPAM) held a technical workshop, **Natural Mortality: Theory, Estimation, and Application in Fishery Stock Assessment Models**, on 14–17 June 2021. The workshop was hosted by NOAA and the University of Washington, in Seattle, Washington, and was conducted via webinar, with morning and afternoon (PDT) sessions timed to accommodate presenters and attendees from time zones across the globe. All talks and discussions were recorded and available for viewing the same day, and recorded keynotes were worked into the agenda in following days during the opposite session from the live presentation. The workshop was the eighth in a series organized by CAPAM as part of its Good Practices in Stock Assessment Modeling Program for improving fishery stock assessments. Some of the papers discussed at the workshop have been published in a special issue of the journal *Fisheries Research*.

Natural mortality, along with selectivity, recruitment, and growth, forms a key process in the age- and/or size-structured population dynamics models on which many fisheries stock assessments are based. It is well known that these four population processes are confounded in principle (Butterworth and Punt 1990, Thompson 1994), and the lack of information in data to distinguish among them makes estimating M difficult. In contrast to data needed to estimate selectivity, recruitment, and growth, data to inform natural mortality are seldom available, making it arguably the most difficult parameter to estimate. Estimation of M within a stock assessment model is often confounded by selectivity, growth, and the form and steepness of the stock-recruitment relationship. M may vary by sex, age, size, and time, and be influenced by the environment, including through predation and prey availability. This complexity adds additional difficulty, whether estimating a single value of M or attempting to capture the complexity in some of these dimensions. This report summarizes the presentations and discussions that occurred during the workshop, and highlights possible best practices for estimating M in stock assessments. The Appendix provides the abstracts of the talks, which are referenced in the text by the name of the author(s) followed by a reference in parentheses to the abstract.

2 Life-History Theory

The diversity and complexity of fish life histories poses a persistent challenge for fisheries management, where practical methods of estimating *M* may work well for one species or stock, but not another. Traditional approaches to stock assessment typically assume that average rates of *M* are constant over individual lifetimes and similar for each sex. Because data availability limits the statistical estimation of parameters for species with complex life histories, *M* is also assumed to be similar in assessments of species with different mating and reproductive systems. Kindsvater (C12) used a comparative approach to model the population dynamics of fished species with different life histories to predict whether variable *M* values change fisheries reference points, including biomass reference points and the spawning potential ratio, with a focus on species that change sex, bear live young, or have parental brood care. These species are often sexually dimorphic, and including sex-specific mortality rates influences the relationship between biomass yield and productivity. Additionally, differences in reproductive mode can change *M* for both adults and juveniles. The results highlighted how complexity in *M*, which drives population demography, can interact in nuanced ways with differences in selectivity arising from management or gear type.

In response to a question on how spawning biomass should be defined for nest-guarding species, Kindsvater noted that for lingcod, the females are overfished and have lower *M*, and every way she ran the models, female limitation arose before limitations due to male nest-guarding effects. Thus, for this case, the effect of the male component was relatively minor. The effects of the interaction between life history and fishing were also noted for crabs in the North Pacific, where "spawning biomass" is taken to be that of males because the fishery is male-only, with limited female discard mortality.

Temporal changes in life history (whether fishing- or environment-induced) are important because changes in growth rate impact both maturation rates and the effects of size-based selectivity on demography. Kindsvater et al. (2017) compared variation in growth rates in both gonochorous and sequentially hermaphroditic species, while Kindsvater and Palkovacs (2017) examined the effect of fishing-induced evolution on maturation rates.

The Beverton–Holt and Ricker stock-recruitment models imply that strong density-dependent early life-history survival effects occur at low biomass levels under most values of the steepness parameter (i.e., survival changes with density even at low densities). Recruitment to a fishery integrates all early life processes, which are likely a combination of density-dependent and density-independent processes.

Kindsvater stated that the size of offspring gets larger as density gets higher. Does this phenomenon occur for pelagic schooling fish such as mackerel, given juvenile *M* likely increases with higher density due to slower growth and lack of food, habitat, and oxygen—i.e., should the fish produce more smaller offspring to compensate the loss by *M*? Kindsvater stated that whether higher *M* selects for larger offspring depends on how tightly the survival of fish is connected to their size.

The typical trajectory of M is one that declines steeply with age from a very high egg and larval mortality rate to a plateau around sexual maturity and a slight decline thereafter. A model that describes this behavior is the reciprocal equation $M(t) = M_a + B/t$ (Caddy 1991), where M_a is the asymptotic mortality and B is a curvature parameter. The Caddy method for estimating the parameters in the reciprocal model is based on several equilibrium assumptions and requires knowledge of the mean lifetime fecundity and the mean parental age, values generally difficult to estimate. In the original method, an iterative procedure, based on the Axiom of Stable Population Size, is applied, and a mortality constraint on the last age class, through a gnomonic age discretization, is considered. Martiradonna (2012) showed that the algorithm may not converge if the initial guess is not close enough to the real parameter. Bitetto et al. (C13) derived the explicit formula to obtain the asymptotic mortality and the curvature parameters, based on the same assumptions of the Caddy method, gaining solution stability and reducing computational cost. They proposed to relax the adult mortality constraint to make the solution independent from the age discretization.

Lorenzen (E1) synthesized current theoretical and empirical knowledge on lifetime patterns and levels of M and their relationships with other life-history traits. Natural mortality rates in most fish and marine invertebrate populations vary over the life cycle, often by orders of magnitude. Driven by physiological (internal) and ecological (external) processes, lifetime mortality schedules show strong regular patterns, but are also influenced by environmental factors and density dependence, particularly during early life stages and for juveniles. Traditionally, fisheries models and stock assessment methods have adopted a highly simplified representation of the life cycle, with a recruited stage where M is described explicitly as a constant rate, and a stock-recruitment relationship that implicitly accounts for juvenile mortality (and the environmental and density-dependent influences upon it). Limitations of this representation and the "constant M" paradigm for the recruited stock are becoming increasingly apparent from practical and theoretical considerations. For example, some fisheries exert heavy fishing pressure on juvenile stages, which must then be explicitly modeled in assessments. At the same time, due to the proliferation of marine reserves, populations where truly "old" fish are well represented are bound to become more common and consideration of senescence effects more relevant. Last but not least, current interest in size-based population dynamics, environmentally driven variation in vital rates, and the evolutionary ecology of aging challenge the constant M paradigm from a scientific perspective.

Fish somatic condition and growth are two interrelated traits closely associated with species life history and fitness, whose trade-off can ultimately impact population dynamics, albeit seldom empirically demonstrated. Kerametsidis et al. (E2) used individual spatiotemporal information in the northwestern Mediterranean Sea to document the existence of a trade-off between condition and growth in regulating survival dynamics in two important fish species and fisheries with contrasting life histories. Juvenile body condition was detected to be negatively associated with growth and positively linked to survival for the European hake (*Merluccius merluccius*), a benthopelagic species. The same pattern was observed for young adult red mullet *Mullus barbatus*, along with a secondary effect of environmental variability. Kerametsidis et al. posited that their results provide ecological support to further implement a dynamic influence of life history in the M information used for the assessment of the two species examined.

3 Approaches to Modeling *M*

A variety of papers presented methods to estimate *M* and applications of these methods to example stocks.

3.1 Conceptual Work

Pope et al. (C1) provided a set of models that aimed to develop *M* for exploited fish stocks, particularly those of the North Sea. Estimates of *M* were first produced by the ICES Multispecies Working Group using Multispecies Virtual Population Analysis (MSVPA) in combination with extensive stomach content data, which demonstrated that predation mortality (*M2*) represents a large portion of *M* for many North Sea fish species, and it varies markedly both by age and by year, thus refuting the then widely adopted hypothesis that *M* was constant. These variations were sufficiently large to overturn single-species predictions of sustainable yield. *M2* results from the 1980s also indicated that mortality levels were related to prey size and species. Size spectra of fish communities from data analysis and a simple trait-based model of the North Sea led to questions about the basis for the coexistence of fish species in an ecosystem, given that egg production scales approximately with asymptotic weight. This led to a plausible hypothesis that differential *M* rates are required that increase with the von Bertalanffy parameters of curvature *K* and asymptotic length L_∞, but decrease with fish length. Data from the literature supported this hypothesis, which was refined into the canonical form $M = K(L_\infty/L)^{1.5}$. However, this hypothesis is questioned because this form might not be compatible with the predicted and observable fact that size-spectra slopes become more negative with increased general levels of fishing. Clearly, changes in size spectra should lead to changes in *M2*. Results of new modeling work suggest that *M* responds both to general levels of fishing and the slope of the ensuing size spectrum. This suggests that a more general expression for predation mortality would be $M2 = \alpha(F)K(L_\infty{}^c)(L^{\beta(F)})$, where *c* is likely to be close to the 1.5 value used in the canonical form. The work thus provides a likely but not necessarily universal formula for *M2*. It remains a hypothesis needing to be tested and perhaps calibrated against monitoring data. Such calibrations might point toward a universal formula for *M2*.

Manabe and Yamakawa (C3) showed that size-dependent *M* is an appropriate principle based on biological, physiological, behavioral, and ecological considerations by constructing functions for each factor in the survival process from initial stages. The possibility that *M* could increase with animal age owing to the costs of aging was discussed.

3.2 New Methods

Tuck and Haddon (A5) proposed to conduct an assessment for orange roughy (*Hoplostethus atlanticus*) in Australia, where a prior for *M* is developed by integrating the posteriors for *M* from four New Zealand orange roughy stock assessments into a beta distribution, and hence, "borrow information" of *M* from similar stocks for which more information on *M* is available. The assessment consequently estimates *M* while accounting for what is known about *M* for other stocks. Given the extreme longevity of orange roughy, indirect methods

are likely inappropriate for this species as the data used to parameterize relationships between *M* and biological parameters would not include many (any) species with life histories like that for orange roughy. In principle, the relationship between M and maximum age should not vary much across ages, though relative onset and impact of senescence will lead to some variability about the relationship.

Trochta and Branch (C2) evaluated previous and new hypotheses explaining reductions in recruitment and/or increases in adult *M* for Pacific herring (*Clupea pallasii*) in Prince William Sound using a Bayesian age-structured stock assessment model (BASA). Factors from the physical environment (e.g., air temperature, the Pacific Decadal Oscillation, and the North Pacific Gyre Oscillation [NPGO]) and interspecific interactions (e.g., abundances of humpback whales [*Megaptera novaeangliae*], walleye pollock [*Gadus chalcogrammus*], and Pacific cod [*Gadus macrocephalus*]) were individually incorporated as covariates or latent variables into the BASA. The resulting suite of models was evaluated using Bayesian model selection criteria (Deviance and Watanabe–Akaike Information Criteria, and Posterior Predictive Loss). The NPGO, walleye pollock spawning biomass, and Pacific cod effects on adult mortality resulted in the best values of all selection criteria and the greatest improvement in model predictions. Furthermore, the magnitudes and even signs of some estimated effects (NPGO and Pacific cod, among others) have changed over time, suggesting nonstationary relationships between herring *M* and ecosystem factors.

Doering et al. (C5) applied a new Bayesian approach to estimating *M* for bivalves based on the articulated valves they leave behind when they die (the "box count" method). The new method was applied to eastern oysters (*Crassostrea virginica*) in 32 areas in Maryland during 1991–2017 using dredge survey data, and the *M* estimates from the model were compared to those derived using the box count method. The spatial and temporal trends in *M* were summarized using dynamic factor analysis (DFA). *M* showed considerable spatial and temporal variation, with median *M* ranging between 0.00 and 0.96/yr. *M* spiked in most regions during 2002 and was lower in more recent years, perhaps due to disease resilience. The Bayesian model estimated slightly higher (0.02/yr higher on average) *M* than the box count method, except for years following high *M*, after which the Bayesian model estimated lower *M*. The DFA revealed two common trends in *M* and a north–south gradient in the loadings on the trends. This work improves the understanding of the variability of oyster *M* in Maryland, and the Bayesian model could be modified for use with oysters in other regions or with other species.

Bravington (C7) summarized how Close-Kin Mark–Recapture (CKMR), an assessment method that requires only tissue samples from dead or live animals, can give precise estimates not just of absolute adult abundance but also of adult *M* and several other desirable quantities. The estimates of *M* and of abundance in CKMR come from different "parts" of the dataset and are statistically orthogonal. No assumptions are needed in CKMR about consistent selectivity or CPUE/other-index reliability. Discussion focused on issues related to survey design and it was noted that it is possible to calculate expected CVs given alternative designs. Discussion also focused on kinship not being independent, e.g., because sampling only occurs in one spawning location and there is spawning-site fidelity. Bravington noted that the conditional independence assumption applied differently to parent–offspring pairs and half-sibling pairs, and was something to consider for each specific application.

It is common for stock assessments, and particularly for U.S. West Coast groundfish, to assume either a single value of *M* or one value of *M* for each sex, although, in reality, *M* can vary with age, size, maturity, and other factors. It is difficult to directly measure even an average *M* across time. Consequently, several meta-analytical approaches using relationships between *M* and other life-history parameters have been developed and used to provide an estimate for *M* in stock assessments. Hamel (2015) developed a method for combining such methods to provide a prior on *M*. An aim of that work was to establish a framework for which it is possible to easily add, omit, or limit data sets and account for nonlinear relationships, interactions between parameters, etc., with any relative weighting desired. Then et al. (2015) provided an updated data set of values of *M* and covariates, and recommended using maximum age alone for estimating *M*, when a reliable value is available. Hamel and Cope (C10) discussed alternative approaches to developing *M* priors based on maximum age information, touching on several previous analyses from the literature and considerations for estimation of both the mean and median value and the width of the prior, including log-transformation of the data on *M* to account for its heteroscedasticity. They recommend a relationship of $M = 5.4/\text{maximum age}$ based on analysis of log-transformed data from Then et al. (2015) and the notion that the relationship between maximum age and *M* should be linear. The resulting estimates of *M* are independent of age because they pertain to adults, for which it is generally assumed that *M* is independent of age. Although this will not be the case if there is senescence, this is only an issue if there are substantial relative numbers at the point of senescence. In cases where there are substantial changes in size during some portion of the "adult" period, the estimated *M* could be used to scale an *M*-at-age relationship.

Food resources often vary seasonally and, as such, individuals must endure periods when they rely on energy reserves to fuel the basic processes of life. Ultimately, limited food resources can lead to starvation-induced mortality and, depending on the scale of the food limitation, can have population-level consequences. While it is widely recognized that starvation plays a key role in the regulation of animal populations, attempts to explicitly account for starvation-induced mortality in population models are rare. Using commonly collected biological data on body condition, Regular et al. (C14) developed a statistical approach to index trends in starvation-induced mortality by estimating the proportion of individuals experiencing severe emaciation. The statistical approach accounts for seasonal patterns in body condition, allowing data collected at any time of year to be included in the model. The method is applied to Canada's northern cod (*Gadus morhua*), where an association was found between *M* estimated using an integrated population model and the index of mortality derived from proportions of cod in poor condition. This index is also associated with the availability of key prey species such as capelin (*Mallotus villosus*) and northern shrimp (*Pandalus borealis*). The results indicate that starvation-induced mortality represents an important component of the *M* experienced by northern cod. Regular et al. argued that explicitly considering prey availability—e.g., through body condition or prey abundance indices—should improve stock assessment modeling efforts and facilitate development of actionable ecosystem-based fisheries management strategies.

Bitetto et al. (C15) integrated fish condition factor into a stock assessment, generalizing the approach developed by Casini et al. (2016), and applied the method to red mullet (*Mullus barbatus*) from the southern Adriatic Sea. The Le Cren condition index (K_n) was selected as the simplest and most reliable indicator of body condition for species allocating energy reserves mostly in muscle. The annual proportion of "starving" individuals by length intervals, defined as having a K_n below a set of thresholds, was used to adjust the annual *M* by age for use in the integrated assessment. This method could be extended to include information on liver condition and parasite level. In relation to a question of whether fish are more likely to be eaten if they are in poor condition, P. Regular stated that the burst speed of individuals in weaker condition was slower so they would be more susceptible to predation and parasites. Fish in poor condition may grow more slowly, so even if they do not die of starvation they will linger longer in the higher mortality length range.

It was noted that care needs to be taken when sampling fish to compute the index developed by Bitetto et al., because only those fish that survived would be available to be captured. S. Barbeaux stated that Pacific cod in the Gulf of Alaska were in good condition in fish targeted by trawls fishing on spawning aggregations and in poorer condition in fixed gear fisheries. This suggests that spawning aggregations consist of fish that are in better condition and that fish in poor condition may skip spawning.

Cope and Hamel (D1) introduced the Natural Mortality Tool,[1] which compiles several empirical estimators of *M* into one application. Users simply input life-history values to obtain estimates of *M*. These estimates can be taken individually or can be combined into a weighted density function that can be used as a prior of *M* that integrates uncertainty across several *M* estimators. Comparing estimators can reveal inconsistencies in life-history values that may lead to further refining of basic biological understanding. It may also reveal poorly estimated life-history parameters, and thus suspect estimates of *M*. Making these estimators and the development of uncertainty in estimating *M* more accessible hopefully provides more transparent and defensible decisions on how to treat *M* and allows more users the ability to evaluate their use of *M* values.

In relation to whether there is a nonsubjective way to weight the *M* estimates, J. Cope noted that multiple methods use the same data (e.g., maximum age) and this needed to be accounted for. He also stated that unrealistic estimates should be removed from any combined estimate. Such estimates may be taxon-specific. For example, the relationship between *M* and *K* is very different in rockfish than in other species.

Hicks (D2) explored methods to estimate *M* in fish stock assessments and identified methods that provide information about the relative difference in *M* between males and females. Data from fisheries and surveys for Pacific halibut (*Hippoglossus stenolepis*), Dover sole (*Microstomus pacificus*), and widow rockfish (*Sebastes entomelas*) were used in age-structured stock assessment models to illustrate the information available to estimate *M*. The estimates of *M* for the separate sexes were correlated, showing that there is information in the data regarding the difference between male *M* and female *M*, even though the absolute

[1] https://github.com/shcaba/Natural-Mortality-Tool

value may not be well informed. Age- and length-composition data that incorporate the sex ratio may be a major source of this information, and structural assumptions about relative selectivity between males and females may contribute to the level of observed correlation in *M* estimates. Using a relative offset for one of the sexes may be useful when estimating *M*, but does not easily facilitate sex-specific prior distributions for *M*.

3.3 Applications

Hart et al. (C4) noted that surveys for sea scallops (*Placopecten magellanicus*) reliably track cohorts two years before they enter the fishery. Additionally, there have been areas closed to fishing for substantial periods of time. This means that both juvenile and adult *M* can be estimated without confounding with fishing mortality. Moreover, there is no assumption regarding steepness in the sea scallop assessment model, as well as independent estimates of survey efficiency. Juvenile (20–90-mm shell height) *M* was estimated for sea scallops in the mid-Atlantic bight using a size-based catch-at-size analysis (CASA) model. Results indicate that substantial increases in *M* were associated with large year classes, suggesting density-dependent mortality. *M* was also estimated for all size classes in the Georges Bank closed areas using the CASA model. *M* stayed within a narrow range except for a short period during a time when there were reports of disease outbreaks. The models that estimated *M* had improved diagnostics (e.g., reduced retrospective patterns and improved fits to survey data), compared to previous models where *M* was fixed.

Eveson et al. (C6) reported on estimates of *M* for southern bluefin tuna (SBT; *Thunnus maccoyii*), which is a rare example where *M*-at-age for the entire lifespan of the species has been derived based on multiple data sources. In particular, extensive tag–recapture studies for SBT have provided valuable information on juvenile *M*, CKMR methods have enabled estimation of adult *M*, and direct age data from catches on the spawning grounds have allowed inference about senescence. It was suggested that it would be interesting to explore how the results of the SBT assessment would change if it was based on an "average *M*," with selectivity (which is dome-shaped for some fleets) re-estimated.

Adams et al. (C9) applied a multispecies statistical catch-at-age analysis, a modeling approach that links multiple single-species age-structured models by time-varying predation mortality and time-invariant residual mortality to data for groundfishes in the Gulf of Alaska (GOA). The model was fitted to data for walleye pollock (*Gadus chalcogrammus*), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), and arrowtooth flounder (*Atheresthes stomias*), species that are the most trophically connected in the GOA. Results demonstrate that recent increases in the biomass of arrowtooth flounder have led to increased mortality on juvenile pollock and cod. Predation mortality was larger for smaller individuals, and the proportion of predation mortality from each species varied through time. However, estimates of biomass were sensitive to the value of residual mortality. Discussion related to the low values for *M2* (0.1/yr for flounder, 0.2/yr for cod, and 0.5/yr for pollock for ages 1–3) and the additional species (e.g., halibut and marine mammals) that could be included in future versions of the model. The authors noted that the consumption estimates used in the analyses were likely biased high because they used theoretical maximum rations and summer temperatures.

Wilberg et al. (C17) conducted stock assessments for eastern oyster in 36 regions of Chesapeake Bay, Maryland. The model was stage-structured and estimated *M* for adult oysters each year during 1999–2018. Estimated *M* varied substantially over space and time. In general, estimated *M*s were higher at the start of the time series and were similar in neighboring regions. It was noted that this work could be extended by analyzing the data simultaneously in a spatiotemporal model. The high *M*s in the northern areas were related to rainfall, which highlights the value of including environmental data in the analyses. However, freshwater effects are very localized and there is also disease, which occurs more at higher salinities, which means that the effect of environmental factors may be complicated.

The status of skipjack tuna (*Katsuwonus pelamis*) in the western-central Pacific Ocean is regularly assessed using the integrated assessment model MULITFAN-CL using catch, standardized and unstandardized effort, mark–recapture, and length-composition data. Vincent et al. (C18) showed that the mark–recapture information obtained from many years of tagging programs, combined with the time series of length-composition data, allows spatially and temporally invariant estimates of *M*-at-age to be estimated, based on the functional form of a cubic spline with five nodes. Tagging data are fit assuming a negative binomial distribution with an estimated overdispersion parameter. Length-frequency data are fit with a robust normal distribution where the effective sample size is capped at 1,000 and then reduced by a specified scalar value. The shape of the curve of *M*-at-age was sensitive to the assumed mixing period for the tagging data, (i.e., time after which tags are included in the likelihood) and the scalar of the length-composition influence. Differing curves for *M*-at-age were attributed to data source conflicts between the tagging data and the longline length composition, the latter being the primary source of observations of the oldest skipjack. The results were also found to be sensitive to growth, which is not estimated in the assessment.

Höffle and Planque (D3) estimated *M* for beaked redfish (*Sebastes mentella*) using 44 estimators from life history, maximum age, and ecological correlates, in two categories—either estimating constant *M,* or *M* dependent on age, length, or weight. The resulting estimates were highly variable, ranging from 0.01–0.49/yr for constant *M* and 0.05–0.62/yr for age- or size-dependent median *M*. These wide ranges demonstrate the sensitivity to the input parameters as well as the pitfalls of using estimators developed for taxa other than that of primary interest. Of the 44 estimates, 24 were considered as potential candidates for updating the stock assessment model.

Impacts of *Karenia brevis* red tide blooms have been an increasing cause of concern for fisheries management on the West Florida Shelf. Red tide mortality has been incorporated into Gulf of Mexico grouper stock assessments since the mid-2000s. Traditionally, this has been achieved by including extra natural mortality during historical years with severe red tides (i.e., 2005), ideally based on analyses of satellite data. The most recent stock assessment of Gulf red grouper (*Epinephelus morio*) was confronted with new challenges of parameterizing red tides during both historical and forecasted time periods, growing uncertainty regarding the standard methods used to quantify red tide severity, as well as suspected mortality due to associated bloom stressors (e.g., hypoxia). Sagarese et al. (F2) discussed how the impacts of multiple red tide events were incorporated into the stock assessment process and how results were communicated to fisheries managers. They reviewed the data streams that were used

to identify severe red tide events and discussed the importance of assumptions made when projecting tactical catch advice required for fisheries management. At the time of a recent assessment, a 2018 red tide event was suspected. However, considerable uncertainty existed regarding the magnitude of the event due to the limited quantitative data available. To account for this, different potential red tide scenarios were evaluated and results were presented in the form of a decision table highlighting the potential risks associated with different catch levels for consideration by managers. In response to a question, it was noted that it is unclear whether red tides impact parameters other than *M*.

The widely used Stock Synthesis modeling platform has a broad range of possible configurations for natural mortality. Methot (F1) provided an overview of the available options, along with a review of common practices used in production stock assessments that utilize Stock Synthesis, along with a demonstration of how various options for setting up *M* behave in a range of existing applications to provide lessons in which setups seems to be most problematic.

3.4 On the Ability To Estimate *M*

Punt et al. (A1) proposed that a best practice for dealing with *M* in assessments was to estimate it with a prior/penalty that reflects information on *M* from sources other than those included in the model likelihood, and to use likelihood profiles to check for model mis-specification and contradictory data. It was noted that estimating *M* within the assessment allows the error associated with estimating *M* to be propagated.

It is common in integrated, age-structured stock assessment models to either 1) fix *M* at an externally derived value using "indirect" methods, or 2) estimate it simultaneously with other parameters. Each method has benefits, but the decision of how to model *M* is often investigated somewhat in isolation of how to treat other key parameters that are difficult to estimate within stock assessment models. Castillo-Jordán et al. (C8) used Monte Carlo simulations to investigate 1) and 2) while simultaneously investigating how the steepness of the stock-recruitment relationship (*h*) affects the results. The consequences of mis-specifying *M*, in terms of estimates of catches that would lead, on average, to a spawning stock biomass that is 40% of the unfished spawning stock biomass, depended on *h*. In particular, estimates of this catch metric were biased when *h* was actually high but fixed at a low value in the stock assessment. Conversely, when *h* was low, estimates of this catch metric were variable.

Cronin-Fine and Punt (C11) explored the ability of stock assessments based on size-structured models to estimate *M* under a variety of scenarios. These scenarios include whether the operating model and estimation method have a terminal molt; whether *M* is constant, time-varying, or sex and maturity stage-specific; the quality/sample size of the biomass index and the size-composition data; and whether growth is estimated simultaneously with *M*.

Perreault and Cadigan (C16) developed natural mortality diagnostic methods for state-space models to better understand how the choice of *M* affects model fit using 1) profile likelihoods, and 2) local influence diagnostics. In traditional stock assessment models, it is straightforward to construct profile likelihood plots that show the likelihood contributions (i.e., the fit) of each data source versus changes in the *M* assumption, since the total negative log likelihood (*nll*) is

simply the sum of the *nll* of each data source. State-space models use an integrated likelihood to account for random effects, and the integrated likelihood cannot be directly split into data likelihood components. Profile likelihoods are used to evaluate the effects of broad changes in *M* across all ages and years on the total model fit to all data and on the fit to individual data sources. Local influence diagnostics are used to assess the influence of age- and year-specific changes in *M* on model fit. This approach could be extended to detect cohort effects, although its results could be confounded with mis-specification in other components of the model.

3.5 General Considerations

3.5.1 Senescence

The workshop discussed possible reasons for senescence, including a reduced ability to feed, swim, and withstand disease, noting that for many long-lived/large species there is not much evidence for high predation pressure on older/larger individuals. However, even if there is senescence, the "grow fast, live short" lifestyle of many fishes means that few individuals will reach the point at which senescence occurs. It was noted that most calculations for reference points assume that *M* is constant above some age, with no maximum possible age.

3.5.2 Best practices for estimating *M* outside of the stock assessment

Maunder et al. (F3) outlined the range of methods available to estimate *M* for use in stock assessment. The methods include those based on maximum age, life-history theory, and relationships between "well known" (those found in the literature and based on data for the stock in consideration) values for *M* and covariates, use of tagging data and catch curve analysis, and estimation within a single- or multispecies stock assessment model. All methods are subject to bias and imprecision due to incorrect assumptions and incomplete data. Furthermore, *M* is generally assumed to be constant over time, age, and sex, but deviations from these assumptions are very hard to detect. Maunder et al. concluded that there is an obvious benefit to directly estimating *M* using data within the stock assessment while assigning a prior based on empirical methods. Carefully examining diagnostics and checking for model mis-specification is required to ensure that the available data and model assumptions are appropriately informative about *M*. For situations where direct estimation is not possible (a condition found in data-limited to data-rich stock assessments), the use of multiple methods with robust sensitivity exploration is recommended. Even when direct data are integrated into a stock assessment model, using other methods to estimate *M* and analyzing the direct data outside the stock assessment model as diagnostic tools is recommended.

Empirical methods for estimating *M* or developing a prior for *M* based on maximum age are gaining popularity. However, these methods rely on an estimate of the maximum age reached, and this age a) may be an ageing error or outlier, b) will depend on how the age-composition data are collected, and c) will depend on past fishing pressure (the estimate of *M* will actually be an estimate of *Z*). Consequently, the best method for estimating *M* outside the stock assessment will likely be species- (or stock-) specific. Nevertheless, if a single indirect method is to be applied, the default seems to be to use a maximum age-based approach. It is always necessary to consider the quality of the available data, which may point to an alternative approach.

Some empirical methods are based on values for *M* and biological parameters that are now considered wrong or are out of date. There would be value in reviewing the basis for the data sets used to estimate empirical relationships for *M*. Also, care should be taken when applying methods developed for teleosts to invertebrates, because the relationship between *K* and *M* differs between these two groups of taxa. In general, care needs to be taken using an empirical relationship that involves extrapolating outside of the range of "data" (including a variety of factors such as range of covariate values, life history, and habitat type) used to determine the original relationship.

Tagging and telemetry studies provide a more direct estimate of natural mortality than those based on life history. Wallace (C19) compared *M* estimates from tagging and telemetry studies to those based on life-history correlates, with varying results.

3.5.3 *M* and model mis-specification

Several papers estimated *M*. Discussion highlighted that many sources of model mis-specification can impact estimation of *M*. One source is misreported (under-reported) catch, which will lead to overestimation of *M* because some component of *F* will be (incorrectly) attributed to *M*. It was noted that the assessment could attempt to estimate a "*q*" for the catch, or use the Rose approach to addressing retrospective patterns (Legault 2020) if under-reported catch is considered likely. It was noted that the *q* approach is only likely to work when the under-reporting bias is constant over time, but this is often not the case (e.g., in the North Sea).

3.5.4 Age and sex variation in *M*

It should be more straightforward to quantify the effect of age and sex variation in *M* than to assess how *M* changes over time. For example, age-specific *M* can be modelled using the Lorenzen curve or based on the results of a multispecies assessment model. There was discussion about whether *M* changes at maturity, and that this probably differs among species depending on life history.

3.5.5 Time variation in *M*

Several papers have modeled time-varying aspects within assessments, but the general pattern is that estimation of time-varying parameters yields more uncertainty in results. It was highlighted that while introducing random effects to account for observed patterns in the data can address retrospective patterns, there is a limit on how many random effects can be estimated from fisheries data. Moreover, Szuwalski et al. (2018) observed that assuming random effects for one process (growth, selectivity, or natural mortality) can mask misfits to data due to unmodelled trends in other processes, resulting in biased estimates of management quantities.

4 Multispecies Approaches to Estimating *M*

Plaganyi et al. (B1) noted that attributing the entire variability in a stock's total mortality rate to variability in fishing mortality *F* may not be valid due to, for example, extreme environmental changes and both direct and indirect trophic interactions—particularly when there are substantial changes in the overlapping abundances of a key predator or prey species. Multispecies models could be used to explicitly capture variation in *M* to more accurately model population dynamics, improve the ability to discriminate between *F* and *M,* and quantify the influences of fishing on the broader ecosystem, consistent with an ecosystem approach to fishing. There are a growing number of approaches to modeling *M* in multispecies models, such as: 1) using diet data to estimate predation mortalities; 2) using predator and prey abundance indices to estimate the net outcome of interactions; 3) using predator breeding success or tag-recapture survival estimates; 4) representing natural mortality risk as a function of size; 5) modeling variability in *M* due to spatiotemporal matches/mismatches; and 6) modeling trophic interactions using Models of Intermediate Complexity for Ecosystem assessments (MICE).

Discussion centered on the extent to which multispecies models could be used for tactical (e.g., status determination and total allowable catch [TAC] setting) rather than strategic Management Strategy Evaluation (MSE) purposes. This is because, as complexity is increased, so is parameter uncertainty. There was general agreement that single-species approaches are currently preferred in terms of tactical management, but that multispecies assessments (or assessments that include environmental drivers of *M*) may be appropriate for questions that are broader and more strategic than status determination and TAC setting.

It was noted that multispecies models could be used to provide bounds on how much *M* can vary over time due to trophic effects. There are limits to the variation in *M* given feedbacks among species and because predators can switch among prey. In relation to the optimal complexity of multispecies models, it was noted that the aim should be to capture most of the mortality on the key modelled species but to restrict the set of modelled species and processes given the data. Moreover, it is desirable to evaluate the robustness of inferences to alternative structural models (e.g., variants of one MICE model or alternative types of ecosystem models, e.g., Atlantis vs. Ecosim). Model building was recognized to be iterative.

Dorn and Barnes (B2) constructed an index of predation mortality for walleye pollock in the GOA. This index accounted for spatiotemporal variation in predator biomass, bioenergetics-based rations, and age-specific proportions of pollock consumed. Evidence was found for intense and highly variable predation on GOA pollock (ranging from 1.86–7.05 million metric tons [mt]). Total pollock consumption estimates were included in the stock assessment model as a survey-like index of removals attributable to natural mortality. This formulation allowed for non-annual data inputs and included a proportionality constant with which to scale consumption. Age-specific *M* was allowed to vary according to a penalized random walk.

There was agreement in the workshop that this was a simple way to include consumption data in single-species assessments, and that, in some cases, allowing for time-varying *M* leads to better fits to the data included conventionally in single-species assessments. It

was noted that there were major discrepancies between the model-predicted consumption of GOA pollock and the absolute size of index. This suggests that either the method for estimating consumption was in error or there was a problem with the assessment models. This surprised some participants because methods such as multispecies Virtual Population Analysis (MSVPA) will simply increase population numbers given (input) consumption estimates, but it was noted that using predation as an index will behave differently. In particular, Dorn and Barnes constrained their model so that additional data on consumption did not lead to a change in the "scale" of the population, as might be expected (at least for recruitment) when consumption data are included in an assessment. The impact of adding consumption data to a single-species assessment would be sensitive to whether the consumption is primarily of pre-recruits, which will lead to higher recruitment, but often to similar estimates of spawning biomass or of older animals. In contrast, estimates of spawning biomass could change if the predation is of older animals that are selected by the fishery or form part of the spawning biomass.

Grüss et al. (B3) developed an approach that fits a spatiotemporal model to both prey-biomass-per-predator-biomass data (i.e., the ratio of prey biomass in stomachs to predator weight) and predator biomass survey data, to predict "predator-expanded stomach contents" (PESC; the product of prey biomass per predator biomass, predator biomass per unit area, and surface area). The PESC estimates can be used to visualize either the annual spatiotemporal variation in predation, or can be aggregated across space to calculate annual variation in diet proportions (variation among prey items and among years). The approach was applied to eastern Bering Sea (EBS) large-size walleye pollock and West Florida Shelf red grouper.

The method outlined by Grüss et al. requires approximately 300 samples, although a "sense" of prey switching can be obtained from 100–200 samples. The current application assumes that the observations are independent, conditional on the covariates and model structure. However, care needs to be taken when analyzing diet data as the process for sampling stomachs is seldom random. It was also noted that information on rations is needed to scale the estimates from the spatiotemporal model to obtain estimates of energetic demand.

There was general agreement that multispecies models provided an appropriate basis for constructing operating models to test the robustness of candidate management systems to sources of uncertainty related to *M*. Multispecies models also have a role to play in defining the range to which *M* can vary over time due to the effects of predation (but not other sources), and perhaps also in assessing some of the long-term effects of climate change as they pertain to changes in *M*. Multispecies models are also able to capture (to some extent) the effect of fishing mortality on predators leading a "release" of mortality on prey.

5 Consequences of Error in Natural Mortality

Natural mortality affects the estimates of biomass, biomass relative to management reference points (e.g., B/B_0, B/B_{MSY}), and catch limits under harvest control rules. The magnitude of error (both bias and variance) when estimating M can be substantial and can be affected by ignoring its variation over time, space, age, sex, and size. Prespecification of M will lead to overly precise measures of uncertainty, while errors in M also impact the ability of model-selection methods to correctly detect the best model from a set of models.

The effects of uncertainty in M can be explored using simulations, which confirm that overestimation of M leads to positively biased estimates of biomass and reference points based on per-recruit methods. The simulation study by Punt et al. (A1) confirmed this result and highlighted that the effects of errors in M could be ameliorated when management was based on feedback (i.e., catch limits are adjusted regularly based on updated assessments). It was noted that the consequences of estimation of M on errors in quantities of management interest depend on the formulation of the population dynamics model (e.g., whether the formulation for selectivity is correctly specified—for example, specifying selectivity to be asymptotic when it is actually dome-shaped will lead to overestimation of M).

Tengvall et al. (A4) investigated how reference points depend on M, and the consequences of errors in assumed M, for three commercially important North Atlantic stocks with different life histories. When other model parameters were fixed, negative correlations were found between M and reference points; high M resulted in low MSY and F_{MSY}. Long-term catches decreased under an F_{MSY} optimized for an M that deviated from true M, but the reference points were much more sensitive to assuming that M was lower than in reality. M could be 35% lower than the parameter value used before exceeding overall assessment uncertainty, while there was only 10% error margin in the opposite direction. This highlights the importance of getting M right, especially when M may have increased, and to determine tolerable levels of error by systematically assessing the effects of M for management purposes.

Tuck and Haddon (A5) reported on estimation of M for orange roughy (*Hoplostethus atlanticus*) in Australia. The base-case value for M has been fixed at 0.04/yr for several assessment cycles. However, this figure is taken from New Zealand, based on an average from two age compositions thought to reflect unfished conditions. A likelihood profile on M from the most recent (2017) assessment suggested that a lower value for M may be more appropriate. Reducing the assumed value for M leads to reductions in catch limits, as determined by the Australian harvest control rule. In the face of uncertainty regarding the appropriate value of M to use, a cross-catch risk assessment was conducted, whereby three years of estimated catches calculated under the Australian harvest control rule for each model were used as fixed catch inputs to the alternative model. While the cross-catch risk assessment showed little short-term risk to the stock, questions remain over how to deal with uncertainty in the value of M in future stock assessments, as this has an influence on catches, the perceived rate of recovery, the perceived risk to the stock given the number of years of unknown recruitment, and future levels of industry investment.

Szuwalski (E3) argued that not allowing for time variation in *M* and catchability (*q*) can result in retrospective patterns in estimated biomass, which results in errors in management advice. Allowing for time variation in these processes can also result in errors in management advice if the estimated time variation does not reflect the underlying variation. Szuwalski presented an assessment for snow crab (*Chionoecetes opilio*) in the eastern Bering Sea that tests different combinations of time variation in *M* and *q*. The management advice for 2020 resulting from these models differed by nearly an order of magnitude. The managing body for snow crab did not adopt any of the models with time variation in *M* or *q* because the estimated variability in *M* and *q* was difficult to explain with any known mechanism, and the management advice differed so drastically among the models. It may be possible to estimate *M* for snow crab using data on shell condition (as a proxy for age). However, for the North Pacific at any rate, shell condition is not a good proxy for age.

Management strategy evaluation (MSE) has been used to examine the consequences of errors to each management goal.

Punt et al. (A1) explored the consequences of age-specific *M* (when *M* is assumed to be independent of time), trends in *M* over time, and the effects of less-informative data when estimating *M*. Time trends in *M* were found to be most consequential in terms of the ability to achieve management goals related to conservation and utilization.

Jacobsen et al. (A2) used MSE to test the ways in which basic harvest control rules and management models perform under different *M* scenarios (constant *M*, decreasing *M*, increasing *M*, and autocorrelated random walk) across a range of species and life-history parameters. They considered two harvest control rules, a constant fishing rate and a "hockey-stick" rule with a lower biomass limit at which the fishery is closed. A state-space surplus production mode was able to estimate reasonable temporal biomass estimates based on total catch and an annual survey in all scenarios, but failed to accurately estimate reference points. Accuracy of estimation depended on life history, in particular maximum length and magnitude of mortality, and was the lowest when mortality was increasing.

Perez-Rodriguez et al. (A3) used GADGET as an operating model to evaluate the consequences of using alternative assumptions about *M* in the single-species assessments for three important commercial stocks (Atlantic cod [*Gadus morhua*], Acadian redfish [*Sebastes fasciatus*], and northern shrimp [*Pandalus borealis*]) on the Flemish Cap fishing ground (NAFO area 3M) for which strong ecological interactions are known. They found that using an ecosystem-based *M* led to better assessments, and that management performance was better when all commercial stocks used the same management approach. They also concluded that life history-based *M* values did not show a clear improvement to a constant *M,* but that allowing *M* to depend on age improved management performance. A final conclusion was that the interaction between *M* in the assessment and the fishing mortality rate implemented in the fishery has an important effect on the real *M* owing to trophic interactions.

Discussion of these papers highlighted that most studies investigating time trends in *M* did so by imposing trends directly within single-species models. However, basing time trends in *M* on the outcomes of multispecies and ecosystem models seems more realistic, albeit at the cost of increased complexity.

6 Research Questions Arising

- Given uncertainty in *M*, will management be more robust if the harvest control rule is *F*-based rather than biomass-based?
- Management strategy evaluations should continue to be used to investigate the structural uncertainty of assessment models in fisheries where the stock has variable biological rates to find the best-performing harvest control rules.
- Simulation studies should examine the consequences of errors in *M* on a broader range of parameters (e.g., survey catchability).
- Multispecies assessment models lead to *M* (and hence optimal harvest rates) for one species depending on the abundance of other species. It remains an open question how to deal with this generically.
- Estimation of *M* is often confounded with estimation of stock-recruitment steepness (*h*), but the exact nature of this relationship remains uncertain and needs to be examined further.
- A lower (assumed) *M* may lead to more precautionary management (except in the case where the higher actual *M* is due to a recent change). This extent to which this is true generally should be explored using MSE.
- There is a need to better understand density dependence in *M* and how that interacts with the stock-recruitment relationship, particularly for low-fecundity species. Does reduced mortality occur close to the carrying capacity or does it also occur at low biomass levels, as implied by the Beverton–Holt and Ricker models?
- Evidence for the survival cost of reproduction is equivocal. To explore this issue, data sets with survival by sex should be examined.
- Some of the empirical methods are based on values for *M* and biological parameters that are now considered wrong or are out of date. The basis for the data sets used to estimate empirical relationships for *M* should be reviewed.
- The link between condition and survival is interesting and should be studied further.
- Disease and density-dependence are not given the attention they might be due and should be studied further.
- How can maximum age data be used more effectively, such as by taking into consideration the effective sample size and age-dependence of *M*? Would this need previous meta-analyses to be repeated using a functional form for age-specific *M* and approximations of sample size?
- Use MSE to determine HCRs that are robust to bias or uncertainty in *M*.

7 Conclusions and Tentative Best Practices

- By default, *M* should be assumed to depend on age and sex, and attempts to model this using a functional form should be made within stock assessments. However, often, a single value may ultimately be used given uncertainty in the form of the relationship, variability, and difficulty in estimation. Develop a prior for *M* (e.g., based on empirical methods not included in the assessment model likelihood), fit the model, and examine standard diagnostics (residual patterns, retrospective analysis, age-structured production model diagnostic, R_0 profile, etc.). This allows the "data to speak for themselves." However, data conflicts and model mis-specification could lead to the estimate of *M* being based more on resolving problems with model specification, and pre-specifying *M* using empirical methods may be more appropriate.
- Many of the problems related to the quality of the data used to estimate *M* within an assessment apply when *M* is estimated outside the assessment. There are some circumstances (e.g., animals in closed areas) where *M* can be estimated inside a stock assessment model and doing so will improve the accuracy of model outputs. Outside of these limited cases, there is an appreciable risk that estimates of *M* will be incorrect owing to confounding with other parameters and/or model mis-specification.
- If a single indirect method is to be applied, the default seems to be to use a maximum age-based approach, but it is always necessary to consider the quality of the available data, which may point to an alternative approach or a correction.
- Local influence diagnostics (i.e., evaluating the influence on model outputs of time and age variability in *M*) should be used to assess the influence of age- and year-specific changes in *M* on model fit.
- "Major" differences between the prior median for *M* and the estimate from an assessment suggest that the estimate is likely driven by model specification, assuming the basis for the prior was well considered (including both the mean/median and width of the prior). In this situation, it may be appropriate to pre-specify *M* to a variety of values and construct a decision table to quantify the consequences of errors in *M* on management-related quantities.
- MICE models are effective as conceptual tools and to examine hypotheses for changing in *M* over time. Multispecies models can be used to guide the construction of single-species assessments and as the basis to test them using simulations, or as part of a management strategy within an MSE.
- Multispecies models could be used to provide bounds on how much *M* can vary over time due to trophic effects.

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Appendix

Session A: Consequences of Error in Natural Mortality Rate Modeling

A1 Consequences of error in natural mortality and its estimation in stock assessment models (Keynote 1)

A. E. Punt, C. A. Castillo-Jordán, O. S. Hamel, J. M. Cope, M. N. Maunder, and *J. N. Ianelli*

Natural mortality (*M*) is often considered to be one of the most important parameters in a fish stock assessment and affects productivity estimates for the population. However, it is also among the most difficult parameters to estimate using commonly available data. The magnitude of error (both bias and variance) when estimating this parameter can be substantial and can be affected by ignoring its variation over time, space, age, and length. In this study, we explore the implications of errors in *M* on estimation and management performance using simulations and illustrative examples. The error in management reference points, such as $F_{35\%}$ and F_{MSY}, is related directly to the error associated with *M*. Estimates of biomass are expected to be positively biased when *M* is overestimated, and vice versa. Use of feedback management strategies reduces the impact of errors in *M*, but performance in meeting management objectives is compromised when *M* is in error. Estimating *M* was found to perform better than pre-specifying *M* in closed-loop simulations. Also, we found that the consequences of setting *M* to an incorrect value were reduced if stock-recruitment steepness was estimated. Based on our study and a review of related work, we advocate estimating *M* within an assessment, ideally with a prior for *M* tailored to the stock concerned.

A2 The impact of natural mortality on reference points and management strategies of forage fish populations

N. S. Jacobsen, *M. C. Siple*, and *T. K. Mildenberger*

Natural mortality (*M*) is an essential parameter in stock assessments and ecological models. For small pelagic species, which play an important role in marine ecosystems as prey for predators, increases in *M* can function similarly to increases in fishing mortality, augmenting the extent and duration of collapse periods. Despite this, stock assessments rarely detect or include changes in *M*, potentially leading to improper estimation of reference points and biomass dynamics for management. Long-term trends in *M*, or shifts in the amount of variability in *M* over time, can have different effects on management performance, depending on how detectable they are and how responsive management is to changes. We use a management strategy evaluation (MSE) approach to test the ways in which basic harvest control rules and management models perform under different *M* scenarios across a range of species and life-history parameters representing 106 stocks. Using an age-structured operating model, we simulate three natural mortality scenarios: a) decreasing, b) increasing, and c) autocorrelated random walk, and compare them to a constant mortality. We compare two simple harvest control rules, a constant fishing rate and a "hockey-stick"

rule with a lower biomass limit at which the fishery is closed. In each year of the simulation, a state-space surplus production model (estimation model, EM) is used to estimate reference points, which are in turn used to determine annual allowable catch. We show that the EM is able to estimate reasonable temporal biomass estimates based on total catch and an annual survey in all scenarios, but fails to accurately estimate reference points. Accuracy of estimation depends on life history, in particular maximum length and magnitude of mortality, and was the lowest when mortality was increasing. We recommend employing MSE to investigate the structural uncertainty of assessment models in fisheries where the stock has variable biological rates to find the best performing harvest control rules.

A3 Impact of a wrong *M* assumption on fisheries management and population risks

A. Perez-Rodriguez, *D. Howell*, and *I. Umar*

Even though the use of alternative estimates of natural mortality (M) is becoming more common, there is still a widespread tendency to assume a constant M across ages and over time in stock assessment models. Recently, some methods based on life-history traits theory are becoming popular to provide models with varying M by age, but still constant over time. In contrast to the rigid assumptions of these approaches, it is known that natural mortality by age can experience strong variations over time due to several factors, but with special relevance for those related to trophic interactions. An excessive simplification in terms of M assumption might lead to higher risk of collapse and reduced fish productivity. In this work, a gadget multispecies model is used as the operating model in a simulation framework to evaluate the consequences of using alternative assumptions on M in a single-species assessment of three important commercial stocks (cod, redfish, and shrimp) of the Flemish Cap fishing ground (NAFO area 3M), for which strong ecological interactions are known.

A4 How natural mortality shapes fisheries reference points: Inference from an age-structured population model

J. Tengvall, *F. Zimmermann*, *A. F. Opdal*, and *K. Enberg*

Natural mortality is a major driver of stock productivity and a key parameter of fisheries models, determining true and perceived stock levels, optimal exploitation rates, and reference points. Despite natural mortality being subject to environmental and ecological dynamics, it is often assumed constant in stock assessments and management simulations. Besides fluctuations in food availability and predation, fishing and other stressors such as climate change or ecosystem shifts can alter natural mortality. Observed and predicted changes in natural mortality highlight the need for exploring the sensitivity of reference points to assumptions on natural mortality. With a stochastic age-structured population model, we investigated how reference points depend on natural mortality and the consequences of errors in assumed natural mortality, using three commercially important North Atlantic stocks with different life histories as case studies. Negative correlations were found between natural mortality and reference points; high natural mortality rates resulted in low MSY and F_{MSY}. Long-term catches decreased under an F_{MSY} optimized for a natural mortality that deviated from true natural mortality, but the reference points were much more sensitive to assuming that natural mortality is lower than in reality. While

natural mortality can be 35% lower than the parameter value used before exceeding overall assessment uncertainty, there was only 10% error margin in the opposite direction. This highlights the importance of getting natural mortality right, especially when natural mortality may have increased, and to determine tolerable levels of error by systematically assessing effects of natural mortality as decision basis for managers and stakeholders.

A5 Uncertainty regarding natural mortality for eastern Australian orange roughy

G. Tuck and *M. Haddon* (Presenter: *P. Burch*)

The eastern Australian stock of orange roughy is very long-lived and highly valued, with a history of considerable exploitation in the late 1980s and early 1990s (peaking at just over 34,000 mt in 1990) before being classified as conservation-dependent only a few years later (catches in the late 2000s were less than 200 mt). Recent assessments have shown an increase in biomass, and a targeted commercial quota has been reinstated. The stock is held as an example of the consequences of overexploitation and of managed recovery and, as such, both conservation and fisheries management place high regard on the status and future of the stock; it is also highly economically valuable to the fishing industry. As a consequence, the assessment is both contentious and highly scrutinized. The current assessment uses the Stock Synthesis platform, with key inputs being annual catches, occasional acoustic surveys, and age-composition data. For the base-case model parameterization, natural mortality has been fixed at $M = 0.04$ for several assessment cycles. However, this figure is taken from New Zealand, based on an average from two age compositions thought to reflect unfished NZ roughy stocks. A likelihood profile on natural mortality from the most recent (2017) assessment suggested that a lower value for M may be more appropriate. Reducing the assumed value for natural mortality leads to reductions in quota, as determined by the Australian harvest control rule. In the face of uncertainty in the appropriate value of natural mortality to use, a cross-catch risk assessment was conducted, whereby three years of estimated catches calculated under the Australian harvest control rule for each model were used as fixed catch inputs to the alternative model. An industry-proposed fixed catch series was also considered, with catches set at an intermediate value between those derived from the lower and higher M scenarios. While the cross-catch risk assessment showed little short-term risk to the stock, questions remain over how to deal with uncertainty in the value of natural mortality in future stock assessments, as this has an influence on catches, the rate of recovery, the risk to the stock given the number of years of unknown recruitment, and future levels of industry investment.

Session B: Multispecies Approaches to Estimating Single-Species Natural Mortality

B1 Multispecies approaches to modeling natural mortality rates (Keynote 2)

É. Plagányi, *L. Blamey*, and *J. Rogers*

Stock assessment models typically assume natural mortality rates, M, are constant, and attribute the variability in a stock's overall mortality rate to variability in fishing mortality, F. However, there are several instances in which this assumption may not be valid. For example,

M can change due to both direct and indirect trophic interactions, particularly when there are substantial changes in the overlapping abundances of a key predator or prey species, and extreme environmental changes. Hence, multispecies models are used to explicitly capture variations in *M* to more accurately model population dynamics, improve the ability to discriminate between F and *M*, and to quantify the influences of fishing on the broader ecosystem, consistent with an ecosystem approach to fishing. There are a growing number of approaches to modeling *M* in multispecies models, and here we consider the following categories: 1) using diet data to estimate predation mortalities; 2) using predator and prey abundance indices to estimate the net outcome of interactions; 3) using predator breeding success or tag–recapture survival estimates; 4) representing natural mortality risk as a function of size; and 5) variability in *M* due to spatiotemporal match/mismatches. We restrict focus to multispecies models developed for tactical applications requiring more rigor and consideration of uncertainty than broad strategic ecosystem models. We present examples using Models of Intermediate Complexity for Ecosystem assessments (MICE). Finally, in light of increasing anthropogenic climate change impacts on marine ecosystems, we summarize use of multispecies models in representing additional sources of mortality due to changing climate.

B2 Predation as a modifier of constant natural mortality for Gulf of Alaska pollock

M. W. Dorn and *C. L. Barnes*

Although highly variable in time and space, predation remains the greatest source of mortality for juvenile and lower trophic-level fishes. As such, cumulative effects of predation can have substantial and long-term effects on the dynamics of these prey. Gulf of Alaska (GOA) walleye pollock (*Gadus chalcogrammus*) is one stock that has shown considerable variability in biomass over the past four decades. During this same time, the GOA transitioned from being dominated by pollock to a demersal fish community comprising primarily upper-trophic-level predators. We estimated time-varying consumption of pollock by five major groundfish species to better understand changes in predation pressure in a "top heavy" system (1990–2017). This index of predation accounted for spatiotemporal variation in predator biomass, bioenergetics-based rations, and age-specific proportions of pollock consumed. We found evidence of intense and highly variable predation on Gulf of Alaska pollock (ranging from 1.86–7.05 million metric tons). Of those examined, Arrowtooth Flounder (*Atheresthes stomias*) was, by far, the dominant pollock predator (relative consumption: 0.74 ± 0.14). The combination of a single dominant predator and synchronous consumption dynamics among focal predators suggests strong top-down control over pollock in this region. To evaluate population-level impacts of predation, total pollock consumption estimates were included in the stock assessment model as a survey-like index of removals attributable to natural mortality. This formulation allowed for non-annual data inputs and included a proportionality constant with which to scale consumption. Age-specific natural mortality was allowed to vary according to a penalized random walk. We found that natural mortality ranged from 43% higher to 50% lower than the long-term mean. Resulting estimates of spawning biomass differed by as much as 20% relative to a model without time-varying natural mortality. We assert that an empirically derived predation index can be used to modify constant natural mortality as a practical means of incorporating ecological information into single-species stock assessments.

B3 Spatiotemporal analyses of marine predator diets from data-rich and data-limited systems

A. Grüss, J. Thorson, G. Carroll, E. Ng, K. Holsman, K. Aydin, S. Kotwicki, H. Morzaria-Luna, C. Ainsworth, and *K. Thompson*

Accounting for variation in prey mortality and predator metabolic potential arising from spatial variation in consumption is an important task in ecology and resource management. However, there exists no statistical method for processing stomach content data that accounts for fine-scale spatiotemporal structure while expanding individual stomach samples to population-level estimates of predation. Therefore, we developed an approach that fits a spatiotemporal model to both prey-biomass-per-predator-biomass data (i.e., the ratio of prey biomass in stomachs to predator weight) and predator biomass survey data, to predict "predator-expanded stomach contents" (PESC; the product of prey biomass per predator biomass, predator biomass per unit area, and surface area). The PESC estimates can be used to visualize either the annual landscape of PESC (spatiotemporal variation), or can be aggregated across space to calculate annual variation in diet proportions (variation among prey items and among years). We demonstrated our approach in two contrasting scenarios: a data-rich situation involving eastern Bering Sea (EBS) large-size walleye pollock (*Gadus chalcogrammus*) for 1992–2015, and a data-limited situation involving West Florida Shelf red grouper (*Epinephelus morio*) for 2011–15. In the large-size walleye pollock case study, PESC was predicted to be higher in very warm years on the Middle Shelf of the EBS, where food is abundant. In the red grouper case study, PESC demonstrated measurable variability in northwestern Florida waters, presumably due to variability in harmful algal bloom severity. The estimates generated by our approach can be employed to parameterize or validate diverse ecosystem models and can serve to address many fundamental ecological questions.

Session C: Approaches to Modeling Natural Mortality

C1 Scrabbling around for an understanding of natural mortality (Keynote 3)

J. G. Pope, H. Gislason, J. C. Rice, and *N. Daan*

The authors have collaborated for the past 40 years on a sequence of initiatives for a range of fisheries and marine ecosystems projects. These had natural mortality (*M*) as a common thread, and have helped increase understanding of this elusive parameter. Here, we provide a reprise as well as an extension of our earlier results. Taken together, these help to develop an understanding of *M* of exploited fish stocks, particularly those of the North Sea. Firstly, a reprisal is given of the key findings about *M* due to predation by important fish stocks of the North Sea. Estimates were first produced by the ICES Multispecies Working Group using multispecies virtual population analysis (MSVPA) in combination with extensive stomach content data, collected for all four quarters and around the whole North Sea during 1981. Results from this initiative demonstrate that predation mortality (*M2*) represents a large portion of *M* for many North Sea fish species, but varies markedly both by age and by year, thus refuting the then-widely adopted hypothesis that *M* was constant. Moreover, these

variations were sufficiently large to overturn single-species predictions of sustainable yield. *M2* results from the 1980s also indicated that mortality levels were related to prey size and species. The paper then reprises results from studies made by the private working group that the authors formed to continue their collaboration. These focused first on size spectra of fish communities both by data analysis and by developing a simple trait-based model (cartoon) of the North Sea—the charmingly simple model (CSM). This modeling led to further questions about the basis of the coexistence of fish species in an ecosystem, given that egg production scales approximately with asymptotic weight. This led to a plausible hypothesis that differential natural mortality rates are required that increase with the von Bertalanffy parameters of curvature, K, and asymptotic length, L_∞, but decrease with fish length. Data from the literature supported this hypothesis, which was further refined into canonical form: $M = K(L_\infty/L)^{1.5}$. However, this hypothesis is also questioned because this form might not be compatible with the predicted and observable fact that size-spectra slopes become more negative with increased general levels of fishing. Clearly, changes in size spectra should cause changes in *M2*. Results of new modeling work are presented where the CSM is modified to include differential natural mortality rates by K and L_∞. The results suggest that M responds both to general levels of fishing and the slope of the ensuing size spectrum. This suggests that a more general expression for predation mortality would be $M2 = \alpha(F)K(L_\infty{}^c)(L^{\beta(F)})$, where c is likely to be close to the 1.5 value used in the canonical form. The work thus provides a likely form for *M2* but by no means a universally applicable formula yet. It remains a hypothesis needing to be tested and perhaps calibrated against data from the sea. Such calibrations might indeed point toward a universal formula for *M2*.

C2 Using Bayesian model selection to evaluate different ecosystem effects on natural mortality in stock assessment of Prince William Sound herring

J. T. Trochta and *T. A. Branch*

The failed recovery of the Prince William Sound herring population following its collapse in the 1990s is not well understood. Many hypotheses explaining reductions in recruitment and/or increases adult mortality have been offered, but little consensus on predominant drivers has been reached. Furthermore, much of the preceding hypothesis-testing work is outdated in light of rapid ecosystem changes as well as improved statistical analysis techniques. Stock assessment models provide a unique tool for hypothesis evaluation because they synthesize and statistically weight various sources of information to produce the best fit of the data. We evaluate previous and new hypotheses with a Bayesian age-structured stock assessment model (BASA) for Prince William Sound herring. Factors from the physical environment (e.g., air temperature, PDO, NPGO) and interspecific interactions (e.g., abundances of humpback whales, walleye pollock, Pacific cod) are individually incorporated as covariates or latent variables into BASA. This produces a suite of models we evaluate using Bayesian model selection criteria (Deviance and Watanabe–Akaike Information Criteria, and Posterior Predictive Loss) and run using a more efficient Bayesian sampling algorithm (the no-U-turn sampler, or NUTS). The use of NUTS allowed us to quickly explore a number of models for selection, as well as check a number of key assumptions for sensitivity. Our results show that NPGO, walleye pollock spawning biomass, and Pacific cod effects on adult mortality resulted in the best values of all selection criteria

and greatest improvement in model predictions (compared to recruitment models as well). Furthermore, we find that the magnitudes and even signs of some estimated effects (NPGO and Pacific Cod among others) have changed over time, suggesting nonstationary relationships between herring mortality and ecosystem factors. These effects represent Gulf of Alaska-wide factors, implying regional bottom-up and/or food-web interactions have a key role in recent adult herring mortality and overall biomass dynamics. By using Bayesian model selection methods with a more efficient sampling algorithm, we demonstrate an efficient framework for incorporating ecosystem information with uncertainty in stock assessment to determine important ecological factors of herring mortality.

C3 Revisit the mechanism: Why is natural mortality size-dependent?

A. Manabe and *T. Yamakawa*

Natural mortality in stock assessments is one of the most pivotal issues that control the consequence of the assessment models. The treatment of natural mortality coefficient *M* has been simplified by assuming a constant value throughout the life history, except for the initial stages owing to the difficulties of estimation and interpretation. However, several empirical studies on natural mortality focus on the allometric relationship between *M* and body size, as well as growth coefficient and environmental temperature (Pauly 1980, Lorenzen 1996, 2000, Gislason et al. 2010). Although the common understanding that the body size acts as a fundamental factor determining natural mortality prevails, the mechanism has not been either discussed precisely or included in stock assessment models. Assuming that the major source of natural mortality of fish is predation, we revisit the successive mechanism of size-dependent mortality by functionalizing each factor in the survival process from initial stages. From the point of view of predator–prey interactions, we discuss the effect of body size and its allometric relationships as the determinant factors of the success/failure rates of the interactions. We then merge all the driving factors of predation to show that the size-dependent natural mortality rate is an appropriate principle based on biological, physiological, behavioral, and ecological points of view.

C4 Estimation of natural mortality in a size-structured stock assessment model for sea scallops

D. R. Hart, *J.-H. Chang*, and *L. D. Jacobson*

Assumed natural mortality rates can strongly affect stock assessment model outputs such as reference points and estimated biomass and fishing mortalities. However, natural mortality can be difficult to estimate, since it is confounded with fishing mortality, survey efficiency (catchability), and/or steepness assumptions. For sea scallops (*Placopecten magellanicus*), surveys reliably track cohorts two years before they enter the fishery. Additionally, there have been areas closed to fishing for substantial periods of time. This means that both juvenile and adult natural mortality can be estimated without confounding with fishing mortality. Moreover, there is no assumption regarding steepness in the sea scallop assessment model, as well as independent estimates of survey efficiency. Thus, the sea scallop assessment is ideally suited for estimating natural mortality. We estimated

juvenile (20–90-mm shell height) natural mortality for sea scallops in the mid-Atlantic bight using a size-based catch-at-size analysis (CASA) model. Results indicate that substantial increases in natural mortality were associated with large year classes, suggesting density-dependent mortality. We also estimated natural mortality for all size classes in the Georges Bank closed areas in the CASA model. Natural mortality stayed within a narrow range except for a short period with elevated natural mortality, during a time where there were reports of disease outbreaks. Mean natural mortality over the time series was somewhat higher than previously reported. The models that estimated natural mortality had improved diagnostics (e.g., reduced retrospective patterns and improved fits to survey data), compared to previous models where natural mortality was fixed. Our results demonstrate that under at least some circumstances, natural mortality can be estimated inside a stock assessment model, and doing so will improve the accuracy of model outputs.

C5 A Bayesian model for estimating bivalve natural mortality with application to oysters in Chesapeake Bay, Maryland

K. L. Doering, *M. J. Wilberg*, *D. Liang*, and *M. Tarnowski*

Bivalves leave behind articulated valves when they die that can be used to estimate natural mortality. However, a common method used to estimate natural mortality in bivalves, known as the box count method, includes several assumptions that may be violated for eastern oysters (*Crassostrea virginica*) in Chesapeake Bay, Maryland. We developed a Bayesian model alternative to the box count method that included modifications to account for potential violations of assumptions. The model was applied to oysters in 32 areas in Maryland during 1991–2017 using dredge survey data, and the natural mortality estimates from the model were compared to ones derived from the box count method. The spatial and temporal trends in natural mortality from the model were summarized using dynamic factor analysis. Natural mortality showed considerable spatial and temporal variation, with median mortality rates ranging between 0.00 and 0.96/yr. Natural mortality spiked in most regions in 2002 and was lower in more recent years. The Bayesian model estimated slightly higher (0.02/yr on average) natural mortality than the box count method, except for years following high natural mortality, after which the Bayesian model estimated lower natural mortality than the box count method. The dynamic factor analysis revealed two common trends in natural mortality and a north–south gradient in the loadings on the trends. This work improves our understanding of the variability of oyster natural mortality in Maryland, and the Bayesian model could be modified for use with oysters in other regions or with other species.

C6 Estimating a natural mortality vector covering the lifespan of southern bluefin tuna

P. Eveson, *R. Hillary*, and *A. Preece*

Natural mortality is one of the most important/influential parameters in fishery stock assessment models; however, it is often assumed constant with age and known due to lack of data with which to estimate it. Southern bluefin tuna (SBT) is a rare example where a natural mortality (M) vector covering the life span of the species has been derived based on

multiple data sources. In particular, extensive tag–recapture studies for SBT have provided valuable information on juvenile natural mortality, Close-Kin Mark–Recapture methods have enabled estimation of adult natural mortality, and direct age data from catches on the spawning grounds have allowed inference about senescence. In this talk I outline how an age-specific *M*-vector for SBT has developed over time.

C7 What can Close-Kin Mark–Recapture estimate: *N*, *M*, what else, and when?

M. Bravington

Close-Kin Mark–Recapture (CKMR) is an assessment method that requires only tissue samples from dead animals, e.g., from commercial catches. It can give precise estimates not just of absolute adult abundance, *N*, but also of adult natural mortality, *M*, and several other desirable quantities that collectively allow, for example, direct estimates of spawner-per-recruit-ratios. The estimates of mortality rate and of abundance in CKMR come from different "parts" of the dataset and are statistically orthogonal, in contrast to conventional stock assessments that rely on relative abundance indices. Further, no uncomfortable assumptions are needed in CKMR about consistent selectivity or CPUE/other-index reliability. In this talk I will explain heuristically how this rather miraculous power of estimation arises, and what the data requirements and limitations really are for two distinct types of animal: "fish" and "sharks." Simulation and study-design results are included.

C8 How high and low steepness of the stock-recruitment relationship changes estimates of natural mortality and management quantities

C. A. Castillo-Jordán, *K. F. Johnson*, *O. S. Hamel*, *K. L. Doering*, *I. G. Taylor*, *C. C. Monnahan*, *J. N. Ianelli*, and *A. E. Punt*

It is common in integrated, age-structured stock assessment models to either 1) fix natural mortality (*M*) at an externally derived value using "indirect" methods, or 2) estimate it simultaneously with other parameters. Each method has benefits, but the decision of how to model *M* is often investigated somewhat in isolation of how to treat other key parameters that are difficult to estimate within stock assessment models. Likelihood profiles, which are typically used to provide support for which parameters (including *M*) to estimate when applying maximum likelihood estimation, largely ignore parameter correlations. Monte Carlo simulations were used to investigate approaches 1) and 2) while simultaneously investigating how the steepness of the stock-recruitment relationship (*h*), another parameter that is commonly fixed at an externally derived value, affects the results. The consequences of mis-specifying *M*, in terms of estimates of catches that would lead, on average, to a spawning stock biomass that is 40% of the unfished spawning stock biomass, depends on *h*. In particular, estimates of this catch metric were biased when *h* was actually high but fixed at a low value in the stock assessment. Conversely, when *h* was low, estimates of this catch metric were variable. Researchers should investigate mis-specification in *M* as another reason for stocks appearing to be more productive, i.e., estimates of *h* appear to be approaching the upper limit of 1.0 with the addition of new data.

C9 Estimates of time-varying natural mortality of groundfish in the Gulf of Alaska

G. Adams, *K. Holsman*, *K. Aydin*, *S. Barbeaux*, *M. Dorn*, *A. B. Hollowed*, *J. N. Ianelli*, *A. E. Punt*, *I. Spies*, and *I. J. Stewart*

An assumption underlying most stock assessment methods is that natural mortality is constant through time, and changes in population status are due only to recruitment, growth, and/or fishing intensity. However, variability in the dynamics of exploited fish stocks has long been understood to be, in part, the result of variation in mortality from predation. Accounting for variation in predation mortality, a component of natural mortality, can be particularly valuable in stock assessment models if the biological realism of the assessment used for management is improved. Multispecies statistical catch-at-age analysis (MSCAA) is one modeling approach that links multiple single-species age-structured models by time-varying predation mortality and time-invariant residual mortality, representing components of natural mortality other than predation. We compare the outputs of single-species stock assessment models and an MSCAA developed for groundfish in the Gulf of Alaska (GOA), which support some of the most valuable fisheries in the region. Specifically, we fit the model to data for walleye pollock (*Gadus chalcogrammus*), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), and arrowtooth flounder (*Atheresthes stomias*), species that are the most trophically connected in the GOA. Results demonstrate that recent increases in the biomass of arrowtooth flounder have led to increased mortality on juvenile pollock and cod. Predation mortality was larger for smaller individuals, and the proportion of predation mortality from each species varied through time. However, estimates of biomass are sensitive to the value of residual mortality. This represents a first step toward tactical ecosystem-based fisheries management in the Gulf of Alaska.

C10 Considerations for developing a longevity-based prior for the natural mortality rate

O. S. Hamel and *J. M. Cope*

The natural mortality rate, *M*, associated with a fishery stock is an important parameter in characterizing the stock productivity, status, and dynamics. It is common for stock assessments, and particularly for U.S. West Coast groundfish assessments, to assume either a single value of *M* or one value of *M* for each sex, though, in reality, *M* can vary with age, size, maturity, and other factors. It is difficult to directly measure even an average *M* across time; thus, a number of meta-analytical approaches using relationships between *M* and other life-history parameters have been developed and used over the years to provide an estimate for *M* in stock assessments. Hamel (2015) developed a method for combining such methods to provide a prior on *M*. Then et al. (2015) provided an updated data set of values of *M* and covariates, and recommended using maximum age alone for estimating *M*, when a reliable value is available. Even so, maximum age can be a tricky value to identify. Here we discuss alternative approaches to developing *M* priors based on maximum age information, touching on a number of previous analyses from the literature and considerations for estimation of both the mean/median value and the width of the prior.

C11 Estimating natural mortality in size-structured models

L. Cronin-Fine and *A. E. Punt*

Natural mortality (M) is crucially important for stock assessment since it strongly influences model outputs such as spawning stock biomasses, MSY, and fishing mortality. Variation in M can occur between sex and maturity stages as well as temporally due to predator–prey interactions and environmental conditions. Estimating M is difficult since it is confounded with several factors including catchability, recruitment, and growth. Many stock assessments pre-specify M. However, studies suggest that it would be better to estimate it. Most studies exploring whether M can be estimated have focused on stock assessments based on age-structured models, since these are commonly used. Unfortunately, several valuable marine species, such as crabs and lobsters, are difficult to age. Therefore, they predominately rely on size-structured models. Size-structured models do not use age data for parameter estimation and have unique characteristics such as a size-transition matrix and possibility a terminal molt that could impact the ability to estimate M. Terminal molt could potentially improve estimation of M because there is no further growth following terminal molt. Therefore, this study explores the ability of stock assessments based on size-structured models to estimate M under a variety of scenarios. These scenarios include whether the operating model and estimation method have a terminal molt, whether M is constant, time-varying, or sex- and maturity-stage-specific, the quality/sample size of the biomass index and the size-composition data, and whether growth is estimated simultaneously with M.

C12 Life-history diversity, natural mortality, and fisheries reference points (Keynote 4)

H. K. Kindsvater

The diversity and complexity of fish life histories poses a persistent challenge for fisheries management, where practical methods of estimating natural mortality may work well for one species or stock, but not another. Traditional approaches to stock assessment typically assume that average rates of natural mortality are constant over individual lifetimes and similar for each sex. Because data availability limits the statistical estimation of parameters for species with complex life histories, natural mortality is also assumed to be similar for species with different mating and reproductive systems. I use a comparative approach to modeling population dynamics of fished species with different life histories to predict if and when including more-realistic natural mortality changes fisheries reference points, including the biomass reference point and the spawning potential ratio. I specifically focus on species that change sex, bear live young, or have parental brood care. These species are often sexually dimorphic, and including sex-specific mortality rates influences the relationship between biomass yield and productivity. Additionally, differences in reproductive mode can change mortality rates of both adults and juveniles. Finally, my results highlight how this complexity in natural mortality, which drives population demography, can interact with differences in selectivity arising from management or gear type in nuanced ways.

C13 Age dependence of natural mortality based on equilibrium assumptions and the adult mortality constraint

I. Bitetto, *A. Martiradonna*, and *M. T. Spedicato*

An extensive literature exists suggesting that, in marine population dynamics, the typical trajectory of natural mortality is steeply declining with age from a very high egg and larval mortality rate to a plateau around sexual maturity and a slight decline thereafter. The model that well describes this behaviour, among the indirect methods, is the reciprocal equation $M(t) = M_a + B/t$ (Caddy 1991), where M_a is the asymptotic mortality and B a curvature parameter. The Caddy method for estimating the parameters in the reciprocal model is based on several equilibrium assumptions and requires knowledge of the mean lifetime fecundity (MLF) and the mean parental age (MPA), values generally difficult to estimate. In the original method, an iterative procedure based on the Axiom of Stable Population Size is applied, and a mortality constraint in the last age class, through a gnomonic age discretization, is taken into account. In Martiradonna (2012), we showed that the algorithm may not converge if the initial guess is not close enough to the real parameters. We derived the explicit formula to obtain the asymptotical mortality and the curvature parameters, based on the same assumptions of the Caddy method, gaining in solution stability and computational cost. We also proposed to relax the adult mortality constraint in order to make the solution independent from the class discretization. In Abella et al. (1998), unlike the Caddy model, the equilibrium assumptions are expressed in terms of production and loss of biomass. Thus, the algorithm (commonly known as ProdBiom) is easier to apply, since it requires only growth and reproduction parameters that are generally available in any age-structured stock assessment. However, this algorithm does not admit a unique solution and we thus proposed a variant (Martiradonna 2012) by imposing an adult mortality constraint that allows us to obtain explicit formulas for the parameter estimation. This variant has been applied recently in literature (Mannini et al. 2020, Pantazi et al. 2020) to some Mediterranean stocks as case studies of statistical catch-at-age assessments. This work is aimed at showing the gain in stability of our finding, applying the two methods to different stocks in the Mediterranean Sea. The natural mortality vectors obtained are compared with other vectorial methods (e.g., Chen and Watanabe 1989, Beyer et al. 1999), evaluating the impact on the stock assessment results (biomass, fishing mortality, and recruitment).

C14 The role of starvation in the collapse and slow recovery of northern cod

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Food resources often vary seasonally and, as such, individuals must endure periods when they rely on energy reserves to fuel the basic processes of life. Ultimately, limited food resources can lead to starvation-induced mortality and, depending on the scale of the food limitation, can have population-level consequences. While it is widely recognized that starvation plays a key role in the regulation of animal populations, attempts to explicitly account for starvation-induced mortality in population models are rare. Using commonly collected biological data on body condition, we develop a statistical approach to

index trends in starvation-induced mortality by estimating the proportion of individuals experiencing severe emaciation in a fish population. The statistical approach accounts for seasonal patterns in body condition, allowing data collected at any time of year to be included in our model. Using Canada's northern cod (*Gadus morhua*) stock as a test case, we found an association between rates of natural mortality estimated by an integrated population model and the index of mortality derived from proportions of cod in poor condition. This index is also associated with the availability of key prey species like capelin (*Mallotus villosus*) and northern shrimp (*Pandalus borealis*). Taken together, our results indicate that starvation-induced mortality represents an important component of the natural mortality experienced by the stock, supporting the idea that food availability contributed to the stock collapse in the early 1990s and, further, that it has been an important factor in the slow recovery of northern cod despite low fishing mortality. Explicitly considering prey availability—e.g., through body condition or prey abundance indices—should improve stock assessment modeling efforts and facilitate development of actionable ecosystem-based fisheries management strategies.

C15 Shaping natural mortality and stock productivity by integrating a fish condition index in the stock assessment

I. Bitetto, *P. Carbonara*, *M. Donnaloia*, *M. T. Spedicato*, and *M. Casini*

In the Mediterranean Sea, only the 9% of the stocks are fished below F_{MSY}. For this reason, reversing the declining trend of Mediterranean fish stocks is a priority of the General Fisheries Commission for the Mediterranean (GFCM) and of the European Union Common Fisheries Policy. As a consequence, there is an increasing focus on monitoring and stock assessment. In recent years, the complexity of the stock assessment models used during the dedicated working groups in the Mediterranean has rapidly increased, together with the availability and quality of the fisheries data. In particular, integrated models were indicated as a possible solution to supplement the information from additional regional indicators of stock status. Natural mortality (*M*) is probably one of the most important, but at the same time difficult, parameters to model within the stock assessment process. In the absence of data to estimate *M* directly, a variety of indirect methods can be used to derive *M* on the basis of life-history traits. Several studies demonstrated that fish condition, or the magnitude of stored energy reserves, is a key attribute of fish, as condition affects other life-history traits such as growth, reproduction, and natural mortality and, consequently, it may have an important influence on stock productivity. The purpose of the present study is to integrate a fish condition factor in stock assessment, generalizing the approach developed by Casini et al. (2016). The red mullet (*Mullus barbatus*) from the southern Adriatic Sea has been selected as a case study. The Le Cren condition index (*Kn*) was selected as the simplest and most reliable indicator of body condition for species allocating energy reserves mostly in muscle, like the red mullet. The annual proportion of "starving" individuals by length intervals, defined as having a *Kn* below a set of thresholds, was used to adjust the annual natural mortality by age used in the integrated assessment. Thereafter, the impact resulting from the integration of the fish condition index in the assessment was evaluated through a sensitivity analysis on the starvation threshold.

C16 Natural mortality diagnostics for state-space stock assessment models

A. M. J. Perreault and *N. G. Cadigan*

State-space stock assessment models that separately include population dynamics process errors and observation errors are increasingly used for fisheries stock assessments and are considered essential for the next-generation stock assessment package. However, diagnostics such as residuals and likelihood profiles are more complicated in state-space models because of the complex dependencies in the data caused by process errors. We develop natural mortality (*M*) diagnostic methods for state-space models to provide an in-depth understanding of how the choice of *M* affects model fit through 1) profile likelihoods and 2) local influence diagnostics. In traditional stock assessment models, it is straightforward to construct profile likelihood plots that show the likelihood contributions (i.e., the fit) of each data source versus changes in the *M* assumption, since the total negative log likelihood (*nll*) is simply the sum of the *nll* of each data source. State-space models use an integrated *nll* to account for random effects (e.g., model process errors), and the integrated *nll* cannot be directly split into data-component *nll*s. The major innovation of our research is the development of methods to provide profile component *nll* contributions in the state-space setting. We use these profile likelihoods to evaluate the effect of broad changes in *M* across all ages and years on the total model fit to all data and on the fit to individual data sources (surveys, landings, age compositions). Additionally, we also use local influence diagnostics to assess the influence of age- and year-specific changes in *M* on model fit. We apply the *M* diagnostics to a case study for American plaice (*Hippoglossoides platessoides*) on the Grand Bank of Newfoundland, and our results indicate that most input data sources are fit better with a higher *M* in recent years. We suggest that *M* diagnostics for state-space models should be examined when formulating an assessment model to improve our understanding of the impacts of *M* specification on model fit and to provide additional insights about the validity of the *M* assumption.

C17 Spatiotemporal patterns in natural mortality estimated using a stage-structured model for oysters in Chesapeake Bay, Maryland

M. J. Wilberg, *M. M. Mace III*, *K. Doering*, *L. Barker*, *A. Larimer*, *F. Marenghi*, *A. Sharov*, and *M. Tarnowski*

Natural mortality is a key driver of population dynamics, particularly for populations affected by episodic disease outbreaks, but it is often difficult to estimate in stock assessment models. A further complication is that natural mortality likely varies over space and time. Some species leave behind evidence of natural mortality that can be included in stock assessment models to estimate natural mortality, such as the articulated valves (i.e., boxes) of deceased bivalves. These auxiliary data can be included by dynamically modeling the abundance of boxes in the environment and fitting the model to the auxiliary data. We conducted stock assessments for eastern oyster (*Crassostrea virginica*) in 36 regions of the Chesapeake Bay, Maryland. The model was stage-structured and estimated natural mortality rates of adult oysters each year during 1999–2018. Estimated natural mortality varied substantially over space and time. In general, estimated natural mortality rates were higher in the beginning of the time series, and were similar in neighboring regions.

C18 Natural mortality estimation from tagging and length composition data for western-central Pacific Ocean skipjack tuna

M. Vincent, *G. Pilling*, and *J. Hampton*

Around 1.8 million mt of skipjack tuna (*Katsuwonus pelamis*) are caught in the western central Pacific Ocean each year. The status of this key tuna stock is regularly assessed using the integrated assessment model MULITFAN-CL. The assessment utilizes catch, standardized and unstandardized effort, mark–recapture, and length-composition data. The significant quantity of mark–recapture information obtained from many years of tagging programs, combined with the time series of length-composition data, allows spatially and temporally invariant estimates of natural mortality at age to be estimated, based on the functional form of a cubic spline with five nodes. Tagging data are fit assuming a negative binomial distribution with an estimated overdispersion parameter. Length-frequency data are fit with a robust normal distribution where the effective sample size is capped at 1,000 and then reduced by a specified scalar value. Biologically plausible estimates of natural mortality at age and overdispersion parameters are obtained, but numerous reporting rate parameters are estimated at the upper bound. The shape of the curve of natural mortality at age was sensitive to the assumed mixing period for the tagging data, (i.e., time after which tags are included in the likelihood) and the scalar of the length-composition influence. Differing curves for natural mortality at age were attributed to data source conflict between the tagging data and the longline length composition; the latter is the primary source of observations of the oldest skipjack. Likelihood profiling shows that both tagging data and length-composition data influence estimates of natural mortality in a size-based integrated assessment.

C19 Comparing life history-based natural mortality estimates to tagging and telemetry studies

J. R. Wallace

Tagging and telemetry studies provide a more direct estimate of natural mortality than those based on life history. I compare and contrast tagging and telemetry studies to life history-based natural mortality for a number of species. The results vary widely.

Session D: Modeling Natural Mortality in Rockfish (*Sebastes*) Stock Assessments

D1 Upgrading from *M* 0.2: An application-based method for accessible estimation, evaluation, and uncertainty characterization of natural mortality (Keynote 5)

J. M. Cope and *O. S. Hamel*

Natural morality (*M*) is a notoriously difficult population parameter to estimate, yet it is also one of the most important measures of life history that sets, as Beverton and Holt called it, "the course of events." Stock assessments that include this parameter often

show great sensitivity to its value, reflecting the need to define not only its value, but also the uncertainty in its estimation. Direct measure of natural mortality is often limited to resource-intensive tag–recapture studies. Indirect measures are more often used, and are built of life-history theory relating natural mortality to traits like age, size, maturity, and reproductive condition. And sometimes you just use 0.2(!). The Natural Mortality Tool attempts to accumulate several empirical estimators of *M* into one application. Users simply input life-history values to obtain estimates of natural mortality. These estimates can be taken individually or can be combined into a weighted density function that can be used as a prior of *M* that integrates uncertainty across several *M* estimators. Comparing estimators can also reveal inconsistencies in life-history values that may lead to further refining of the basic biological understanding. Making these estimators and the development of uncertainty in estimating natural mortality more accessible hopefully provides more transparent and defensible decisions on treating this important population parameter.

D2 Estimation of sex-specific natural mortality in fish stock assessments

A. Hicks

Natural mortality is an important parameter in fish stock assessments and likely differs for females and males. The actual value of natural mortality for each sex can be difficult to estimate given the data typically available to stock assessments, but these data may contain information that informs the relative difference in natural mortality between sexes. We explore different methods to estimate natural mortality in fish stock assessments and identify methods that leverage the data and provide information about the relative difference in natural mortality between males and females. Data from fisheries and surveys for three fish species, Pacific halibut (*Hippoglossus stenolepis*), Dover sole (*Microstomus pacificus*), and widow rockfish (*Sebastes entomelas*), are used in age-structured stock assessment models to illustrate the information available to estimate natural mortality. The estimates of natural mortality for the separate sexes were correlated, showing that there is information in the data regarding the difference between male natural mortality and female natural mortality, even though the absolute value may not be well informed. Age- and length-composition data that incorporate the sex ratio may be a major source of this information, and structural assumptions about relative selectivity between males and females may contribute to the level of observed correlation in *M* estimates. A relative offset for one of the sexes may be useful when estimating natural mortality, but does not easily incorporate sex-specific prior distributions.

D3 Estimating natural mortality for an ovoviviparous fish: Beaked redfish (*Sebastes mentella*) in the northeastern arctic

H. Höffle and *B. Planque*

Beaked redfish (*Sebastes mentella*) is one of the few commercially important fish species producing living offspring. Like many other deep-water fishes, it is slow-growing, late maturing, and long-lived, getting as old as 65 or even 75 years in some populations. The stock in the Norwegian and Barents Seas is analytically assessed since 2012, assuming a natural

mortality (*M*) of 0.05 across all ages based on Hoenig's longevity-based estimator. Since then, several reviews and new studies have been published, affording a reevaluation of the natural mortality in the assessment model. We estimated natural mortality of beaked redfish using 44 different estimators in two categories: either estimating *M* across the population, or dependent on age, length, or weight. The obtained estimates were highly variable, ranging from 0.01–0.49 for estimates across the population, and 0.05–0.62 for age-or size-dependent median *M*. These wide ranges demonstrate the sensitivity to the input parameters as well as the pitfalls of using estimators developed for distant taxa. Of the 44 estimates, 24 were considered as potential candidates for updating the stock assessment model. Here, we present an overview of the tested estimators, the criteria we used for selecting potential candidates, and our recommendation for further use in the assessment model.

Session E: Life-History Theory

E1 Natural mortality and life history: A primer for fisheries scientists (Keynote 6)

K. Lorenzen

Natural mortality rates in most fish and marine invertebrate populations vary over the life cycle, often by orders of magnitude. Driven by physiological (internal) and ecological (external) processes, lifetime mortality schedules show strong patterns of regularity but are also influenced by environmental factors and density dependence, particularly in early life stages and juveniles. Traditionally, fisheries models and stock assessment methods have adopted a highly simplified representation of the life cycle, with a recruited stage where natural mortality is described explicitly as a constant rate, and a stock-recruitment relationship that implicitly accounts for juvenile mortality (and the environmental and density-dependent influences upon it). Limitations of this representation and the "constant *M*" paradigm for the recruited stock are becoming increasingly apparent from practical and theoretical considerations. For example, some fisheries exert heavy fishing pressure on juvenile stages, which must then be explicitly modeled in assessments. At the same time, due to the proliferation of marine reserves, populations where truly "old" fish are well represented are bound to become more common and consideration of senescence effects more relevant. Last but not least, current interest in size-based population dynamics, environmentally driven variation in vital rates, and the evolutionary ecology of aging challenge the "constant *M*" paradigm from a scientific perspective. For this keynote, I will synthesize current theoretical and empirical knowledge on lifetime patterns and levels of natural mortality and their relationships with other life-history traits. Based on this synthesis, I will aim to provide practical guidance on selecting appropriate natural mortality models for various fisheries assessment and research situations.

E2 The trade-off between condition and growth shapes juveniles' survival of harvested demersal fish of the Mediterranean Sea

G. Kerametsidis, *L. Rueda*, and *M. Hidalgo*

Fish somatic condition and growth are two interrelated traits closely associated with species life history and fitness, whose trade-off can ultimately impact population dynamics—albeit seldom empirically demonstrated. For instance, they can intricately affect survival rates, which are particularly relevant for species under exploitation. Using individual spatiotemporal information in the northwestern Mediterranean Sea, we document for the first time the existence of a trade-off between condition and growth in regulating survival dynamics in two important fish species for Mediterranean marine ecosystems and fisheries with contrasting life histories. For European hake (*Merluccius merluccius*), a benthopelagic species, juveniles' body condition was detected to be negatively associated with growth and positively linked to their survival. For the red mullet (*Mullus barbatus*), the same pattern was observed for young adults along with a secondary effect of environmental variability. As it has been previously shown that natural mortality (M) is highly dynamic and influenced by condition and other life-history traits, we posit that our results provide well founded ecological support to further implement a dynamic influence of life history in the natural mortality information used for the assessment of the two species examined.

E3 Time variation in confounded processes in population dynamics modeling: A case study for snow crab in the eastern Bering Sea

C. Szuwalski

Population dynamics models used to provide management advice for harvested natural resources often assume a constant natural mortality (M) over time. However, M is often not constant over time in reality, and it is confounded with other processes within population dynamics models like catchability (q) and growth, which may also vary over time. Not allowing for time variation in these processes can result in retrospective patterns in estimated biomass, which result in errors in management advice. Allowing for time variation in these processes can also result in errors in management advice if the estimated time variation does not reflect the underlying variation. Here I present an assessment for snow crab in the eastern Bering Sea that tests different combinations of time variation in M and q. The management advice for 2020 resulting from these models differed by nearly an order of magnitude. The managing body for snow crab did not adopt any of the models with time variation in M or q for management because the estimated variability in M and q was difficult to explain with any known mechanism and the management advice differed so drastically among the models.

Session F: Modeling Natural Mortality Using the Stock Synthesis Modeling Framework

F1 Modeling natural mortality in Stock Synthesis: Options available, common practices, and what to avoid (Keynote 7)

R. D. Methot

The widely used Stock Synthesis modeling platform has a broad range of possible configurations for natural mortality. An overview of the available options is provided, along with a review of common practices used in production stock assessments which utilize Stock Synthesis. The configuration of natural mortality is changed to illustrate how other options behave in a range of existing applications and to provide lessons in what setups seems to be most problematic.

F2 Enhancing single-species stock assessments through socioeconomic and ecosystem contributions: Accounting for red tide mortality in past and future population dynamics for Gulf of Mexico red grouper (*Epinephelus morio*)

S. Sagarese, *N. Vaughan*, *J. F. Walter III*, and *M. Karnauskas*

Impacts of *Karenia brevis* red tide blooms have been an increasing cause of concern for fisheries management on the West Florida Shelf. Red tide mortality has been incorporated into Gulf of Mexico grouper stock assessments since the mid-2000s. Traditionally, this has been achieved by including extra natural mortality during historical years with severe red tides (i.e., 2005), ideally based on analyses of satellite data. The most recent Gulf red grouper stock assessment was confronted with new challenges of: parameterizing red tides during both historical and forecasted time-periods, growing uncertainty regarding the standard methods used to quantify red tide severity, as well as suspected mortality due to associated bloom stressors (e.g., hypoxia). We will discuss how the impacts of multiple red tide events were incorporated into the stock assessment process and how results were communicated to fisheries managers. We first review data streams that were used to identify severe red tide events and discuss the importance of assumptions made when projecting tactical catch advice required for fisheries management. At the time of the assessment, a 2018 red tide event was suspected; however, considerable uncertainty existed in the magnitude of the event due to the limited quantitative data available. To account for this, different potential red tide scenarios were evaluated and results were presented in the form of a decision table highlighting the potential risks associated with different catch levels for consideration by managers. Collectively, these results emphasize the importance of ecological considerations in the management process and highlight a situation where status quo management may have led to unintended consequences. Ultimately, catch advice was recommended assuming that red tide mortality in 2018 approximated 2005. This decision was validated by a recent interim analysis, which found that the 2019 abundance index derived from the NMFS bottom longline survey was consistent with red tide magnitude similar to 2005.

F3 A review of estimation methods for natural mortality and their performance in the context of fishery stock assessment

M. N. Maunder, *H.-H. Lee*, *K. R. Piner*, *O. S. Hamel*, *J. M. Cope*, *A. E. Punt*, *J. N. Ianelli*, and *R. D. Methot*

Natural mortality (*M*) is one of the most influential parameters in fisheries stock assessment and management. It relates directly to stock productivity and important reference points used for fisheries management advice. Unfortunately, *M* is also very difficult to estimate, and hence very uncertain. This paper outlines the range of methods available to estimate *M* for use in stock assessment. The methods include those based on maximum age, life-history theory, and relationships between "well known" (those found in the literature and based on data for the stock in consideration) values for *M* and covariates, use of tagging data and catch curve analysis, and estimation within a single- or multispecies stock assessment model. All methods are subject to bias and imprecision due to incorrect assumptions and incomplete data. Furthermore, *M* is generally assumed to be constant over time, age, and sex, but deviations from these assumptions are very hard to detect. Based on our review, there is an obvious benefit to directly estimating *M* with data and within the stock assessment while assigning a prior via empirical methods. Carefully examining diagnostics and checking for model mis-specification is required to ensure that the available data and model assumptions are appropriately informative about *M*. For situations where direct estimation is not possible (a condition found in data-limited to data-rich stock assessments), the use of multiple methods with robust sensitivity exploration is recommended. Even when direct data are integrated into a stock assessment model, we recommend using other methods to estimate *M* and analyzing the direct data outside the stock assessment model as diagnostic tools.

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