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A REVIEW OF NATURAL MORTALITY (*M*) VALUES RELEVANT TO COASTAL PELAGIC SPECIES (CPS) FINFISH MANAGED UNDER THE PACIFIC FISHERY MANAGEMENT COUNCIL CPS FISHERY MANAGEMENT PLAN

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A review of natural mortality (*M*) values relevant to coastal pelagic species (CPS) finfish managed under the Pacific Fishery Management Council CPS Fishery Management Plan

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Abstract

The coastal pelagic species (CPS) fisheries along the U.S. West Coast in the Northeast Pacific Ocean are managed under the CPS Fisheries Management Plan and include four finfish species: Pacific jack mackerel (*Trachurus symmetricus*), northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax caerulea*), and Pacific mackerel (*Scomber japonicus*). The instantaneous rate of natural mortality (*M*) is an important parameter for assessment and management of these and other species. A synthesis of literature on *M* for each of these species has the potential to contextualize and improve estimation of *M* in future stock assessments. To this end, a brief synthesis of various methods for deriving estimates, inferences, or assumed values of *M* for managed CPS finfish along the U.S. West Coast was conducted. The synthesis included a review of literature cited in recent assessments for the U.S. West Coast, scientific reports from prominent fisheries and assessment-focused organizations, and Google Scholar queries. First, the report briefly describes the primary means of estimating *M* in fisheries management (i.e., empirical relationships across stocks found between estimates of *M* and more readily observed traits, mark-recapture analysis, catch-at-age analysis, and estimation within stock assessments) and summarizes best practices for modeling *M* in stock assessments. Reported values of *M* for CPS finfish are subsequently summarized and compared. For the U.S. West Coast, estimates of *M* for Pacific jack mackerel and northern anchovy are scant relative to those for Pacific sardine and Pacific mackerel, highlighting potential data gaps. Values of *M* were generally greatest for northern anchovy, followed by Pacific sardine and Pacific mackerel, and were lowest for Pacific jack mackerel. Values of *M* from conspecific stocks from other parts of the Pacific Ocean or closely related species were generally similar to those for CPS finfish off the U.S. West Coast and help contextualize available estimates for the region. Differences in values of *M* obtained from recent stock assessments and other estimation or inference methods were observed for both Pacific mackerel and northern anchovy; these differences may merit further consideration in future assessments. Finally, proposed research and modeling directions are discussed.

1. Introduction

The coastal pelagic species fisheries encompass historical and present fishing effort for a variety of vertebrate and invertebrate species along the U.S. West Coast in the Northeast Pacific Ocean. The CPS fishery is managed under the CPS Fishery Management Plan (FMP) by the Pacific Fishery Management Council (PFMC 2023). Species considered part of the CPS fishery by the PFMC include the following four finfish species, in addition to market squid (*Doryteuthis opalescens*) and multiple euphausiid species: Pacific jack mackerel (*Trachurus symmetricus*), northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax caerulea*), and Pacific mackerel (*Scomber japonicus*) (PFMC 2023). While Pacific sardine, Pacific mackerel, and the central subpopulation of northern anchovy are formally assessed, other CPS including the northern subpopulation of northern anchovy, Pacific jack mackerel, and market squid are monitored to ensure stock stability but are not regularly assessed (PFMC 2024). Two additional species, Pacific herring (*Clupea pallasii*) and jacksmelt (*Atherinopsis californiensis*), are included in the CPS FMP as ecosystem component species; ecosystem component species are non-target, not considered to be subject to overfishing or the risk of overfishing, and not generally kept for commercial or personal use.

Assessment of CPS finfish stocks requires, among many other components, specification of the instantaneous rate of naturality mortality, *M*. Natural mortality is an important parameter for fisheries assessments and management, with implications for productivity and management reference points (Maunder et al. 2023). Misspecification of *M* can produce biased estimates of other fishery parameters, like steepness in stock recruitment, and result in poor estimates of quantities relevant to management (e.g., virgin biomass) (He et al. 2011). Estimation of *M*, either independent from or within stock assessments, is challenged by limited informative data and confounding with other estimated parameters in assessments.

The specification and/or estimation of *M* in stock assessments can be informed by conducting an evaluation of *M* for each assessed species, including a review of relevant data and estimates (Maunder et al. 2023). Additionally, a review of a recent stock assessment for Pacific mackerel by the stock assessment review (STAR) panel recommended exploring and summarizing broad information on *M* for CPS (STAR 2023). Based in part on these recommendations, and the importance of *M* in CPS stock assessments, this report was developed to briefly summarize available information on *M* for the four CPS finfish species managed under the CPS FMP (excluding ecosystem component species), with an emphasis on stocks off the U.S. West Coast: Pacific jack mackerel, northern anchovy, Pacific sardine, and Pacific mackerel. The report is intended to accomplish the following objectives: 1) explore and synthesize available literature on the estimation and specification of *M* for CPS finfish, 2) summarize methods for estimating or inferring *M* independent from and within stock assessments, 3) summarize reported values of *M* for each of the CPS finfish species, with a focus on stocks along the U.S. West Coast but including contextual information from other conspecific stocks or related species in the Pacific Ocean, and 4) provide recommended directions for future research.

2. Description of data sources and literature review

The review of available data sources and literature featured obtaining all references pertaining to *M* in the most recent assessments for northern anchovy, Pacific sardine, and Pacific mackerel, and identifying all additional, relevant data sources and references cited within these references (Kuriyama et al. 2022; Kuriyama et al. 2023; Kuriyama et al. 2024). Published values of natural mortality for Pacific jack mackerel, which is not currently assessed, were obtained through a literature review of publications. Literature reviews also were conducted for the four CPS finfish species from either a) conspecific stocks outside of the U.S. West Coast (preferred) or b) from closely related species in the Pacific Ocean using the following keywords (via Google Scholar within the first 50 returns):

- Pacific jack mackerel:
    - jack mackerel *Trachurus symmetricus* natural mortality (conducted 10/28/24)
- Northern anchovy:
    - Northern anchovy *Engraulis mordax* natural mortality (conducted 10/29/24)
    - Anchoveta *Engraulis ringens* natural mortality (conducted 10/29/24)
- Pacific mackerel:
    - *Scomber japonicus* natural mortality (conducted 8/16/24)
- Pacific sardine:
    - Pacific sardine *Sardinops sagax* natural mortality (conducted 9/10/24)

No new, relevant results were obtained from the first Google scholar search for *E. mordax*, which prompted the second query for estimates of *M* for anchoveta. Additionally, recent scientific reports from the International Council for the Exploration of the Sea (ICES; https://www.ices.dk/Science/publications/ Pages/Scientific-reports.aspx) (i.e., 2022-onward) and all scientific reports from the North Pacific Marine Science Organization (PICES; https://meetings.pices.int/publications/scientific-reports) relevant to the estimation of natural mortality or life history characteristics for CPS finfish were obtained, in addition to all workshop reports and proceedings from the Center for the Advancement of Population Assessment Methodology (CAPAM; https://www.capamresearch.org/) and National Stock Assessment Workshops (NSAW; https://www.fisheries.noaa.gov/population-assessments/national-stock-assessment-workshops). Finally, a literature search with the NOAA Fisheries Scientific Publications Office (SPO; https://spo.nmfs.noaa.gov/) was conducted using the key word "natural mortality".

The literature search methods were intended to include the most relevant sources of information and provide a meaningful summary of current information on natural mortality for CPS finfish, but they should not be considered exhaustive. It is likely that relevant values of *M* or estimation methodologies were not captured as part of the described queries, particularly for stocks outside of the U.S. West Coast or closely related species. However, the estimates and methodologies presented in this report are expected to comprise a representative dataset for characterizing current information and best practices for the specification of natural mortality in CPS finfish stock assessments.

Estimates or assumed values of *M* for stocks of CPS finfish off the U.S. West Coast are primarily summarized in this review, although relevant estimates of *M* for conspecific stocks or for closely related species are included for context. The literature review also revealed numerous studies reporting CPS finfish egg or larval mortality (e.g., Hunter 1976; Lo et al. 1989; Smith et al. 1989; Butler et al. 1993). Although mortality of early life stages is a relevant process for population dynamics and management, it does not reflect the natural mortality of fish after recruitment to fishery and therefore is not summarized in this report. These studies may be relevant for future syntheses on recruitment processes for CPS finfish.

3. Methods for estimating *M*

3.1. *Overview*

There are several published schemes for categorizing methods for estimating or inferring *M*, both independent from and within stock assessments (e.g., Brodziak et al. 2011; Hoenig et al. 2016; Maunder et al. 2023). For convenience, the categorization in Maunder et al. (2023) is adopted in this review, which separates estimation methodology into two broad groups: 1) estimation independently from a stock assessment and 2) estimation within integrated population models. Brief overviews of the types of methodologies are provided below, in addition to summaries of their application to estimating *M* for CPS finfish; details and discussion on the relative performance of each can be found in Maunder et al. (2023). These overviews are intended to contextualize the methods used to generate reported values of *M* for CPS finfish.

*3.2. **Estimation independent from stock assessments***

For estimation methods independent from stock assessment, Maunder et al. (2023) defined three broad methodology groups: 1) empirical relationships, 2) mark-recapture analysis, and 3) analysis of catch-at-age data.

3.2.1. **Empirical relationships**

Broadly defined, "empirical" methods for estimating *M* are based on predictive relationships between existing estimates of *M* and some attribute(s) of species life history, including characteristics like maximum age, age-at-maturity, and growth. The basis of many empirical relationships is rooted in life history theory, in which relationships between *M* and a life history characteristic are defined based on assumed structural forms of population dynamics.

Empirical relationships between *M* and life history characteristics have been employed extensively to infer the natural mortality of CPS finfish. Relationships between *M* and maximum age developed by Beverton (1963), Hoenig (1982), Hoenig (1983), and Hamel and Cope (2022) have been applied to infer natural mortality for Pacific sardine, Pacific mackerel, northern anchovy, and Pacific jack mackerel. Relationships between *M* and growth developed by Beverton and Holt 1959 and Pauly (1980) have been applied to Pacific sardine, Pacific mackerel, and Pacific jack mackerel. A relationship between *M* and age-at-maturity developed by Charnov and Berrigan (1990) has been applied to Pacific mackerel. Other types of relationships not applied formally to CPS include relationships between *M* and size and reproductive effort (e.g., Lorenzen 1996; Gunderson and Dygert 1988). Methods to integrate estimates of *M* using multiple relationships, reported in Hamel (2015) and Cope and Hamel (2022), have been developed and used to specify priors on *M* in recent CPS assessments.

3.2.2. Mark-recapture analysis

Mark-recapture analysis of tagging data is an established method of estimating *M*. Mark-recapture analyses using physical tag recoveries have provided estimates of *M* for Pacific sardine and Pacific mackerel (Clark and Janssen 1945; Fry and Roedel 1949; Clark and Marr 1955). Methods of mark-recapture that can provide estimates of M without the need for physical recaptures or recoveries include electronic tagging (e.g., acoustic telemetry), archival tagging, and genetic tagging (e.g., close-kin mark-recapture); none have yet been applied to CPS finfish (e.g., Bravington et al. 2016; Peterson et al. 2021).

3.2.3. Catch-at-age analysis

Catch-at-age data, typically collected from commercial fisheries or fisheries-independent surveys, can be analyzed to estimate total mortality *Z,* and in some cases fishing mortality *F* and *M* specifically, using methods commonly referred to as catch curve analysis. Catch curve analysis is predicated on the assumption that cohort abundances decline over time as a function of *Z*. Separate estimates of *F* and *M* can be obtained under conditions of insignificant fishing mortality or by regressing estimates of *Z* on fishing effort. Analyses can be performed with either a single year or multiple years of catch-at-age data; however, analyses on one year require the assumptions that selectivity is constant across ages and recruitment is constant over time, while analyses with multiple years only require assuming constant selectivity across ages. Catch curve analysis can also be conducted using length-frequency data if an age-length key is applied.

Estimates of *M* have been generated for Pacific sardine, Pacific mackerel, and northern anchovy using catch curve methods reported in Silliman (1943), Silliman (1945), Widrig (1954), Beverton and Holt (1956), Chapman and Robson (1960), Murphy (1966), and Ricker (1975).

3.3. Estimation within stock assessments

Estimation of *M* can occur within the major packages used for stock assessments, often with optional features to estimate *M* as a function of age, sex, and/or time. Estimation of *M* can be informed with the specification of a prior on *M* using data independent from the assessment, either formally within a Bayesian model or as part of a likelihood in a penalized likelihood model, depending on the utilized assessment package. Recent stock assessments for Pacific sardine, Pacific mackerel, and northern anchovy have estimated *M* in various forms (e.g., Kuriyama et al. 2022; Kuriyama et al. 2023; Kuriyama et al. 2024). Additionally, although not typically recommended as a formal method for estimating *M*, goodness-of-fit evaluations and sensitivity analyses from stock assessment efforts for Pacific sardine, Pacific mackerel, and northern anchovy historically have been used to justify the selection of values for *M* (Murphy 1966; Parrish 1974; Methot 1989; Hill et al. 2017).

3.4. Best practices

Recent workshops and publications on the recommended handling of *M* in stock assessments generally agree on the following best practices (i.e., Then et al. 2015; Hamel et al. 2023; Hamel and Cope 2023; Maunder et al. 2023; Punt et al. 2023):

- Estimate *M* within stock assessments, assuming that *M* varies as a function of age or size (e.g., using relationships in Lorenzen 1996; Lorenzen 2022)
    - If practical, also consider estimating *M* as a function of sex
- When estimating *M* within a stock assessment, specify a prior based on information not used in that stock assessment
- Empirical relationships between *M* and life history characteristics are the most reliable method for specifying prior values
    - If a single method is to be used and a reasonable estimate of maximum age is available (i.e., stock has representative sampling of ages, accurate ageing, and no heavy sustained fishing pressure), the relationship between maximum age and *M* from Hamel and Cope (2022) is generally considered to be the most reliable. This approach puts broad bounds on *M* to constrain the model to somewhat realistic values but still allows for data to influence the estimated value of *M*
    - If a reliable estimate of maximum age is not available but other estimates of life history characteristics are available (e.g., growth rate, age-at-maturity) are available, meta-analytical priors may also be developed using multiple empirical relationships and methods developed in Hamel (2015) and Cope and Hamel (2022)

- Evaluate the sensitivity of assessment results, and particularly quantities relevant to management, to a range of fixed values of *M* (i.e., as part of likelihood profiling), especially if estimated *M* differs from the prior value

4. Reported values of *M* for CPS finfish

4.1. Pacific jack mackerel

The few reported values of *M* (defined on an annual basis, with units yr^{-1}, throughout this review) for Pacific jack mackerel off the U.S. West Coast are summarized in Table 4.1. The earliest study reported *M* is expected to be less than 0.25 based on empirical relationships between *M* and both growth rate and maximum age (MacCall et al. 1980). A subsequent study inferred *M* to be 0.23 using a combination of growth rate parameters and water temperature (MacCall and Stauffer 1983). No estimates of *M* from U.S. stock assessments are available because Pacific jack mackerel have not been and are not currently assessed (PFMC 2024).

Table 4.1. Reported values of Pacific jack mackerel natural mortality for the U.S. West Coast.

Source	Estimate (yr^{-1})	Method (citation)	Details
MacCall et al. 1980	<0.25	Empirical relationship with growth rate	Applied K=0.09 yr^{-1}
	<0.25	Empirical relationship with maximum age	Applied T_{max}=30
MacCall and Stauffer 1983	0.23	Empirical relationship with growth parameters and water temperature (Pauly 1980)	Applied L_{inf}=60.3 cm, K=0.0935 yr^{-1}, T=14°C

The distribution of Pacific jack mackerel is restricted to the Northeast Pacific Ocean, and no other values of *M* throughout its range were obtained. However, values of *M* for closely related jack mackerel species (i.e., *Trachurus* spp.) in the Pacific Ocean are available, and ranged from 0.23 to 0.38. *M* for Chilean jack mackerel (*T. murphyi*) was inferred to be 0.4 using a combination of growth rate parameters and water temperature, was estimated at 0.38 using catch-at-age analyses, and has been specified at 0.23 and 0.3 in stock assessments (Serra 1983; Cubillos et al. 1998a; Serra and Canales 2009; Table 4.2). Estimates of *M* for *T. novaezelandiae* and *T. declivis*, both harvested in New Zealand waters, ranged between 0.17 and 0.20 based on catch-at-age analyses (Horn 1991).

Table 4.2. Reported values of *Trachurus* spp. natural mortality in the Pacific Ocean, excluding *T. symmetricus*. Values used in stock assessments are considered fixed unless estimates of *M* are obtained directly from assessment model fitting.

Source (sp.)	Estimate (yr^{-1})	Method (citation)	Details
Serra 1983 (*T. murphyi*)	0.4	Empirical relationship with growth parameters and water temperature (Pauly 1980)	Applied both L_{inf}=45.9 cm, K=0.167 yr^{-1}, T=18°C, and L_{inf}=44.3 cm, K=0.181 yr^{-1}, T=15°C
Horn 1991 (*T. novaezelandiae*, *T. declivis*)	0.17 – 0.20	Catch-at-age analysis	Analysis of age-length data from 1975-1976
Cubillos et al. 1998a (*T. murphyi*)	0.38	Catch-at-age analysis	Analyzed size frequency data collected off Chile in 1973
	0.3	Stock assessment (fixed)	Applied fixed value in stock assessment
Serra and Canales 2009 (*T. murphyi*)	0.23	Stock assessment (fixed)	Applied fixed value in stock assessment

Reported values of *M* for multiple *Trachurus* spp. in the Pacific Ocean are summarized in Figure 4.1. Although not suited for detailed statistical analyses, the summary suggests reported values of *M* for Pacific jack mackerel fall within the range of reported values for other jack mackerel species. However, the limited number of *M* values for Pacific jack mackerel warrants caution in placing too much emphasis on this comparison. In comparing values among studies for Pacific jack mackerel and for other CPS finfish species, it is also worth emphasizing that observed variation in reported values of *M* may be caused to varying degrees by true biological differences (i.e., due to environmental variability over time and space as well as differences among isolated stocks or species) and differences in the data collection and estimation methodologies. Just considering the aspect of methodology, different approaches to inferring *M* (e.g., empirical relationships, catch-at-age analysis, assessments) each have varying tradeoffs with regards to aspects including ease of estimation, expected realism, and intended application (Maunder et al. 2023). Therefore, any comparisons of values of *M* will be necessarily coarse in nature, and differences or similarities in reported *M* among studies should be evaluated with these complexities in mind.

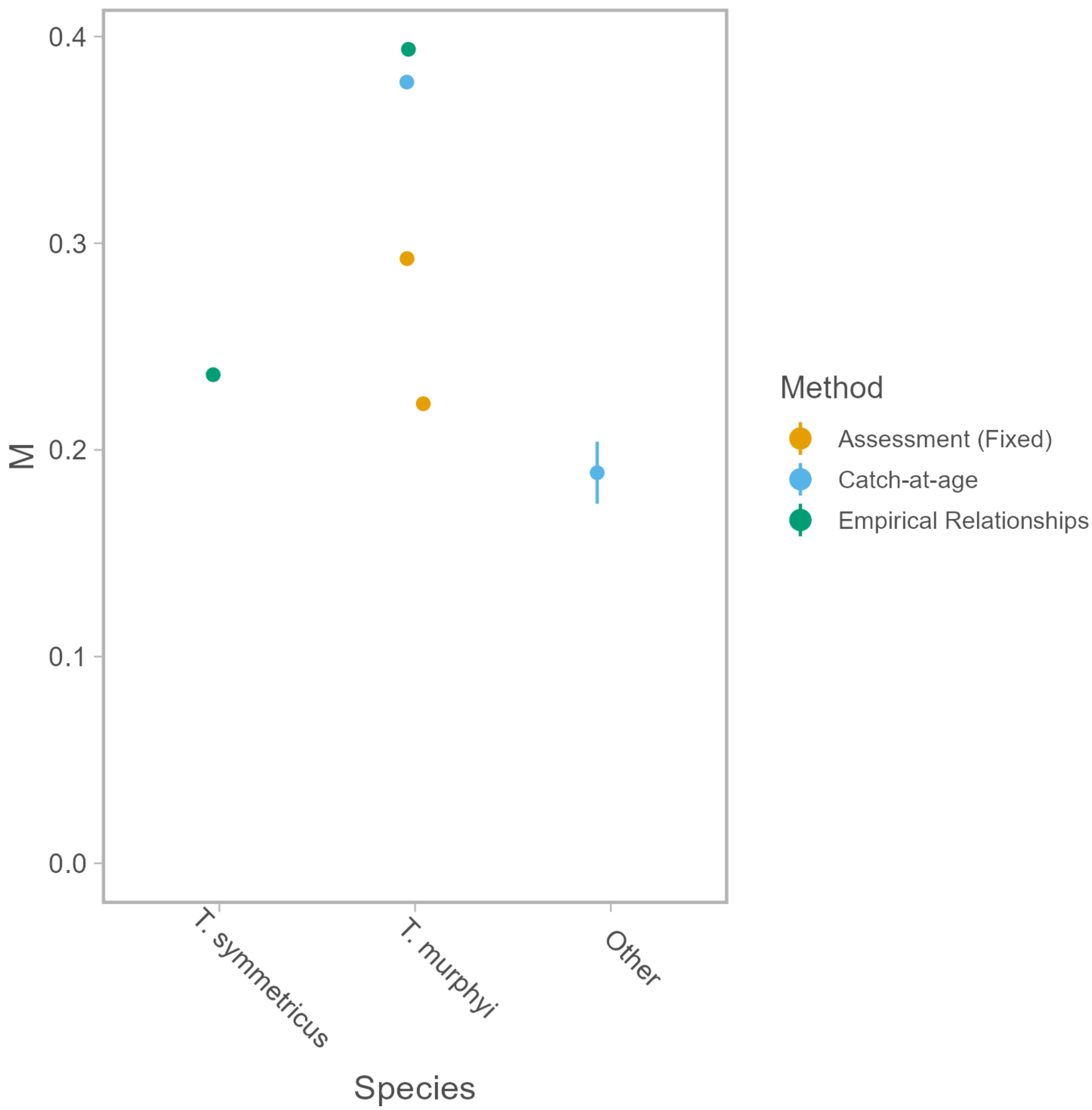

Figure 4.1. Reported values of *M* for *Trachurus* spp. in the Pacific Ocean (Tables 4.1, 4.2). A slight horizontal jitter is provided to distinguish identical values of *M* among studies. For studies in which a range of possible *M* values were provided (e.g., Horn 1991), the bounds and mean of the bounds are plotted. Inferred values of *M* from MacCall et al. (1980) are excluded because only the upper bounds are provided. The contents of the plot are intended for coarse comparisons among methods and species only.

4.2. Northern anchovy

Available values of natural mortality for northern anchovy off the U.S. West Coast are summarized in Table 4.3. One of the earliest reported estimates of *M* was 1.06, using catch-at-age analysis for 16 years of survey data collected off southern California (MacCall 1973).

MacCall (1973) also summarized previously published estimates of *Z* for northern anchovy based on catch-at-age analyses but described various methodological or documentation-based issues for each (i.e., *Z*=0.9, Beverton 1963; *Z*=1.7, Bayliff 1967; *Z*=1.1, Schaefer 1967). MacCall (1973) also noted *Z* appears to increase with age for northern anchovy, supporting a similar observation by Beverton (1963). An updated estimate of *Z* (*Z*=0.97) was calculated using an extended time series of catch data (Hanan 1981).

Methot (1989) conducted a stock assessment for northern anchovy using fisheries-dependent and fisheries-independent data, including estimates of age-composition, landings, and biomass, and evaluated the performance of three fixed values of *M* (i.e., 0.4, 0.6, and 0.8) in addition to three coefficients (i.e., 0.4, 0.6, 0.8) for the influence of Pacific mackerel biomass on *M*. A fixed value of 0.6 was selected for *M* along with 0.4 for the coefficient of Pacific mackerel biomass. With a Pacific mackerel biomass equal to the level expected in 1989 (i.e., 400,000 tons), estimated *M* at that time was approximately 0.76.

A subsequent biomass dynamics model for northern anchovy, developed by Jacobson (1994), fixed *M* at 0.8, with partial justification for selecting this value based on an empirical relationship between *M* and an assumed maximum age of 7 (Hoenig 1983). The fixed value was applied in subsequent assessments until the most recent assessment in 2022 (e.g., Jacobson et al. 1995).

Natural mortality was first estimated within a U.S. stock assessment for northern anchovy in the most recent benchmark assessment in 2022, in which a constant (i.e., sex-, age/size-, and time-invariant) *M* was estimated with no specified prior (Kuriyama et al. 2022). The estimated value of *M* was 0.4142. A likelihood profile calculated over fixed values of *M*, ranging from 0.3 to 0.9, indicated values of *M* between 0.4 and 0.6 were reasonably well supported by the data sources.

Table 4.3. Reported values of northern anchovy natural mortality for the U.S. West Coast.

Source	Estimate (yr^{-1})	Method (citation)	Details
MacCall 1973	1.06	Catch-at-age analysis (Chapman and Robson 1960)	Analyzed survey catch data from 16 cruises, spanning 1966-1971
Methot 1989	0.76	Stock assessment (fixed)	Evaluated three fixed values of *M* in addition to three coefficients for Pacific mackerel biomass
Jacobson 1994	0.8	Stock assessment (fixed), informed by empirical relationship with maximum age (Hoenig 1983)	Applied fixed value based in part on empirical relationship with maximum age (T_{max}=7)
Kuriyama et al. 2022	0.41	Stock assessment (estimated)	Estimated constant M

Aside from an inferred value of *M* for northern anchovy in the Gulf of California (*M*=1.49 based on an empirical relationship; Cisneros et al. 1990), other values of *M* in the Pacific Ocean were not available; this may have occurred in part because the range of northern anchovy is restricted to the Northeast Pacific Ocean. However, reported values of *M* for the closely related anchoveta (*Engraulis ringens*) in the Southeast Pacific Ocean were available in reports obtained from Google Scholar, and ranged from 0.69 to 3.0 (Table 4.4). Inferred values of *M* based on empirical relationships included 0.69, 1.2, and 1.3 (Serra 1983; Cubillos 1991; Cubillos et al. 1998b; Canales and Leal 2009). Year-specific estimates of *M* obtained from fitting stock assessments models ranged from 0.8 to 3.0 (Pauly and Palomares 1989). Fixed values of *M* specified in stock assessments included 0.8 and 1.0 (Csirke et al. 1996).

Table 4.4. Reported values of northern anchovy natural mortality in the Gulf of California and anchoveta natural mortality in the Southeast Pacific Ocean. All values are for anchoveta except the value for northern anchovy provided by Cisneros et al. (1990).

Source	Estimate (yr^{-1})	Method (citation)	Details
Serra 1983	1.3	Empirical relationship with growth parameters and water temperature (Pauly 1980)	Applied L_{inf}=19.04 cm, K=0.73 yr^{-1}, T=17°C
Pauly and Palomares 1989	0.8 – 3.0	Stock assessment (estimated)	Estimated year-specific *M* using virtual population analyses
Cisneros et al. 1990	1.49	Empirical relationship with growth parameters and water temperature	Applied L_{inf}=153 mm, K=0.70 yr^{-1}
Cubillos 1991	1.2	Empirical relationship with growth parameters and water temperature (Pauly 1980)	Applied L_{inf}=20.25 cm, K=0.875 yr^{-1}, T=18°C
Csirke et al. 1996	0.8 – 1.0	Stock assessment (fixed)	Applied fixed values for different periods in stock assessment
Cubillos et al. 1998b	0.69	Empirical relationships	Obtained weighted average of *M* from multiple empirical relationships
Canales and Leal 2009	1.3	Empirical relationships	Averaged estimates of *M* from four published empirical relationships

Values of *M* for northern anchovy and anchoveta in the Pacific Ocean are summarized in Figure 4.2. Although not suited for detailed statistical analyses, the summary suggests reported values of *M* for northern anchovy off the U.S. West Coast are generally similar if slightly lower than those reported for anchoveta. The estimated *M* from the most recent stock assessment for northern anchovy off the U.S. West Coast falls outside the range of other reported values for either northern anchovy or anchoveta. More details on model fitting from the most recent assessment, and associated challenges of integrating multiple data sources, can be found in Kuriyama et al. (2022).

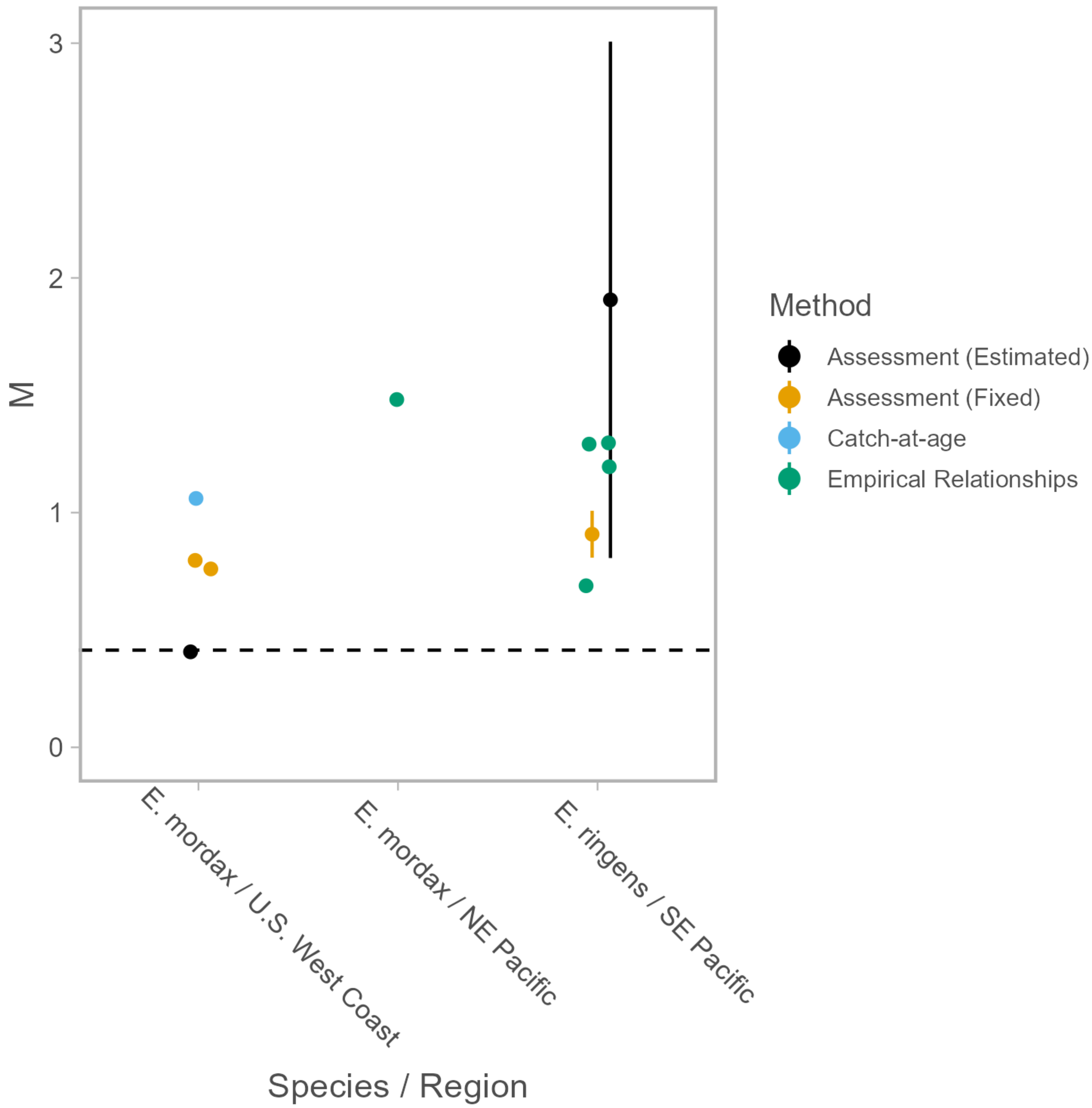

Figure 4.2. Reported values of *M* for northern anchovy (*E. mordax*) and anchoveta (*E. ringens*) off the U.S. West Coast, in other parts of the Northeast Pacific Ocean (including the Gulf of California), and in the Southeast Pacific Ocean (Tables 4.3, 4.4). A slight horizontal jitter is provided to distinguish identical values of *M* among studies. For studies in which a range of possible *M* values were provided (e.g., Pauly and Palomares 1989), the bounds and mean of the bounds are plotted. The horizontal line represents the estimate of *M* from the most recent U.S. stock assessment (Kuriyama et al. 2022). The contents of the plot are intended for coarse comparisons among methods and regions only.

4.3. Pacific sardine

Reported values of natural mortality for Pacific sardine off the U.S. West Coast are summarized in Table 4.5. Re-analysis of mark-recapture data from physical tagging experiments between 1937 and 1942, described in Clark and Janssen (1945) and Janssen (1948), resulted in estimates of *M* between 0.4 and 0.49 (Clark and Marr 1955). Murphy (1966) also reported that the original analyses in Clark and Janssen (1945) would have produced year-specific estimates of *M* between 0.27 and 0.45 and an overall value of 0.39. Additional analyses of catch-at-age data resulted in an estimated *M* of 0.51 (Clark and Marr 1955). Subsequent analyses of catch-at-age data, using a regression of *Z* on fishing effort for the periods 1925-1932 and 1937-1945, produced estimates of *M* between 0.2965 and 0.4222; 0.4 was selected as the best value of *M* for modeling population dynamics and estimating biomass for 1932-1950 (Murphy 1966). Poor modeled fit after 1948 led Murphy (1966) to apply an *M* of 0.8 to model dynamics for 1949-1960. Zwolinski and Demer (2013) fit an exponential population dynamics model to acoustics-based estimates of sardine abundance for 2008, 2010, and 2011 to estimate an *M* of 0.52.

There also were several attempts to estimate or infer *M* using varying methods that resulted in variable and unreliable estimates of *Z* and *M* (i.e., based on negative reported values and/or flawed methodologies) that are not included in Table 4.5. Catch-at-age analyses by Widrig (1954) produced a negative estimate of *M*. Silliman (1943) estimated *Z*=0.51 for 1925-1933 and *Z*=1.61 for 1937-1942, and subsequent regression of *Z* on fishing effort produced an estimated *M* of 0.153. Murphy (1966) also reports Marr (1960) produced year-specific estimates of *M* from 1950-1957 ranging between 0.25 and 3.91, but describes numerous concerns with the estimation methodology. Additional reported values of *M* based on catch-at-age analyses, assessments, and empirical relationships ranged from 0.35-0.75, 0.34-0.4, and 0.14-0.3, respectively (Yamanaka 1959). Hayasi (1988) estimated age-specific values of *Z* for Pacific sardine off California ranging from -0.09 to 1.23, with *Z* increasing with age. An ecosystem-based modeling approach was also used to estimate *M* for Pacific sardine at 0.24 based on expected predation pressure; however, the authors concluded the estimate was likely biased low, possibly due to the exclusion of some predators of Pacific sardine (Hannesson et al. 2009).

Pacific sardine stock assessments following Murphy 1966 applied *M* as a fixed value of 0.4 until recently (e.g., MacCall 1979; Hill et al. 2014). Hill et al. (2017) updated *M* in their benchmark assessment to a fixed value of 0.6, based in part on recent estimates of *M* (e.g., Zwolinski and Demer 2013) and a likelihood profile for *M*. The 2020 benchmark assessment was the first stock assessment in which *M* was estimated within a stock assessment for Pacific sardine instead of being fixed at a constant (Kuriyama et al. 2020). Natural mortality was estimated as a constant, using a lognormal prior with mean of -0.59 (*M*=0.554) and standard deviation of 0.39. The prior was derived from a meta-analysis using an assumed maximum age of 10 and six estimates of growth rate K from previous assessments, following the meta-analysis methods in Then et al. (2015) and Hamel (2015). The estimated value of *M* from the stock assessment was 0.585, and a likelihood profile calculated over fixed values of *M*, ranging from 0.3 to 0.9, indicated values between 0.5 and 0.6 were generally supported across data sources.

For the next U.S. benchmark assessment in 2024, natural mortality was estimated to be age-specific and time-invariant (Kuriyama et al. 2024). A longevity-based prior with a mean of -

0.393 (*M*=0.675, based on an assumed maximum age of 8) and standard deviation of 0.31 was applied, based on Hamel and Cope (2022). Estimated *M* was adjusted within the model to take on age-specific values, following the Lorenzen *M* specification in Stock Synthesis (Lorenzen 1996). The estimated *M* from the assessment was 0.546. A likelihood profile calculated over fixed values of *M*, ranging from 0.2 to 1.0, indicated values of *M* between 0.5 and 0.6 were well supported by the acoustic trawl survey index data, as well as all age-composition data.

Table 4.5. Reported values of Pacific sardine natural mortality for the U.S. West Coast.

Source	Estimate (yr^{-1})	Method (citation)	Details
Clark and Marr 1955	0.4 – 0.49	Mark-recapture analysis	Re-analysis of data from Clark and Janssen (1945), Janssen (1948)
	0.51	Catch-at-age analysis	Analyzed change in year-class abundance using data from 1950-1951 (Radovich 1952)
Murphy 1966	0.4 (best estimate based on estimates of 0.30, 0.34, 0.42)	Catch-at-age analysis (Silliman 1943, Widrig 1954)	Regression of *Z* on fishing effort for the periods 1925-1932 and 1937-1945
	0.80	Stock assessment (fixed)	Manually selected to fit abundance trends for 1949-1960
Zwolinski and Demer 2013	0.52	Catch-at-age analysis	Fit population dynamics model to annual acoustic estimates of abundance
Hill et al. 2017	0.6	Stock assessment (fixed)	Justified selection using recent literature and *M* likelihood profile
Kuriyama et al. 2020	0.55	Empirical relationship with maximum age, growth (Hamel 2015; Then et al. 2015)	Meta-analysis using T_{max}=10 and six estimates of growth rate K; used as prior in assessment
	0.59	Stock assessment (estimated)	Estimated constant *M*
Kuriyama et al. 2024	0.68	Empirical relationship with maximum age (Hamel and Cope 2022)	Applied T_{max}=8; used as prior in assessment
	0.55	Stock assessment (estimated)	Estimated constant *M* with age-specific adjustments

Reported values of *M* for *S. sagax* (of which *S. sagax caeruleus* is a subspecies) in other parts of its range in the East Pacific Ocean range from 0.17 to 1.46 (Table 4.6). Catch-at-age analyses from catches off the west coast of the Baja California Peninsula provided an estimate of 0.6 for use in virtual population analyses (Morales-Bojórquez et al. 2003) and empirical relationships provided an inferred value of 1.1 (Cisneros et al. 1990). A recent stock assessment for *S. sagax* off the west coast of the Baja California Peninsula specified a fixed value of approximately 0.54 for *M* based on the average of two estimates from empirical relationships (Enciso Enciso et al. 2022; Enciso-Enciso et al. 2023). Numerous values for *M* are available for *S. sagax* in the Gulf of California, including values of 0.77 (Cisneros-Mata et al. 1991, as reported in Nevárez-Martínez et al. 1999) and 1.46, 0.73, and 0.37 for early adult, adult, and late adult life stages, respectively, based on empirical relationships (Martínez-Aguilar et al. 2005). A recent stock assessment for the Gulf of California fixed *M* at 0.7 based on past reported empirical relationships (Nevárez-Martínez et al. 2023). Estimates of *M* for *S. sagax* off the coast of Chile included values between 0.68 to 0.76 based on catch-at-age analyses, values between 0.17 to 0.54 based on multiple empirical relationships, and a value of 0.4 based on an empirical relationship with growth and water temperature (Serra 1983; Garland 1993).

Table 4.6. Reported values of *S. sagax* natural mortality in and near the East Pacific Ocean, excluding the U.S. West Coast.

Source	Estimate (yr^{-1})	Method (citation)	Details
Serra 1983	0.4	Empirical relationship with growth parameters and water temperature (Pauly 1980)	Applied L_{inf}=42 cm, K=0.19 yr^{-1}, T=18°C
Cisneros et al. 1990	1.1	Empirical relationship with growth parameters and water temperature	Applied L_{inf}=225 mm, K=0.60 yr^{-1}
Cisneros-Mata et al. 1991	0.77	Empirical relationship	None available
Garland 1993	0.68 – 0.76	Catch-at-age analyses	For multiple data sources from 1985-1986, constructed catch curves based on length
	0.17 – 0.54	Empirical relationships	For multiple data sources, averaged estimates of *M* from four published empirical relationships
Morales-Bojórquez et al. 2003	0.6	Catch-at-age analyses (Ricker 1975)	Analyzed data from 1981-1993
Martínez-Aguilar et al. 2005	0.37 – 1.46	Empirical relationships	Applied the gnomonic-interval natural-mortality method
Enciso Enciso 2022	0.54 – 0.55	Empirical relationships (Pauly 1980; Hewitt and Hoenig 2005)	Applied T_{max}=8 years, T=19.5°C
Nevárez-Martínez et al. 2023	0.7	Stock assessment (fixed)	Applied fixed value based in part on empirical relationships applied in Nevárez-Martínez et al. (1999)

Values of *M* for *S. sagax* are summarized in Figure 4.3. Although not suited for detailed statistical analyses, the summary suggests reported values of *M* from the U.S. West Coast are generally similar to those from other regions in the East Pacific Ocean. The estimate of *M* from the most recent assessment for the U.S. West Coast falls within the range of *M* values obtained across a variety of methods and across the East Pacific Ocean.

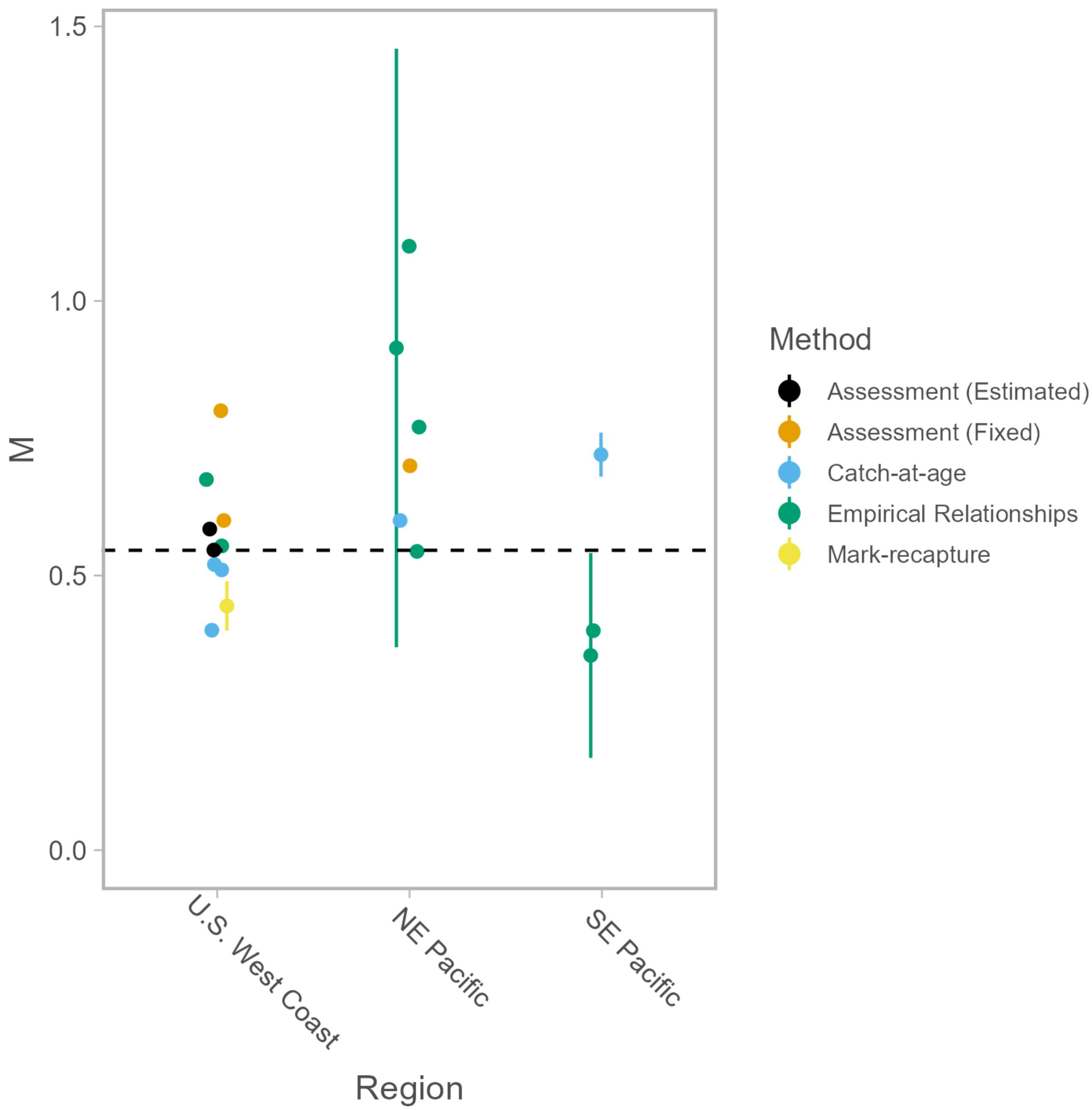

Figure 4.3. Reported values of *M* for *S. sagax* from the U.S. West Coast, other parts of the Northeast Pacific Ocean (including the Gulf of California), and Southeast Pacific Ocean (Tables 4.5, 4.6). A slight horizontal jitter is provided to distinguish similar values of *M* among studies. For studies in which a range of possible *M* values were provided (e.g., Clark and Marr 1955), the bounds and mean of the bounds are plotted. The horizontal line represents the estimate of *M* from the most recent U.S. stock assessment (Kuriyama et al. 2024). The contents of the plot are intended for coarse comparisons among methods and regions only.

4.4. Pacific mackerel

Values of natural mortality for Pacific mackerel off the U.S. West Coast are summarized in Table 4.7. The earliest inferred value of *M* was obtained from a stock assessment, in which values of 0.4, 0.7, and 1.0 were evaluated for their ability to produce realistic estimates of biomass and exploitation rates; a value of 0.7 was selected as the best estimate (Parrish 1974). Parrish and MacCall (1978) reported several values of *M* based on a combination of catch-at-age analyses and empirical relationships. Analysis of length-frequency data from fishery landings in 1929-1930 and 1930-1931 produced estimates of *Z* of 0.317 and 0.424, leading the authors to conclude estimates of *M* between 0.3 and 0.5 were reasonable. Regressions of *Z* on fishing effort produced estimates of *M* between 0.4 and 0.6, and the authors concluded *M*=0.5 was the best estimate from these methods. An empirical relationship between *M* and maximum age (i.e., Beverton 1963), assuming a maximum age of 11 years, suggested values of *M* between 0.3 and 0.7 were reasonable. An empirical relationship between *M* and growth rate K (i.e., Beverton and Holt 1959), assuming K was either 0.244 or 0.221, produced values of *M* between 0.4 and 0.6. Across all lines of evidence, Parrish and MacCall (1978) selected *M*=0.5 as the best value for population modeling. It is worth noting that Fry and Roedel (1949) produced estimates of *M* between 1.1 and 1.3 using mark-recapture data from physical tagging experiments between 1937 and 1946; these estimates are excluded from Table 4.7 because the authors concluded the estimates are biased high and unreliable based on unequal spatial distribution of tagging, limited tag returns, and inaccurate estimation of tagging mortality.

Until the benchmark stock assessment in 2019, stock assessments for Pacific mackerel since 1978 specified a fixed value of 0.5 for *M* (e.g., Crone et al. 2011). For the stock assessment in 2019, *M* was estimated as constant, using a lognormal prior with mean of -0.5 (*M*=0.61) and a standard deviation of 0.32, following meta-analysis methods in Then et al. (2015) and Hamel (2015) (Crone et al. 2019). Three empirical relationships between life history parameters and *M* were used to identify the lognormal prior on *M*: maximum age (Hoenig 1982), maximum size and growth rate (Pauly 1980) and age-at-50% maturity (Charnov and Berrigan 1990). The estimated value of *M* from the stock assessment was 0.811. A likelihood profile calculated over fixed values of *M*, ranging from 0.5 to 1.1, indicated values of *M* greater than 0.7 were well supported by the data.

For the subsequent benchmark assessment in 2023, *M* was estimated with an age-specific, time-invariant structure using a longevity-based prior with a mean of -0.393 (*M*=0.675, based an assumed maximum age of 8) and standard deviation of 0.31 (Hamel and Cope 2022; Kuriyama et al. 2023). The estimated mean value of *M* was 0.8512. A likelihood profile calculated over fixed values of *M*, ranging from 0.3 to 1.0, indicated values of *M* greater than 0.7 were well supported by all data.

Table 4.7. Reported values of Pacific mackerel natural mortality for the U.S. West Coast.

Source	Estimate (yr^{-1})	Method (citation)	Details
Parrish 1974	0.7	Stock assessment (fixed)	Evaluated *M*=0.4, 0.7, 1.0 for ability to produce realistic outputs
Parrish and MacCall 1978	0.3 – 0.5 (from *Z*=0.32-0.42)	Catch-at-age analysis (Beverton and Holt 1956)	Analysis of length frequency catch data
	0.5 (from *M*=0.4-0.6)	Catch-at-age analysis	Regression of *Z* on fishing effort
	0.3 – 0.7	Empirical relationship with maximum age (Beverton 1963)	Applied T_{max}=11
	0.4 – 0.6	Empirical relationship with growth (Beverton and Holt 1959)	Applied K=0.244, 0.221
Crone et al. 2019	0.61	Empirical relationships with maximum age, maximum size and growth rate, and age-at-50% maturity (Hamel 2015; Then et al. 2015)	Meta-analysis across empirical relationships; used as prior in assessment
	0.81	Stock assessment (estimated)	Estimated constant *M*
Kuriyama et al. 2023	0.68	Empirical relationship with maximum age (Hamel and Cope 2022)	Applied T_{max}=8; used as prior in assessment
	0.85	Stock assessment (estimated)	Estimated constant *M* with age-specific adjustments

Values of *M* for Pacific mackerel in other parts of their range ranged between 0.3 and 1.01 (Table 4.8). The highest value of 1.01, based on an empirical relationship, was reported in the Gulf of California (Cisneros et al. 1990). *M* was inferred to be 0.52 to 0.53 off the coast of Peru using an empirical relationship (Caramantin-Soriano et al. 2008). Values from waters off Chile include 0.3 (Serra 1983) and values between 0.34 and 0.70 (Cerna and Plaza 2014), all based on empirical relationships. In the Northwest Pacific Ocean, values of *M* range from 0.39 to 0.72 using empirical relationships, values of 0.4 and 0.41 have been applied as fixed values in stock assessments based on varying analyses, and a value of 0.37 was estimated using sensitivity analyses within a stock assessment model (Hiyama et al. 2002; Nishijima et al. 2021; Cai et al. 2023; Yoon et al. 2024).

Table 4.8. Reported values of Pacific mackerel natural mortality in and near the Pacific Ocean, excluding the U.S. West Coast.

Source	Estimate (yr^{-1})	Method (citation)	Details
Serra 1983	0.3	Empirical relationship with growth parameters and water temperature (Pauly 1980)	Applied L_{inf}=44.6 cm, K=0.16 yr^{-1}, T=18°C
Cisneros et al. 1990	1.01	Empirical relationship with growth parameters and water temperature	Applied L_{inf}=293 mm, K=0.50 yr^{-1}
Hiyama et al. 2002	0.4	Stock assessment (fixed)	Applied fixed value in stock assessment
Caramantin-Soriano et al. 2008	0.52 – 0.53	Empirical relationship with growth parameters and water temperature (Pauly 1980)	Applied mean L_{inf}=41.3 cm, K=0.39 yr^{-1}
Cerna and Plaza 2014	0.34 – 0.70	Empirical relationships (Pauly 1980; Hewitt and Hoenig 2005)	Applied relationships based on growth parameters and on maximum age
Nishijima et al. 2021	0.39 – 0.72	Empirical relationships	Multiple empirical relationships applied to varying data sources
Cai et al. 2023	0.41	Stock assessment (fixed)	Applied fixed value in stock assessment
Yoon et al. 2024	0.37	Stock assessment (fixed)	Used sensitivity analyses to identify best fitting *M* value

Values of *M* for Pacific mackerel across the Pacific Ocean, including those off the U.S. West Coast, are summarized in Figure 4.4. Although not suited for detailed statistical analyses, the summary suggests reported values of *M* from the U.S. West Coast generally exceed those from other parts of the species' range. Within estimates from the U.S. West Coast, values of *M* estimated within recent stock assessments generally exceed those obtained from other methods. More details on model fitting from the most recent assessment, including model fit to competing data sources, can be found in Kuriyama et al. (2023).

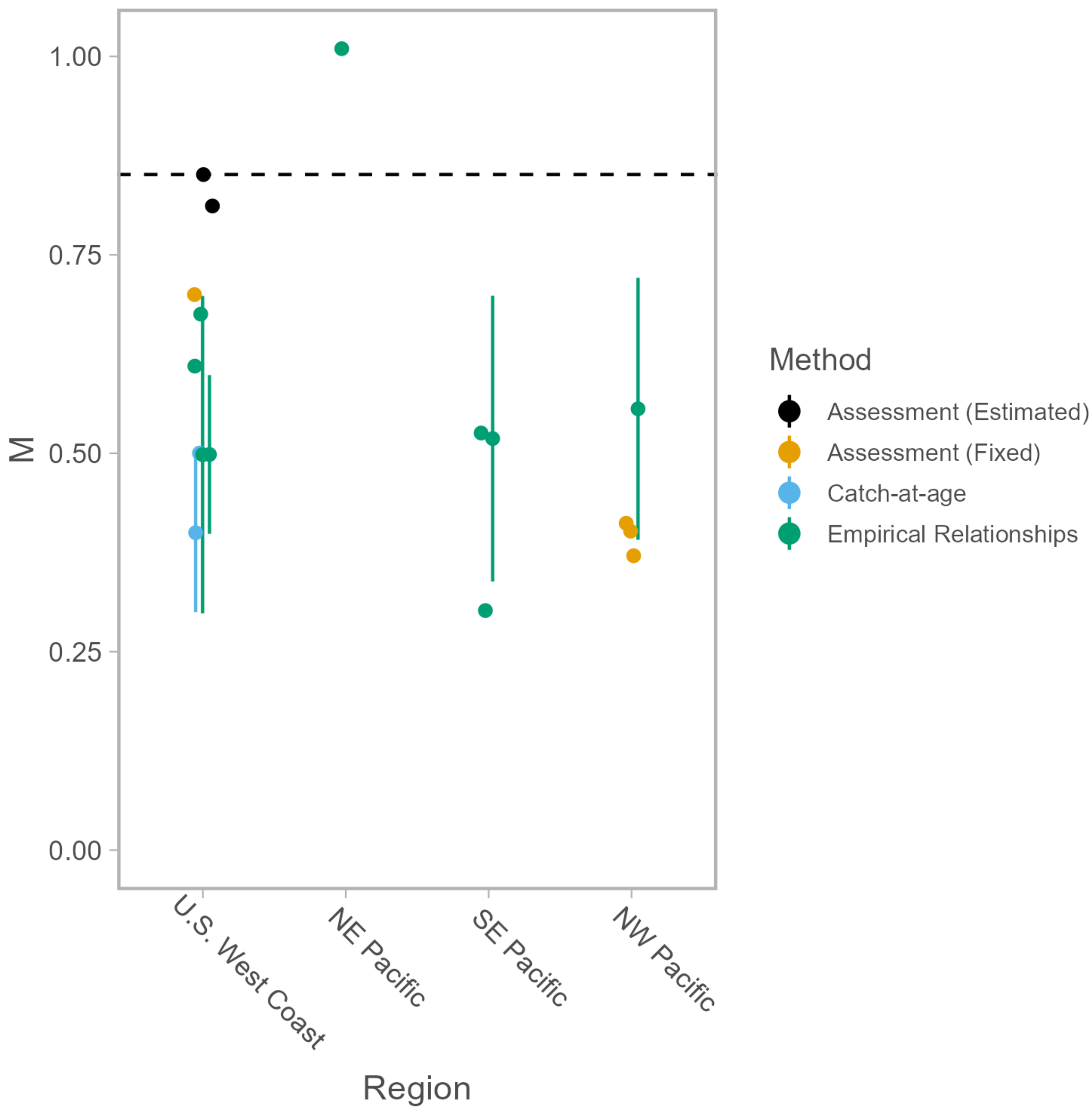

Figure 4.4. Reported values of *M* for Pacific mackerel from the U.S. West Coast, other parts of the Northeast Pacific Ocean (including the Gulf of California), Southeast Pacific Ocean, and Northwest Pacific Ocean (Tables 4.7, 4.8). A slight horizontal jitter is provided to distinguish identical values of *M* among studies. For studies in which a range of possible *M* values were provided (e.g., Parrish and MacCall 1978), the bounds and mean of the bounds are plotted. The horizontal line represents the estimate of *M* from the most recent U.S. stock assessment (Kuriyama et al. 2023). The contents of the plot are intended for coarse comparisons among methods and regions only.

5. Future research priorities for *M*

Although values of *M* for CPS finfish recently have been generated based on a combination of empirical relationships, specification of fixed values for stock assessments, and formal estimation within stock assessments, direct estimates of *M* through catch-at-age and mark-recapture analyses have been rare since the 1980's. New direct estimation of *M* for CPS finfish, particularly through tagging efforts like close-kin mark-recapture, has the potential to contextualize and inform the estimation of *M* within stock assessments, including age-specific mortality; however, these methods can cost-prohibitive, especially if they are repeated over several years to characterize time-varying *M* (Maunder et al. 2023). Tagging data increasingly can be incorporated directly into stock assessments to aid estimation of parameters like *M* (Punt et al. 2024). The disparity in the number of available values of *M* among CPS finfish, in which Pacific jack mackerel and northern anchovy had fewer available, recent values of *M*, also represents a possible data gap that may be addressed with further research depending on management priorities.

A major challenge with estimating *M* within stock assessments is that *M* is confounded with other parameters that can be even more difficult to estimate, including steepness and catchability. Steepness and catchabilities were fixed in the most recent benchmark stock assessments for CPS finfish, with the exception of catchability for Pacific mackerel, and estimates of *M* are conditioned on these assumptions. Additionally, *M* likely varies with time, particularly for CPS, but time-varying *M* values can be difficult to estimate, due in part to issues with model misspecification (Johnson et al. 2015). These challenges can be alleviated in the short-term by continuing to refine and provide reasonable constraints on *M* for estimation within stock assessments. Possible long-term analyses to address the challenges include the following: 1) evaluation of model sensitivity to alternative priors for *M*, 2) evaluation of model sensitivity to modified data weighting (e.g., down-weight age composition data for Pacific mackerel), 3) evaluation of model performance with alternative structures for *M,* such as time-varying *M* expressed as a function of environmental covariates, 4) simulation analyses to assess possible model misspecification (e.g., Piner et al. 2011), and 5) exploration of correlations and confounding among estimated parameters using Bayesian model fitting. The general effects of data availability, assessment methodology, and environmental stochasticity on variability and uncertainty in estimates of *M* also may be addressed with additional simulation-based analyses; better understanding of these effects and the magnitude of uncertainty in *M* can improve communication of modeling results and subsequent management actions. Finally, management strategy evaluation can be employed to address the performance of different harvest strategies to varying levels of uncertainty or misspecification of *M*. For example, Wildermuth et al. (2024) evaluated the robustness of harvest control rules, including the direct use of survey indices of biomass in management and estimation of dynamic reference points, to variability in Pacific sardine recruitment. A similar evaluation with respect to *M*, including management approaches that are less dependent on assumptions about *M*, could inform the expected performance of different harvest control rules for CPS finfish.

6. Conclusions

Among CPS finfish off the U.S. West Coast, values of *M* generally were greatest for northern anchovy, intermediate and similar for Pacific sardine and Pacific mackerel, and lowest for jack mackerel (Fig. 6.1). It is again worth emphasizing that these comparisons are coarse in nature and should not be taken as prescriptive, as they include values generated for a variety of different regions, time periods, and stocks by studies that employed a variety of estimation methodologies and data sources. Although values of *M* for northern anchovy for the U.S. West Coast ranged between 0.76 and 1.06 based on empirical relationships and catch-at-age analyses, the most recent assessment estimated a lower *M* at 0.41. Values of *M* for the closely related anchoveta were similarly higher than those from the assessment, ranging from 0.69 and 3.0. The most recent U.S. stock assessment for northern anchovy estimated *M* as a constant value but did not specify an informed prior. For Pacific sardine, reported values of *M* were relatively consistent across methodologies for the U.S. West Coast, ranging from approximately 0.4 to 0.7. Available *M* values were similar but more variable for Pacific sardine in other regions of the Pacific Ocean, varying between 0.17 and 1.46. The most recent stock assessments for Pacific sardine followed best practices for modeling *M* (i.e., according to Punt 2024) by specifying *M* as both age-specific and time-invariant and providing an informed prior based on an empirical relationship with maximum age. For Pacific mackerel, values of *M* from the U.S. West Coast varied between 0.3 and 0.85, and recent stock assessments in 2020 and 2024 estimated the highest reported values of 0.81 and 0.85, respectively. With the exception of one outlier value (M=1.01), values of *M* for Pacific mackerel from other parts of the Pacific Ocean, ranging from 0.3 to 0.72, were lower than estimates from recent assessments for the U.S. West Coast. The most recent stock assessment for Pacific mackerel also followed best practices for modeling *M.* Finally, for Pacific jack mackerel, the few inferred values of *M* available for jack mackerel based on empirical relationships were consistently less than 0.25. Values of *M* for closely related jack mackerel species in the Pacific Ocean are similarly low, ranging between 0.17 and 0.4. No recent assessment has been conducted for Pacific jack mackerel off the U.S. West Coast.

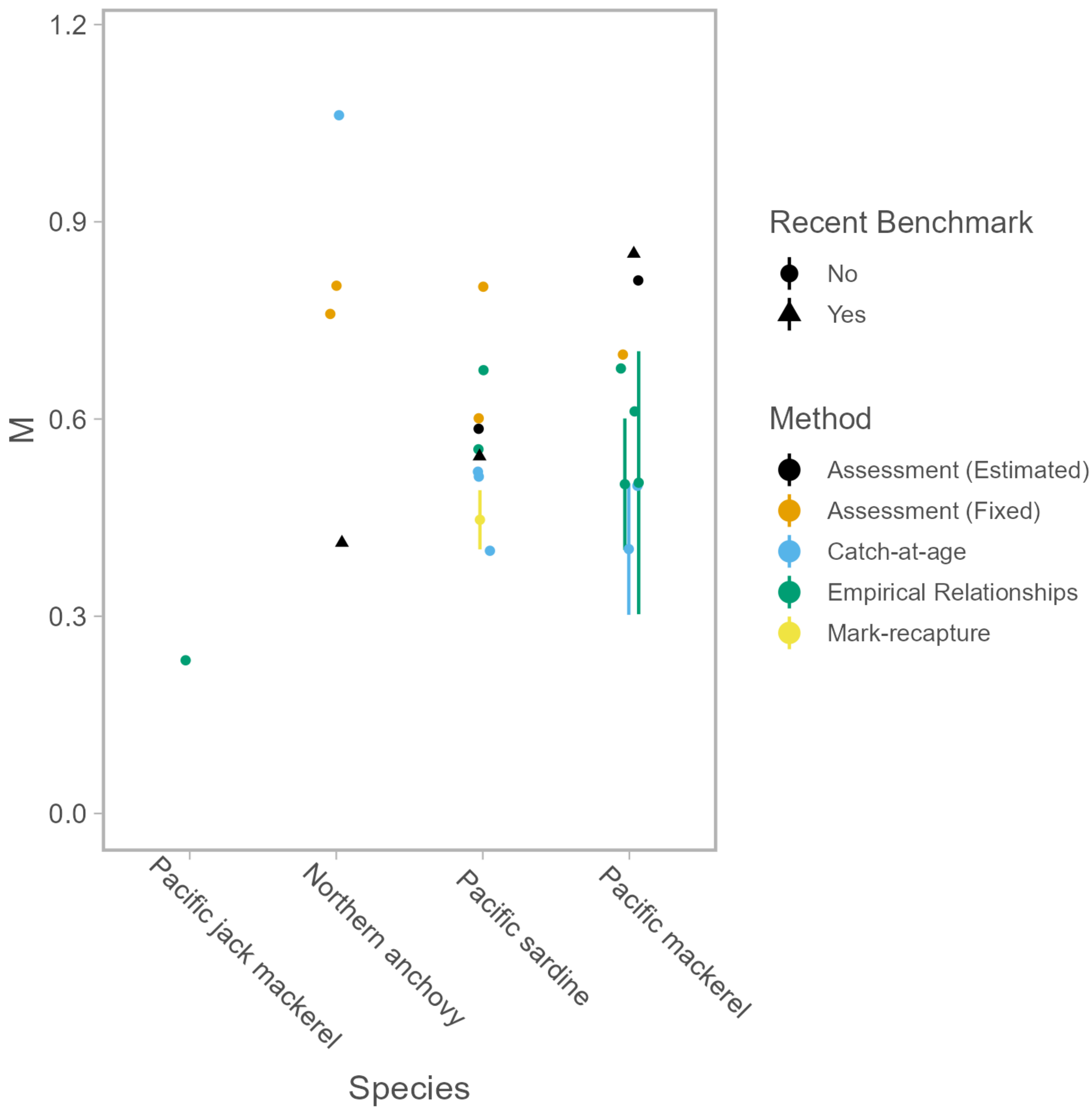

Figure 6.1. Reported values of *M* for Pacific jack mackerel, northern anchovy, Pacific sardine, and Pacific mackerel from the U.S. West Coast. A slight horizontal jitter is provided to distinguish identical values of *M* among studies. For studies in which a range of possible *M* values were provided (e.g., Parrish and MacCall 1978), the bounds and mean of the bounds are plotted. The triangular points represent the estimates of *M* from the most recent U.S. stock assessment for each stock, if available. The contents of the plot are intended for coarse comparisons among species and methods only.

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