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Even low levels of cannibalism can bias population estimates for Pacific hake

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Abstract

By incorporating trophic interactions and temperature-dependent bioenergetics, multi-species models such as CEATTLE (climate-enhanced age-based model with temperature-specific trophic linkages and energetics) are a step towards ecosystem-based stock assessment and management of high-value commercial species such as Pacific hake (*Merluccius productus*). Hake are generalist predators and previous studies in the California Current Ecosystem have determined that their diet consists of ∼30% cannibalism. We used CEATTLE to include cannibalism in a model of hake population dynamics and re-examined hake diet data to determine the proportion by age that can attributed to cannibalism. The proportion was highly variable, ranging between 0 and 80% of stomach contents by weight. When included in the CEATTLE model, the estimated spawning biomass, total biomass, and recruitment increased by 15, 23, and 58%, on average, relative to the single-species model, due to the estimation of time- and age-varying predation mortality, primarily for age-1 hake. The effects of cannibalism varied over time, with further increases in total biomass and recruitment resulting from the age structure of the population following large cohorts in 1980 and 1984. Results from the cannibalism model could be used to inform the estimation of time- and age-varying mortality in the single-species assessment and as a pathway for including ecosystem information in management through environmental and trophic drivers of variability in mortality.

Keywords: multi-species; ecosystem-based fisheries management; trophic interactions; natural mortality; stock assessment

Introduction

There is an increasing need for holistic models of marine systems to support management strategies that adapt to changing ocean conditions. Re-examining data inputs and model assumptions can improve implementation and our understanding of the ecosystem (Link et al. 2020, Karp et al. 2023). For example, a multi-species model of the role of Pacific sardine (*Sardinops sagax*) in the population dynamics of their predators in the California Current Ecosystem (CCE) indicated that brown pelicans (*Pelecanus occidentalis*) were vulnerable to variability due to sardine depletion (Kaplan et al. 2019). Multi-species models, which provide a more holistic view of the ecosystem, are under the umbrella of ecosystem-based fisheries management (EBFM; Marshall et al. 2019, Howell et al. 2021). Approaches to EBFM range in complexity. Models of intermediate complexity (MICE) fall between single-species assessments (Methot and Wetzel 2013, Nielsen and Berg 2014) and end-to-end ecosystem models, such as Atlantis (Fulton et al. 2011) and Ecopath with Ecosim (Christensen and Walters 2004). MICE address specific management questions by estimating the population dynamics of a few species (Plagányi et al. 2014). They are useful for targeted questions in EBFM because of their parsimony relative to end-to-end ecosystem models and because parameters, and uncertainty, are estimated by fitting to data (Plagányi et al. 2014). Within MICE, multispecies statistical catch-at-age analysis (MSCAA) incorporates trophic dynamics by linking species through predation derived from bioenergetics and diet proportions (Kinzey and Punt 2008, Holsman et al. 2016).

MSCAA can be compared to and used alongside traditional single-species assessment models because they can be parameterized similarly. Management advice that uses multiple models, including MSCAA, is a step towards operationalizing EBFM, which has been stymied by institutional inertia, resource limitation, and modeling issues (Karp et al. 2023). Specifically, MSCAA can be used to estimate time- and age-varying natural mortality (M) by explicitly modeling environmental and trophic processes (Moffitt et al. 2016, Holsman et al. 2021, Plagányi et al. 2022). For example, predation by Atlantic cod (*Gadus morhua*) is explicit in the assessment of Barents Sea capelin (*Mallotus villosus*; Bogstad et al. 2022), while the MSCAA Gadget (Begley and Howell 2004) was used to demonstrate the importance of including species interactions when estimating stock status and M for Flemish Cap commercial species (Atlantic cod, redfish [*Sebastes* spp.], and northern shrimp [*Pandalus borealis*]; Pérez-Rodríguez et al. 2017). CEATTLE (climate-enhanced age-based model with temperature-specific trophic linkages and energetics), an MSCAA, has been used to model the trophic interactions of groundfish species in the Gulf of Alaska (USA; Adams et al. 2022), and as a multi-species stock assessment for walleye pollock (*Gadus chalcogrammus*), Pacific cod (*Gadus macrocephalus*), and arrowtooth flounder (*Atheresthes stomas*) in the Bering Sea (USA; Holsman et al. 2021). These models are also presented in Ecosystem Status Reports: suites of environmental and trophic indicators for their regions (Ferriss and Zador 2022, Siddon 2022).

Improving estimates of *M* and recruitment, and the development of dynamic reference points, are priorities for the management of Pacific hake (*Merluccius productus*; Hamel et al. 2023). By including predation mortality as a component of *M*, models such as CEATTLE estimate age- and time-varying *M* as a direct consequence of changes in predation pressure (Plagányi et al. 2022). Hake is an abundant commercial species in the CCE (Koehn et al. 2016, Marshall et al. 2017) and currently supports the highest-volume commercial finfish fishery. The stock is assessed using a single-species model (Grandin et al. 2020). Hake primarily consume euphausiids (Ressler et al. 2007), but they are considered generalists (Methot and Dorn 1995, Ruzicka et al. 2012), with their diet also containing juvenile salmon, pandalid shrimp, herring, anchovy, and smelt, with varying records of cannibalism (Buckley and Livingston 1997, Field and Francis 2006, Koehn et al. 2016, Bizzarro et al. 2017). An analysis of hake trophoscapes identified three diet clusters dominated by euphausiids, myctophids, and juvenile hake (Wells et al. 2023). Additionally, hake serve as prey for larger fishes and marine mammals (Buckley et al. 1999, Brodeur et al. 2014, Koehn et al. 2016). Hake consumption of euphausiids versus teleosts depends on time of year, age, and location, with higher euphausiid consumption during the summer and evidence for increased piscivory with age and during periods of late or weak upwelling, when hake generally forage on the shelf (Tanasichuk et al. 1991, Buckley and Livingston 1997, Nelson 2004, Wells et al. 2023).

Previous studies have determined variable amounts of cannibalism in Pacific hake diets, estimated at an average of 30% by weight (Field 2004) and surpassing 75% by weight in 1991 (Buckley and Livingston 1997, Buckley et al. 1999). More recent surveys of hake stomach contents from 2005 to 2019 (de Blois 2020) detected lower cannibalism than the diet studies conducted during the 1980s and 1990s. As there has not been a study dedicated to exploring why recent observations of cannibalism have declined, the prevailing understanding of hake cannibalism is greatly informed by the high level found in these 1990s studies. Field (2004) notes that cannibalism levels had varied in the past and were low or non-evident from the late 1960s to the early 1980s.

Cannibalism has been suggested as a mechanism for creating and destabilizing population cycles and driving the discrete generations seen in age-structured population models for species such as hake (Claessen et al. 2004, Persson and De Roos 2006, Grandin et al. 2020). As hake cannibalism has been shown to increase with body size and to be on primarily age-1 fish, increases in cannibalism corresponding with low subsequent recruitment have been theorized to drive declines in the hake population, or depress recruitment further (Buckley et al. 1999, Field 2004). Additionally, the spatial distribution and recruitment variability of hake have been linked to environmental variables (Malick et al. 2020), with additional implications for their prey. The CCE is dominated by upwelling, with interannual and decadal temperature fluctuations driven by the Pacific Decadal Oscillation, the North Pacific Gyre Oscillation, and the El Niño Southern Oscillation (Black et al. 2011, King et al. 2011), likely leading to variability in predator/prey abundance and overlap (Wells et al. 2023). The effect of cannibalism on the estimation of *M* and population size has been considered for the assessment of cod (*Gadus morhua*) in the northeast Arctic, where inclusion of cannibalism in the assessment improved estimation of mortality and the stock size time series (Yaragina et al. 2018).

Treating hake as both a predator and prey in a multispecies model is a way to investigate how predation mortality from cannibalism affects estimates of quantities of management interest: biomass, recruitment, and relative spawning biomass, as the output from CEATTLE can be directly compared to that of single-species stock assessments. The time- and age-variation in estimated predation mortality can also inform approaches for introducing time- and age-variation into estimates of *M* for single-species models. Additionally, though previous studies (Buckley and Livingston 1997, Buckley et al. 1999, Field 2004) have determined that cannibalism comprises ~30% of hake diets, recent observations of cannibalism are lower. Exploring the effect of variable cannibalism proportions on these quantities provides insight into the interactions between cannibalism and population dynamics and how any increase in cannibalism in the future may affect the stock, with implications for the management of Pacific hake and related species.

Methods

Study area

Pacific hake is a pelagic species distributed throughout the CCE from British Columbia, Canada, to Baja California, USA (de Blois 2020, Shelton et al. 2022). The coastal population migrates seasonally and is generally found in offshore, southern waters during the winter for the spawning season, and in shallower waters farther north for the spring, summer, and fall when the fishery takes place (Malick et al. 2020, Phillips et al. 2023, Wells et al. 2023).

Diet data

The proportion of cannibalism, by weight, in Pacific hake stomachs was sourced from the California Current Trophic Database (CCTD), which is comprised of stomachs collected from multiple sources in 1988–1991, 1995–1999, 2002, 2005, 2007, 2009, 2011–2013, 2015, 2017, and 2019 (Bizzarro et al. 2023). The hake diet data were primarily from two sources: collected as part of the Pacific Coast continental shelf and upper continental slope survey conducted by the NOAA's Alaska Fisheries Science Center from 1980 to 2001 (Buckley and Livingston 1997, Buckley et al. 1999), and from the hake acoustic-trawl survey conducted by the NOAA's Northwest Fisheries Science Center (NWFSC) from 2005 to 2019. Of the 143 species included in the CCTD, hake diet data ranked highest in overall data quality (Bizzarro et al. 2017, 2023). In total, there were 17 802 hake stomachs in the CCTD, including empty stomachs, with high variation in sampling intensity, location, and time of year (Fig. 1). There were 5066 predator hake with full stomachs.

We parameterized cannibalism using the multispecies virtual population analysis (MSVPA) Type II suitability function from Jurado-Molina et al. (2005), which requires mean age-structured diet proportions by weight, so the proportion by weight of prey-hake-at-age in each predator hake stomach was calculated (Magnusson 1995, Supplementary Table S2).

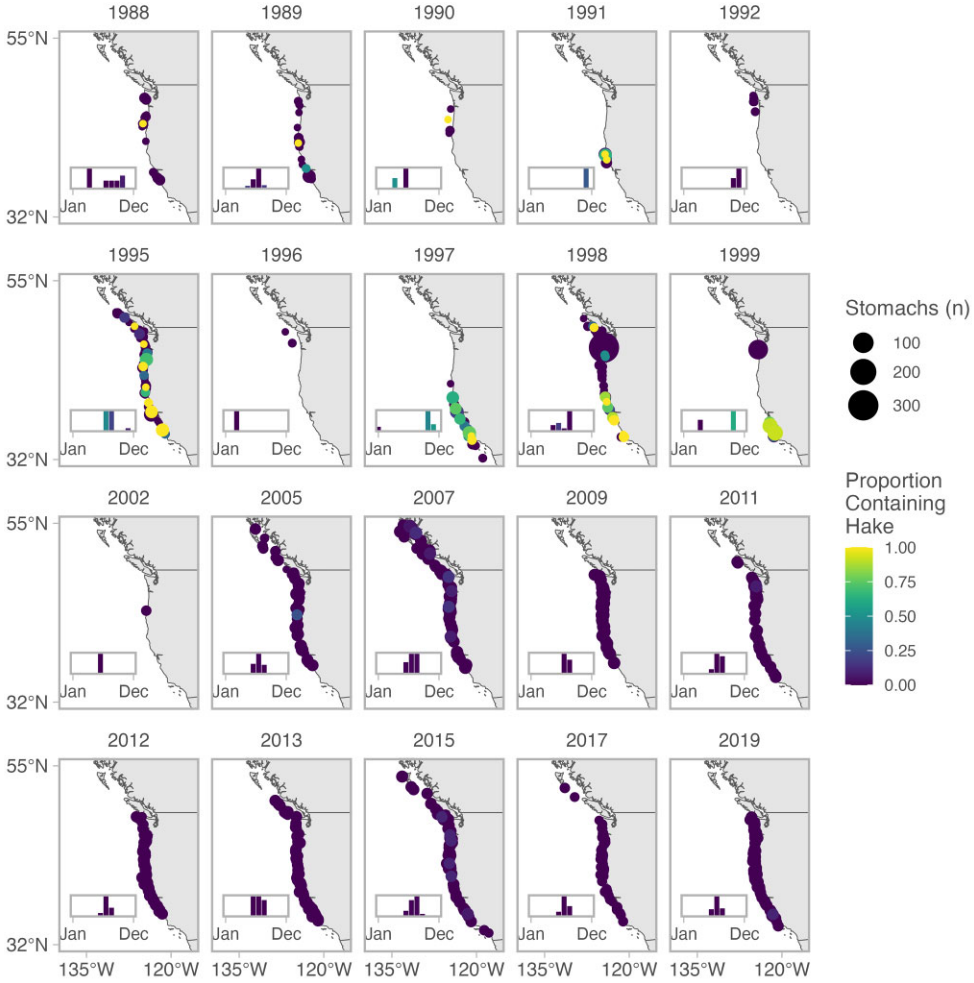

Figure 1. Proportion of Pacific hake stomachs containing Pacific hake by location and sampling month (insets), by year of sampling.

We chose the MSVPA Type II suitability rather than including the diet data in the model likelihood and estimating suitability parameters (*sensu* Trijoulet et al. 2019) to allow the model to match cannibalism-at-age directly and avoid misspecification due to other model parameters. Additionally, estimating diet externally allows the likelihoods of models with and without cannibalism to be compared. Hake in the CCTD were assigned lengths, not ages, so ages were estimated using a von Bertalanffy growth curve, parameterized with the length-at-age data from the acoustic-trawl survey (de Blois 2020). Estimated ages <1 were assigned to age 1 and estimated ages >15 were assigned to a 15+ group. None of the fish aged by the NWFSC's Fisheries Engineering and Acoustic Technologies Team (FEAT) in the stomach dataset were outside of this range (Supplementary Fig. S1).

A Dirichlet reweighting technique designed for concatenating diet data from multiple field studies (Ainsworth et al. 2010) was adapted to average the stomach content data across years. In the absence of consistent annual data, we used the mean for the time period. Given the gaps in the available diet data, the uneven distribution of sampling effort, and the variability in diet composition, annual estimates of diet proportions would not have been representative of true interannual variability (Supplementary Fig. S2). Diet data were averaged across the predators-at-age, then bootstrapped to generate a distribution of diet proportions, which were fit to a Dirichlet function, resulting in maximum-likelihood estimates of the mean diet proportions for each predator-at-age and prey-at-age combination, with uncertainty (Ainsworth et al. 2010, Supplementary Fig. S3).

Population model

Although CEATTLE was designed as a multi-species model, only Pacific hake was included for this implementation. As an age-structured model, CEATTLE follows cohorts of species through time (Adams et al. 2022). Natural mortality (*M*) is partitioned into residual mortality (*M1*) and predation mortality (*M2*). The latter was modeled following previous MSCAA models, where *M2* from predators-at-age is determined using empirically derived suitability coefficients (representing prey- and age-preference, calculated from the proportion by weight of prey-at-age in the stomachs of predators-at-age; Supplementary Fig. S4), estimated prey biomass of the species included in the model and from other species in the system, and estimates of annual consumption (Adams et al. 2022). *M1* was estimated with a lognormal prior with a median of 0.2 y^{-1} and a log standard deviation of 0.1 y^{-1}, as in the 2020 stock assessment of Pacific hake, conducted by NOAA's National Marine Fisheries Service (NMFS) and Fisheries and Oceans Canada (DFO) (Grandin et al. 2020) using Stock Synthesis 3.0 (Methot and Wetzel 2013). In

CEATTLE, $M2$ can be set to zero, resulting in a single-species model.

The model was parameterized similarly to the 2020 stock assessment and was fit to data from 1980 to 2019. For the CEATTLE model, some values and parameters were prespecified to those from the 2020 assessment, including empirical weight-at-age (Supplementary Fig. S5) and maturity-at-age (Supplementary Table S3). The model was not sex-specific, consistent with the assessment (Grandin et al. 2020). The values of the remaining parameters were estimated by fitting the model to a time series of fishery and survey age-composition data and survey biomass estimates (Supplementary Table S4).

Projection period and harvest control rule

The model was projected for 3 years assuming mean annual recruitment and terminal maturity, selectivity, and weight-at-age, and diet suitability parameters for the last 5 years. Catch was determined by applying a projected fishing mortality rate (F_{proj} y^{-1}) based on a harvest control rule (HCR) applied to the estimated population. The HCR was based on the US and Canada Pacific Hake/Whiting Agreement default harvest policy, which includes a "40–10" control rule, triggered when spawning biomass (SB) is <40% of the unfished level (SB_0). The catch limit is then reduced in a straight line until SB is at 10% of SB_0, where the total allowable catch would equal zero (Powell 2004).

F_{target} was based on spawner-per-recruit-based proxies for maximum sustainable yield ($F_{target} = F_{40\%}$) for the single-species models and depletion-based proxies ($F_{target} = F_{40}$) for the cannibalism (multi-species) models (Holsman et al. 2016, Grandin et al. 2020), where SB_0 was determined by projecting the model forward under no fishing until year 2100 (Supplementary Fig. S6). Note that when the model is single species, $F_{40\%} = F_{40}$. However, when the model is multi-species, there is no clear choice for selecting M for deriving $F_{40\%}$ because M is conditional on predator biomass. Therefore, the depletion-based F_{40} was used instead for F_{target} for the cannibalism model. For year y of the projection period, $F_{proj,\ y}$ was calculated as follows:

(i) Stock status: $SB_y > SB_{40}$.
  - $F_{proj,y} = F_{target}$.

(ii) Stock status: $SB_{10} < SB_y \le SB_{40}$.
  - $F_{proj,y} = F_{target}\frac{4}{3} \times \frac{SB_y - SB_{10}}{SB_y}$.

(iii) Stock status: $SB_y < SB_{10}$.
  - $F_{proj,y} = 0$,

where SB_y is the spawning stock biomass during year y.

Bioenergetics and temperature

Predation was parameterized using a temperature-specific predation ration as defined in Holsman and Aydin (2015). The consumption rate was modeled as dependent on temperature and fish weight, following Kitchell et al. (1977). Temperature-dependent consumption is summarized as:

$$F\left(T\right) = V^X \times e^{X(1-V)}, \tag{1}$$

where:

$$V = \frac{T_{CM} - T}{T_{CM} - T_{CO}}, \tag{2a}$$

$$X = Z^2 \times \frac{\left[1 + \left(1 + \frac{40}{Y}\right)^{0.5}\right]^2}{400}, \tag{2b}$$

$$Z = ln\ \left(C_Q\right)\ \times \left(T_{CM} - T_{CO}\right), \tag{2c}$$

$$Y = ln\ \left(C_Q\right)\ \times \left(T_{CM} - T_{CO} + 2\right), \tag{2d}$$

and T is the temperature experienced by Pacific hake, and T_{CM} and T_{CO} are the maximum and optimal temperatures, respectively. C_Q represents the effect of temperature on consumption rate and would typically be derived from laboratory weight- and temperature-specific consumption experiments, but there are no such studies for Pacific hake. For comparison, Holsman et al. (2016), modeling walleye pollock, Pacific cod, and arrowtooth flounder, relied on laboratory-derived bioenergetic parameters (Holsman and Aydin 2015) available for these or related species. Without such studies for hake or other Merlucciidae, we assumed $C_Q = 2.5$: slightly lower than for pollock and near the value for other Gadiformes, as summarized by Deslauriers et al. (2017) (Supplementary Fig. S7). Our value for C_Q is also consistent with the global meta-analysis of the related Q_{10} parameter, the change in consumption rate when the temperature is changed by 10°C (Dell et al. 2011).

The maximum and optimal temperatures for the hake consumption rate, T_{CM} and T_{CO}, were derived from observed temperatures when hake were present during the hake acoustic-trawl survey because there are no temperature-specific consumption experiments for hake. Previously, Malick et al. (2020) kriged the temperature data collected at 100 m during the survey to create a spatial grid across the survey area and assigned hake biomass estimates to each grid cell. We filtered these kriged values for when hake were present (biomass > 0), which coincided with a median temperature of 8°C and a maximum temperature of 10.5°C (Supplementary Fig. S8). These values were assigned to T_{CM} and T_{CO}, respectively (Supplementary Fig. S7). The maximum temperature for the survey area was higher (14.5°C) than the maximum estimate for the kriged temperatures filtered for when hake were present, but the median temperature was the same.

To provide a full time series of annual temperatures for the calculation of temperature-dependent consumption, estimates for the California Current were derived from Regional Ocean Modeling System (ROMS; Shchepetkin and McWilliams 2005) output for 1980–2019, representing mean temperature from 50 to 350 m at the shelf break over the 100–200 m isobaths, from 42 to 47°N. The annual ROMS estimate was lower than the survey temperature observations by 0.45°C, on average. The annual temperature estimate used to parameterize the consumption ration never exceeded T_{CM}, as the ROMS estimate varied between 7 and 8.3°C (Supplementary Figs S7 and S8).

The estimates for the rate of consumption with weight for Pacific hake were derived from Francis (1983) according to:

$$C = C_A \times weight^{C_B}, \tag{3}$$

where C_A is the consumption by a 1 g fish at optimal temperature and C_B is the allometric scaling coefficient of consumption (per gram of predator) with predator weight. Francis (1983) notes that the estimated value of C_A (0.167), resulting from modeling the feeding-growing season, equated to 1.1–0.7% body weight consumed per day and that annual values would be approximately half this: 0.4–0.5% body weight per day (corresponding to $C_A = 0.0835$; Supplementary Fig. S9). Consumption in CEATTLE is scaled to an estimate of the number of foraging days per year, which was set to 182.5 days, the estimate for the duration of the feeding-growing season from Francis (1983) for late April–October. So, the original Francis (1983) estimate of C_A for the feeding-growing season was used. C_B in (3) was assumed equal to 0.54, based on Francis (1983), and this was implemented in CEATTLE as the mass-specific equivalent (0.54–1 = −0.46).

Modeling varying cannibalism proportions

The overall mean proportion of cannibalism in the Pacific hake diet belies the potential impact of cannibalism on hake population dynamics, given the variability in the rates across the time series and the mean diet proportions used. To test the effect of varying levels of cannibalism on model-derived quantities (*M*, recruitment, and biomass), the diet data were scaled to a maximum proportion of 0.05, 0.10, 0.5, and 0.75 cannibalism by weight, maintaining the age structure in the observed data (Supplementary Fig. S10). To approximate the time-varying response to cannibalism for the model period, CEATTLE was also fit (for all years) using the diet proportion for periods of high (1988–1999) and low (2005–2019) cannibalism as suggested by the observations in the CCTD. The diet proportions for these periods were also determined using the Dirichlet-reweighting approach (Supplementary Fig. S11).

Likelihood profile of natural mortality (*M*)

A likelihood profile of *M1*, over the range 0.15–0.3 y^{-1} was constructed for the single-species and cannibalism models to explore the information in the data on *M1*. The lowest negative log likelihood value (NLL) from the *M1* values tested was then subtracted from each NLL to determine the change in NLL and likelihood components.

Results

Pacific hake diet

On average across ages, cannibalism comprised 24.1% of Pacific hake diets by weight in the CCE, although the amount of cannibalism observed was highly variable (Figs 1 and 2). Across the time series, cannibalism was primarily on age-1 hake, with no records of predation on hake older than age 5 (Fig. 2). Cannibalism reached a maximum of 76.4% of stomach contents for ages 15+ by weight during the 1990s (estimated from the Dirichlet resampling), whereas the cannibalism inferred from the data collected during the acoustic-trawl survey (2005–2019) accounted for a maximum of 5.6% by weight for age 14 (Fig. 2). There were 16 instances of cannibalism out of 3995 stomachs (including empty stomachs) sampled from 2005 to 2019. In the CCTD dataset, cannibalism was the largest contributor by weight to hake diet between 1988 and 2019. The timing and location of cannibalism were variable, with evidence in some years of a higher proportion of stomachs that included hake at the southern end of the sampling area (below ~42°N) and when sampling took place later during the year. These trends are visible in 1998 and 1999 and without a latitudinal trend in 1995 and 1997 (Fig. 1).

Single-species model fit and comparison to the stock assessment

For the hindcast, the single-species CEATTLE model led to the same estimate of *M1* (0.21 y^{-1}, corresponding to *M* for the single-species model) and similar estimates of derived quantities of interest (*SB*, total biomass, and recruitment) as in the 2020 assessment (Fig. 3). Estimated *SB*, averaged across the hindcast, was 1.4% lower (mean difference of -0.06 ± 0.147 million tons [Mt]) and total biomass was 1.4% higher (0.06 ± 0.23 Mt) than estimated in the stock assessment (Fig. 3). Average estimated recruitment was 8.7% lower for the single-species CEATTLE model than the stock assessment, on average (Fig. 3; -0.29 ± 0.68 million). The single-species CEATTLE model and the assessment model predicted a declining trend in *SB* and total biomass during the projection period, with the single-species CEATTLE model projecting higher *SB* and total biomass than the assessment (Fig. 3).

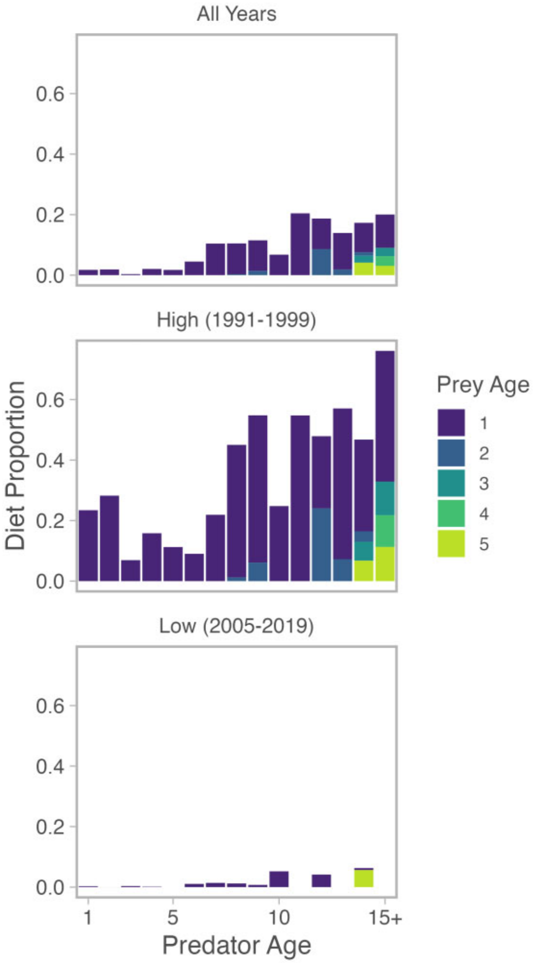

Figure 2. Dirichlet-weighted diet proportions by weight of cannibalism by predator and prey age for three periods: all years in the dataset (1988–2019), the period of high observed cannibalism (1991–1999), and the period of low observed cannibalism (2005–2019).

Cannibalism model using CEATTLE

The cannibalism and single-species models led to similar AICs and fits to data (Table 1). However, mean *SB*, estimated using the cannibalism model and averaged across the hindcast, was 15% higher, total biomass 23% higher, and recruitment 58% higher than using the single-species model, with greater uncertainty for the cannibalism model (Fig. 3; mean difference of 0.44 ± 0.22 Mt, 1.12 ± 1.03 Mt, and 4.10 ± 6.94 million). Estimated *M1* was higher, at 0.24 y^{-1} in the cannibalism model. Total biomass increased more than *SB* with cannibalism. During the projection period, the cannibalism model

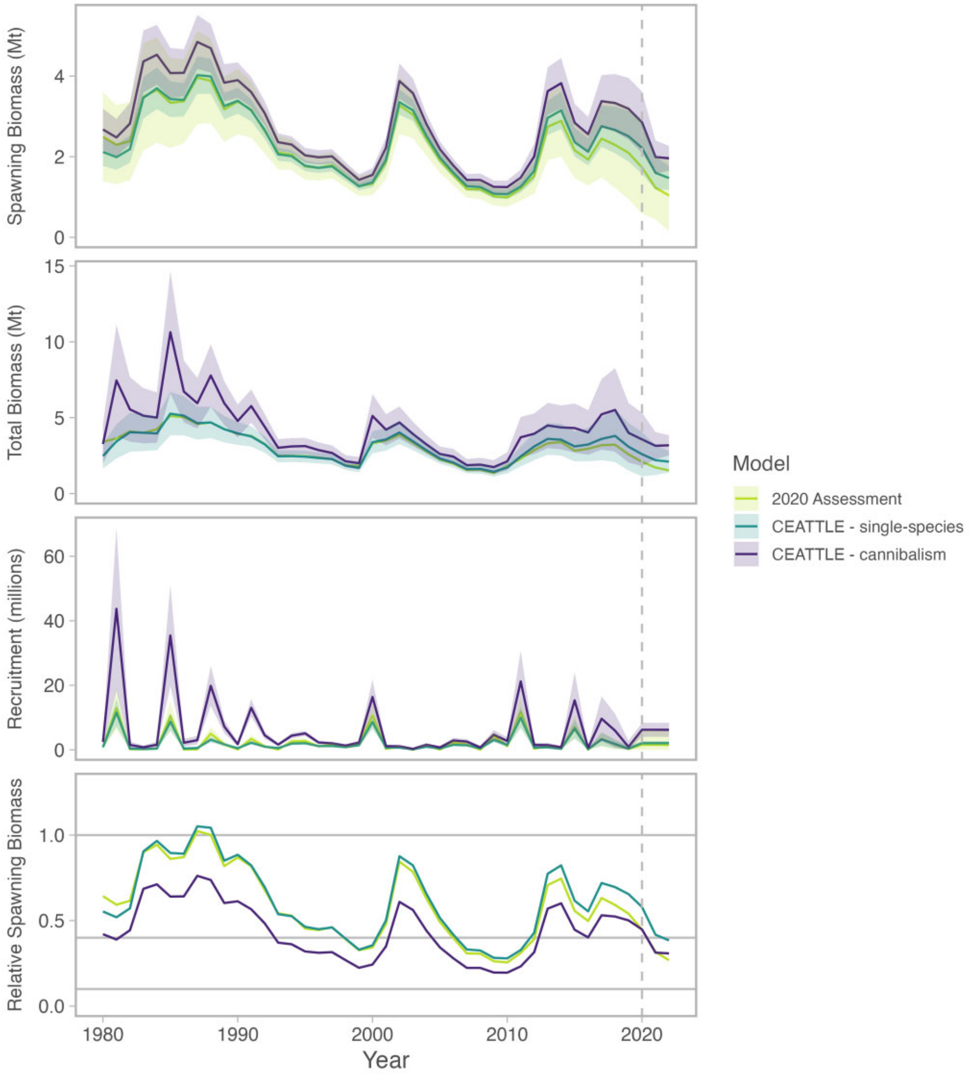

Figure 3. Spawning biomass (*SB*; Mt), total biomass (Mt), and age-1 recruitment (millions) with 95% confidence intervals (shaded region) and relative spawning biomass, *SB/SB₀*, for Pacific hake from CEATTLE in single-species mode, in cannibalism mode with the average proportion of cannibalism for the entire period, and from the 2020 stock assessment. The vertical line represents the start of the projection period (2020). Horizontal lines for relative spawning biomass represent *SB₀* (1.0), the management target (0.4), and the minimum stock size threshold (0.1).

Table 1. CEATTLE model variants and negative log-likelihood components for single-species and multi-species (cannibalism) models, and the sensitivity to the maximum scaled proportion and varying periods of cannibalism.

Base models	NLL	AIC	Survey	Catch	F comp	S comp	Sel	Init	Rec	F
Single species	867	1737	3.6	−146	479	104	328	29	62	11
Cannibalism	877	1757	3.9	−147	479	106	328	31	66	12
Scaled proportions of cannibalism										
0.05	867	1736	3.6	−147	479	104	328	29	62	11
0.1	871	1745	3.7	−147	497	105	328	30	63	12
0.5	905	1804	5.7	−147	481	113	328	33	74	12
0.75	936	1875	9.8	−145	486	126	328	37	80	12
Varying time periods of cannibalism										
High (1980–1999)	1034	2070	21	−147	502	126	331	59	127	15
Low (2005–2019)	867	1737	3.6	−147	479	104	328	29	62	11

NLL = joint negative log likelihood; AIC = Akaike information criterion; Survey = survey index negative log-likelihood (NLL); Catch = fisheries catch NLL; F comp = fishery age-composition data NLL; S comp = survey age-composition data NLL; Sel = selectivity deviates penalty; Init = initial abundance deviates penalty; Rec = recruitment deviates penalty; and F = fishing mortality deviates penalty.

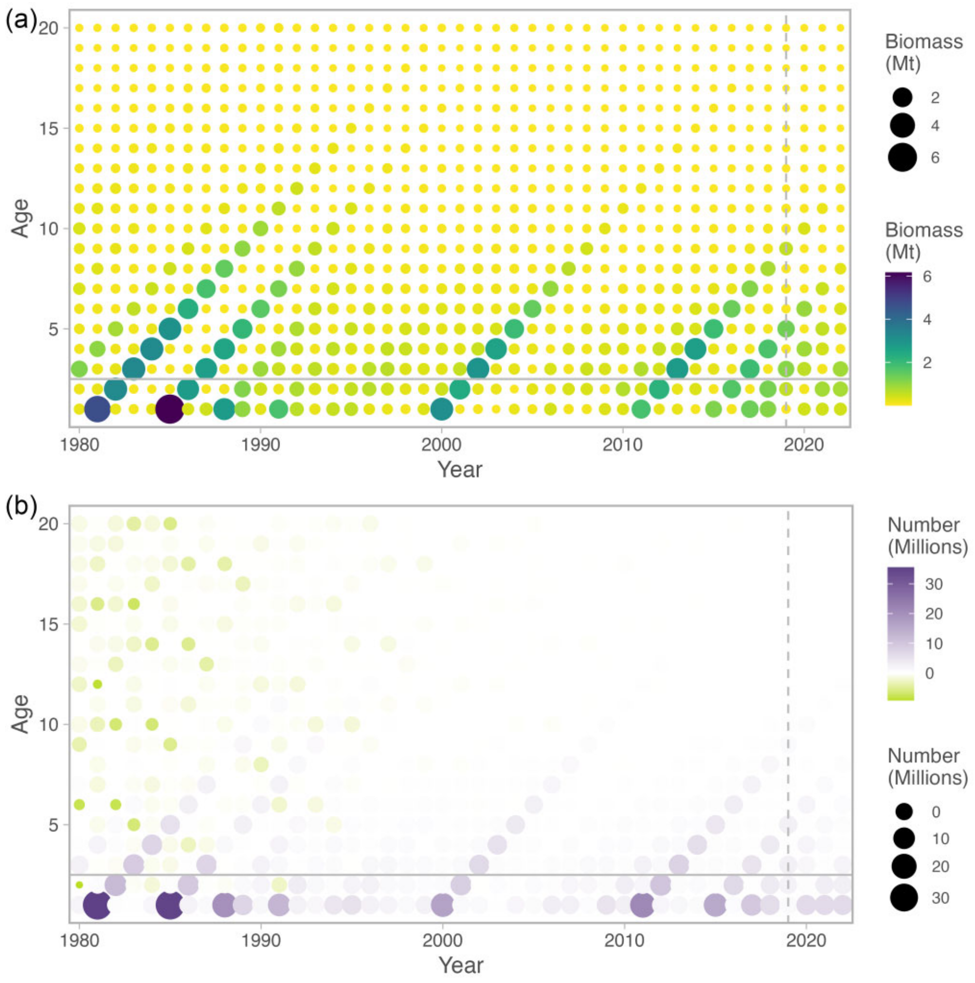

Figure 4. (a) Biomass-at-age (Mt) for the CEATTLE cannibalism model and (b) numbers-at-age for the 2020 stock assessment subtracted from those for the CEATTLE model using the averaged proportion of cannibalism. The horizontal line represents the age at 50% maturity (2.5) for Pacific hake from the 2020 stock assessment. The vertical line represents the start of the projection period.

Table 2. Biological reference points.

Quantity	Single species	Cannibalism
Unfished total biomass (B_0, Mt)	3.83	8.01
Unfished spawning biomass (SB_0, Mt)	1.91	3.18
Unfished recruitment (R_0, millions)	0.39	0.86
Target fishing mortality rate (F_{target})	0.44	0.51

predicted higher *SB* and, to a lesser extent total biomass, for the final year, compared to the single-species model (Fig. 3). The increase in recruitment relative to the single-species model was greater earlier in the time series, corresponding to years following strong cohorts in 1980 and 1984 (Grandin et al. 2020), when there were more larger individuals in the population (Fig. 4a). This trend was also apparent following other strong cohorts in 1999 and 2010 (Figs 3 and 4a). The estimate of the number of individuals-at-age for the cannibalism model, relative to the 2020 assessment, varied over time, with lower numbers of estimated individuals above ∼age 5 during the 1980s and 1990s, in addition to higher estimated numbers of age-1 hake (Fig. 4b). Estimated total *M* ($M1 + M2$) in the cannibalism model for age-1 hake ranged between 0.5 y^{-1} in 2009 and 1.43 y^{-1} in 1986, with higher *M2* during the late 1980s and early 1990s (Supplementary Table S5).

Biological reference points

Estimated unfished total biomass (B_0) and spawning biomass (SB_0) were higher for the cannibalism model than for the single-species model (Table 2) and the 2020 assessment (3.8 and 1.8 Mt; Grandin et al. 2020). The estimate of relative *SB* at the end of the hindcast (*SB* at the start of 2020 divided by SB_0) for the cannibalism model (45%) was near the management target (40%) and lower than the estimate from the single-species CEATTLE model (58%; Fig. 3). Estimated *F* was lower for the cannibalism model than the single-species CEATTLE model for the entire time series (Supplementary Fig. S12), though F_{target} was slightly higher for the cannibalism model than for the single-species model (Table 2).

Sensitivity to diet proportion

Variants of the cannibalism model were fit using the observed cannibalism proportion-at-age, described above, rescaled to a maximum proportion of 0.05, 0.1, 0.5, and 0.75 prey hake by weight, preserving the relative proportion of cannibalism-at-age, to represent the range of cannibalism in the CCTD dataset (Supplementary Fig. S10). The AIC and NLL of the model

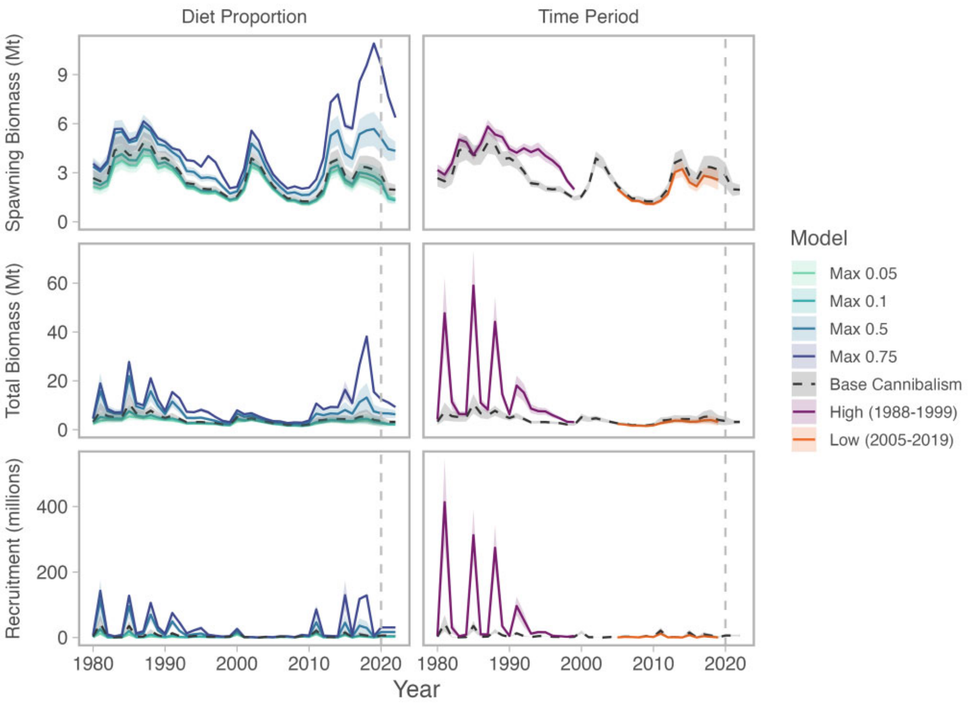

Figure 5. Spawning biomass (Mt), total biomass (Mt), and recruitment (millions) with 95% confidence intervals (shaded region) for models testing the sensitivity to the diet proportion: using base cannibalism data and the base data scaled to a maximum cannibalism proportion-by-weight of 0.05, 0.1, 0.5, and 0.75; for models testing varying periods of cannibalism: using the diet data for the period of high observed cannibalism (1980–1999) and the period of low cannibalism (2005–2019). The time series for the varying periods of cannibalism are displayed only for that period. The vertical line represents the start of the projection period.

with 0.05 cannibalism were similar to those of the single-species model and the AIC and NLL of the model with 0.1 cannibalism were between the single-species model and the base cannibalism model (with the observed diet proportions; Table 1). The models with 0.5 and 0.75 cannibalism had a higher AIC and NLL than the base cannibalism model (Table 1). The fits to the survey biomass, age-composition data, and recruitment and initial abundance deviations deteriorated as the cannibalism proportion increased (Table 1). Generally, *SB*, total biomass, and recruitment increased with cannibalism. The effect of increasing cannibalism is most apparent at the end of the time series and into the projection period (Fig. 5). The estimated value for *M1* increased with cannibalism, leveling off for the higher proportions (0.22, 0.23, 0.26, and 0.27 y^{-1} for maximum proportions of 0.05, 0.1, 0.5, and 0.75).

Varying periods of hake cannibalism

CEATTLE was fit with the Dirichlet-reweighted diet proportions for the periods of high (1980–1999) and low (2005–2019) cannibalism (Supplementary Fig. S11) to approximate the diet observed during these periods of regular sampling (Fig. 2). For the high-cannibalism period, the model led to much higher estimates for total biomass and recruitment than the base cannibalism model, increasing by 155 and 432% (Fig. 5; mean difference of 7.62 ± 9.82 Mt, 38.41 ± 72.29 million). Estimated *SB* was 53% higher (Fig. 5; 1.26 ± 0.06 Mt). The differences between the base and low-cannibalism models were less substantial, with average *SB* and total biomass for the low-cannibalism model estimated 14 and 19% lower and recruitment 45% lower, on average (Fig. 5; −0.35 ± 0.20 Mt, −0.71 ± 0.44 Mt, −2.26 ± 2.97 million). Estimated *M* for age-1 hake almost doubled for the high-cannibalism model (0.58–2.1 y^{-1}) and was substantially lower for the low-cannibalism model (0.26–0.44 y^{-1}). The AIC and NLL for the low-cannibalism model were comparable to the 0.05 cannibalism proportion model; the high-cannibalism model had the highest AIC and NLL of any model tested (Table 1).

M1 likelihood profile

The *M1* profile indicated that *M1* estimated without a prior would be higher than *M1* estimated with a prior for the single-species and cannibalism models. In the profile, higher values of *M1* corresponded to lower NLL for initial abundance and recruitment deviates for both models (Fig. 6). The likelihoods for the other components were mostly flat; NLL for fishing mortality deviations decreased with lower values of *M1* (Fig. 6). Increasing *M1* led to an increase in the estimated size of the stock, but not a change in the trend in stock size over time (Supplementary Fig. S13).

Discussion

Our analysis benefited from the new, long-term diet database (CCTD) for the CCE (Bizzarro et al. 2023), as the proportion-by-weight of cannibalism in Pacific hake stomachs appears to be highly variable. The (Dirichlet-weighted) cannibalism proportion for the entire time series was lower than the estimate by Wells et al. (2023) and the average proportion for the period of higher cannibalism was consistent with previous estimates of cannibalism from studies of hake diets in the CCE, the data for which are included in the CCTD (Buckley and Livingston 1997, Buckley et al. 1999, Field 2004). These higher proportions have informed the prevailing understanding of hake diets (Buckley et al. 1999, Field and Francis 2006),

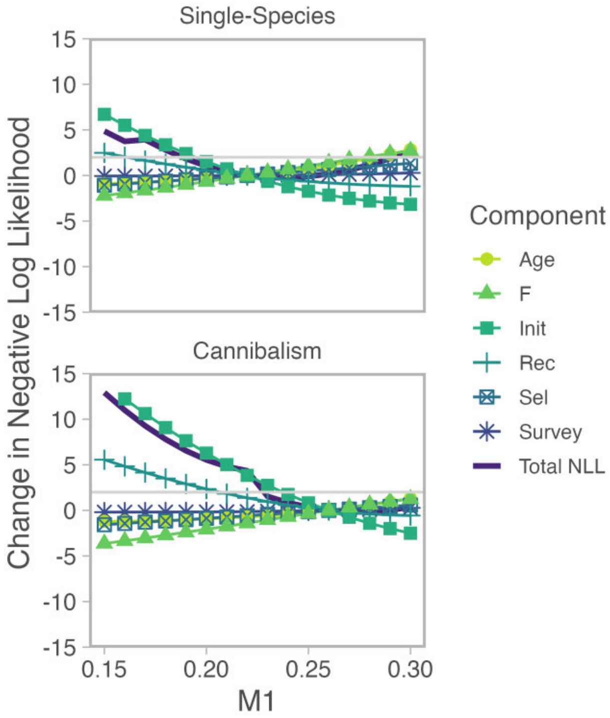

Figure 6. Change in the total negative log likelihood (NLL) and likelihood components for the single-species and cannibalism CEATTLE models with fixed values of residual mortality (*M1*). Age = survey and fishery age composition data NLL; F = fishing mortality deviates penalty; Init = initial abundance deviates penalty; Rec = recruitment deviates penalty; Sel = selectivity deviates penalty; and Survey = survey index NLL. Horizontal line is at the threshold for significant improvements in likelihood.

although Field (2004) noted that the proportion of cannibalism was lower during the late 1960s. The cannibalism detected using stomach samples collected during the acoustic-trawl survey was lower than all published estimates. The predator- and prey-hake ages were consistent with other diet studies, as piscivory increases with age (Nelson 2004).

Ideally, using time-varying diet proportions would have captured the temporal variability and hence the resulting effect on population dynamics. However, with missing years and high variability in the number of stomachs and predator ages sampled, there was insufficient support for extrapolating the missing years and predator–prey age structure. Averaging the diet for the entire time series biases the estimation of population dynamics, even with low-quality or uneven diet data, and the bias can be reduced by averaging over periods of up to 10 years (Trijoulet et al. 2019). We believe, however, that any interpolation of or substitution for the missing years during the transition between the high and low observed cannibalism states (2000–2004) would be a misrepresentation. The models of scaled diet proportion and time periods of cannibalism contextualize the averaged diet data and approximate the temporal variability in cannibalism without assuming the diet proportions for 2000–2004.

Despite the low proportion of cannibalism, when averaged across all years and samples in the CCTD, including cannibalism in a model of hake population dynamics increased estimates of population size and decreased the estimate of fishing mortality (*F*) for the hindcast. Multi-species estimation models are free to estimate higher levels of recruitment to compensate for the addition of *M2*, with all other parameters kept constant. Most of the increase in *M* pertains to age-1 hake, due to the age structure of the population following strong cohorts in 1980 and 1984 (and to a lesser degree in 1999 and 2010), resulting in an older population that consumes more age-1 hake. This translates to higher estimated numbers to compensate. The long interval between large cohorts for 1985-2020 may have inhibited cannibalism from altering the age structure and periodicity of the population (a mechanism described by Claessen et al. 2004). The decrease in *F* for the cannibalism model results from the relative increase in the estimated biomass, as the catch time series was the same for both models.

The perception of a lower stock status for the cannibalism model is consistent with the conclusion by Tyrrell et al. (2011) that including predation in the calculation of reference points reflects ecological realities and, due to the increase in mortality, leads to more conservative reference points. Holsman et al. (2016) found that SB_0 was lower in multi-species models, consistent with previous studies, but that the calculation of SB_0 was highly dependent on the harvest rates and resulted from predation mortality due to other species in the model. In this study, there were no other predatory species and cannibalism was observed primarily for age-1 individuals. To account for the higher mortality on younger ages, estimated recruitment almost doubled, but with the steep decline in cannibalism at older ages, more age-2+ fish survive and contribute to spawning biomass. Alternative reference points have been proposed for multi-species models, where SB_0 is defined as the biomass that occurs under equilibrium and no fishing for the target species, but various levels of fishing occur for other species in the system (e.g. Holsman et al. 2016, Moffitt et al. 2016). However, in the case of a cannibalism-only model, defining SB_0 as the spawning biomass that occurs under equilibrium and no fishing is the most parsimonious approach.

Impact of predation mortality from cannibalism on estimated population dynamics

While previous studies have noted the role of cannibalism in population dynamics (e.g. Buckley and Livingston 1997, Buckley et al. 1999, Claessen et al. 2004, Field and Francis 2006), none have quantified its potential impact on quantities of management interest. When the cannibalism model is used, the effect of *M2* on *SB* is less dramatic than the effect on total biomass or recruitment, though the effects are magnified during the period of higher cannibalism.

Model misspecification, leading to a bias in estimates of mortality, can affect quantities of management interest, with a positive bias in *M* leading to an overestimation of biomass (Johnson et al. 2015, Punt et al. 2021, Maunder et al. 2023). Without evidence to suggest that the estimated values for the CEATTLE models are too high, these findings suggest that the value for *M* estimated in the assessment may be low. The hake assessment has used a longevity-based prior from Hoenig (1983) since 2011 (Hicks et al. 2013, Grandin et al. 2020). Estimation of *M* for the assessment could be improved by including time- and age-variation, as indicated by the results of the cannibalism model, with substantially higher *M* for age-1 hake and variability across the time series.

Including *M2* introduces temporal variability and increased pressure on age-1 fish. As described by Plagányi et al. (2022), MICE are a tool for re-evaluating natural mortality assumptions, as multi-species models can account for changes in predation pressure and environmental conditions not considered in most single-species estimates of *M*. Maunder et al. (2023) note that most assessments assume *M* to be age- and time-invariant, despite the common knowledge that *M* is higher for younger fish and varies through time. The cannibalism model provides a data-driven source of estimates of increased *M* for age 1–5 hake. Even without time-varying diet, the interaction between cannibalism and the age structure of the population is made explicit, with the increased *M* during the late 1980s and 1990s likely underestimating the cannibalism pressure at that time.

Ignoring trophic interactions, especially cannibalism, can bias estimates of population size and status (Trijoulet et al. 2020). Cannibalism contributes to the energy transfer from recruits to older individuals in a population (Persson and De Roos 2006). The proportion of cannibalism may change depending on periods of high density, when more larger individuals spatially overlap with small individuals, when this overlap is driven by environmental conditions, or when other small prey are scarce (Persson and De Roos 2006, Pereira et al. 2017, Malick et al. 2020). Analyses of diet trends for Cape hake (*Merluccius capensis*) off southern Africa differ in their conclusions on prey preference. Macpherson and Gordoa (1994) suggest that cannibalism for Namibian Cape hake is not density-dependent, but the result of a preference for smaller conspecifics, whereas Pillar and Wilkinson (1995) determined that cannibalism is the result of density-dependence and overlap of small and large individuals in certain areas off South Africa.

Variability in hake diets

While it may be expected that some of the variability in the stomach content data is due to differences in sampling protocols for the studies included in the CCTD, such as species-of-interest, season, and spatial extent, it appears that more cannibalism occurred during the late 1980s and 1990s. This increase in cannibalism was observed during a period of intense sampling when stomachs were collected across seasons. In contrast, the sampling conducted during the acoustic-trawl survey from 2005 to 2019 was summer-only. The location and depth of the acoustic-trawl survey—both latitudinally and relative to the coast—may also contribute to the relative lack of observations of cannibalism in this later period.

The diet of Pacific hake in the CCE appears to be driven by the environment. Their co-occurrence with euphausiids varies spatially and is lower during warmer conditions (Phillips et al. 2023). Wells et al. (2023) conducted a spatial analysis of hake trophodynamics and determined that increased consumption of fishes when foraging inshore could allow hake to adapt to changing environmental conditions, specifically weaker upwelling, when the euphausiid biomass also decreases. A trend towards increased piscivory in weak upwelling conditions could interact with overlap of age classes to drive cannibalism. Hake cannibalism has not been specifically addressed since the initial analyses of the diet data collected during the 1980s and 1990s. A more up-to-date analysis, including an investigation of environmental covariates and spatial variability potentially leading to density-dependent consumption, would help determine the drivers of trends in cannibalism.

Buckley and Livingston (1997) suggest that cannibalism most likely occurs off central and southern California from late autumn to early spring, whereas the acoustic-trawl survey occurs during the summer when hake are consuming more euphausiids (Tanasichuk et al. 1991, Buckley and Livingston 1997, Buckley et al. 1999). Though euphausiids dominate hake diets in most years, when cannibalism occurs, it is a substantial portion of their nutritional intake. Larger hake are generally found off the coast of British Columbia, though in warmer years, the entire population migrates farther north during the summer (de Blois 2020, Grandin et al. 2020, Malick et al. 2020). This higher rate of cannibalism to the south aligns with spatio-temporal patterns in juvenile hake occurrence from 2003 to 2017, where the most consistent hotspot was <35°N, with higher variability in juvenile hake density than other species studied (Tolimieri et al. 2020).

It is difficult to disentangle changes in the time and location of sampling from a shift in hake trophic ecology. Development of an index of predation, including cannibalism, that accounts for seasonal and spatial trends could better inform future modeling efforts. While further analysis of the trends in hake predators or prey was outside the scope of this study, there is evidence of a similar trend in the proportion of hake present in the diets of California sea lions (*Zalophus californianus*), an abundant predator in the CCE (Koehn et al. 2016, Lowry et al. 2022). There were more records of hake detected in sea lion scat during the 1990s than during the 2000s and onwards (Supplementary Fig. S14). The sea lion scat records in the CCTD are from San Clemente and San Nicholas Islands in southern California and were collected quarterly from 1988 to 2015, with higher rates of hake predation in the summer, in contrast to the suggestion by Buckley and Livingston (1997) that cannibalism occurs off southern California during the winter (Supplementary Fig. S14). These data may corroborate the trend in hake cannibalism, indicating a spatial or temporal change in hake population dynamics, manifesting in predation by their conspecifics and sea lions.

Importance of accounting for cannibalism in Pacific hake management

The increase in estimated recruitment and biomass at the mean proportion of observed cannibalism indicates that even a low rate can affect estimates of population size. The results of the CEATTLE models are comparable to those from the single-species assessment because of the similarities in parameterization. The only extra data requirements for CEATTLE are the temperature time series, bioenergetic parameters, and diet data, none of which contribute to the likelihood function. CEATTLE adapts to the excess predation mortality from cannibalism by inferring a higher *M* for predated hake. Overall, most cannibalism was on age-1 hake and despite the typically low selectivity of age-1 fish by the fishery, our results show that the single-species stock assessment of Pacific hake underestimates hake total biomass (consisting largely of age-1+ fish) and spawning biomass, but overestimates the relative *SB*, given that some cannibalism likely occurs.

In addition to estimating biomass and recruitment, CEATTLE provides a basis for estimating time- and age-varying *M*. Therefore, CEATTLE, applied alongside the single-species hake assessment, could inform estimates of *M* in the assessment and more accurately reflect the impact of cannibalism and other sources of predation mortality (Plagányi et al. 2022). There is precedent for using multi-species models to inform a single-species assessment, as a CEATTLE model for walleye pollock, Pacific cod (*Gadus macrocephalus*), and arrowtooth flounder (*Atheresthes stomias*) is used to inform the management of Bering Sea pollock (Holsman et al. 2021). The CEATTLE model is included in the appendix of the pollock stock assessment to represent the impact of predation by Pacific cod and arrowtooth flounder. Additionally, mortality and consumption rates determined from the model are included in the Ecosystem Status Reports, which collate a suite of indicators for the Eastern Bering Sea and the Gulf of Alaska (Ferriss and Zador 2022, Siddon 2022).

Even when averaged across the time series, there is a clear effect of cannibalism on the population dynamics of Pacific hake, accentuating peaks in recruitment and total biomass. The single-species assessment introduces bias into the estimation of biomass and recruitment, especially earlier in the time series, by ignoring time- and age-specific variation in *M*. In contrast to the higher rates of cannibalism detected during the 1980s and 1990s, the more recent rates from 2005 to 2019 do not contribute to as large of an increase in estimated biomass or recruitment. The lower rate of cannibalism in recent years suggests that the single-species model is more representative of the population as it is now. This assumes, however, that the diet data collected during the survey are representative of the population and it is possible that cannibalism will increase in the future, given the past. There is no consensus on the cause or consequence of cannibalism across fishes, though the physiological traits, lower species richness, and/or decreased spatial segregation of juveniles and adults in ecosystems at higher latitudes have been theorized to drive increased cannibalism with latitude (Pillar and Wilkinson 1995, Pereira et al. 2017).

Even if the cannibalism proportion is low, the entire time series of the population also affects the calculation of reference points, such as SB_0. Additionally, high variability in recruitment, driven by the environment, is a central reason why dynamic reference points, which allow variability in how the stock-recruitment relationship is modeled, can better represent population fluctuations for species such as hake (Haltuch et al. 2009). Cannibalism may be an important driver of recruitment variability, but our ability to detect and respond to changes in cannibalism depends on continued monitoring of hake stomach contents. Our understanding of their diet would be amplified by collecting stomachs outside of the summer survey season and further offshore, potentially from the fishery.

The effects of cannibalism demonstrate the importance of considering trophic interactions in stock assessment. The variability in hake diets over time also underscores how monitoring the foraging ecology of target species remains a priority, especially with climate change. While the impact of temperature on Pacific hake diets is beyond the scope of this study, cannibalism was more prevalent during the 1980s and early 1990s when the mean temperature was slightly elevated. Relying on decades-old data collection can bias our understanding of trophic dynamics and our estimation of population size, as can assumptions of time- and age-invariant *M* in single-species models (Maunder et al. 2023). Considering a multi-species CEATTLE model alongside the single-species assessment for Pacific hake could inform mortality specification.

The applicability of cannibalism-only models to fisheries assessment and management will depend on which ages are predated. One would expect *M1*, as "residual" mortality, to decrease as *M2* increases. The increased M1 for the cannibalism model may be due to the lack of predation of older ages—removing excess individuals in the population not taken through fishing—but also increasing the total *M* of fish aged 1–5 as *M1* is time and age-invariant. Only including cannibalism also ignores the variability in predation mortality from other sources. Pacific hake was found in the stomachs of 25 species in the CCTD, accounting for >5% of stomach contents (by occurrence in all diet samples) for marine mammals and fish of management interest such as California sea lion, lingcod (*Ophiodon elongatus*), sablefish (*Anoplopoma fimbria*), and arrowtooth flounder (Supplementary Fig. S15). Future expansions of this model, and its utility in EBFM, would benefit from the inclusion of additional predators to provide a more complete picture of predation mortality. Including multiple predators could provide information on the predation of hake beyond the range of the survey, as with the inclusion of California sea lion and brown pelican as predators in a model of Pacific sardine in the CCE (Kaplan et al. 2019).

Despite this limitation, cannibalism models provide insight into the "chicken and egg" relationship of cannibalism and population dynamics. Explorations of cannibalism for Pacific hake, and other species, will be enhanced by a better understanding of spatiotemporal trends in diets, especially in relation to density dependence (Claessen et al. 2004). The development of spatial stock assessment methods will be a critical tool in the assessment of wide-ranging and commercially important species when combined with spatiotemporal diet studies, such as the development of trophoscapes for hake by Wells et al. (2023).

This study and the CEATTLE model can provide a framework for similar investigations into the impact of trophic dynamics on single-species models where high variability in recruitment and other dynamics is likely to be related to ecosystem conditions. The direct comparability to single-species assessments and relatively low data costs make MSCAA a crucial tool in the operationalization of EBFM. The models for Barents Sea capelin (Bogstad et al. 2022) and Flemish Cap commercial species (Pérez-Rodríguez et al. 2017), demonstrate the utility of MSCAA in exploring the impact of predation on population dynamics, as do simpler approaches, as in the assessment of Northeast Arctic cod (Yaragina et al. 2018), where predation mortality from cannibalism is applied directly. These models are also useful as part of an ensemble of models, as for Pacific sardine (Kaplan et al. 2019). While end-to-end ecosystem models are an admirable goal for underscoring EBFM, in the shorter term, models such as CEATTLE can address the dearth of ecosystem information in fisheries assessment and management.

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Author contributions

All authors contributed significantly to the project, agreed to be listed, and approve of the submitted manuscript. S.N.W. led the analysis and manuscript preparation under the guidance of A.E.P., M.A.H., I.C.K., and K.N.M. G.D.A. developed the modeling framework and particiated in the analysis and manuscript preparation.

Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

Conflict of interest

The authors declare that they have no known conflicts of financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The data underlying this article are available via the California Current Trophic Database, at https://doi.org/10.14284/597, and via GitHub, at https://github.com/sowasser/hake-CEATTLE.

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