Reviews in Fish Biology and Fisheries (Author's Accepted Manuscript)

Hungry like the fish: Evidence and implications of starvation mortality on marine animal population dynamics

Authors: Robertson, M.D.[1*], Cadigan, N.G.[1], & Eddy, T.D.[1], Eliason, E.J.[2,3]

1. *Centre for Fisheries Ecosystems Research, Fisheries and Marine Institute of Memorial University, P.O. Box 4920, St. John's, NL, A1C 5R3, Canada*
2. *Department of Ecology, Evolution & Marine Biology, University of California, Santa Barbara, CA 93106, USA*
3. *Pacific Science Enterprise Centre, Fisheries and Oceans Canada, West Vancouver, British Columbia, V7V 1H2 Canada*

*Corresponding author. Email: matthew.robertson@mi.mun.ca

ORCID:

Robertson, M.D. 0000-0003-3252-9956

Cadigan, N.G. 0000-0002-5922-1014

Eddy, T.D. 0000-0002-2833-9407

Eliason, E.J. 0000-0002-0120-7498

Running title: Hungry like the fish

Keywords: ecosystem-based fisheries management, energy, life-history, natural mortality, stock assessment

Abstract

Stock assessment models are simplifications of a stock's population dynamics. One commonly simplified component of population dynamics is natural mortality, which refers to all components of mortality that are not attributed to harvest, including predation, starvation, disease, and senescence. Although recent modeling advances have improved our ability to estimate natural mortality, most research has focused on either estimating aggregate natural mortality or predation mortality rates, while continuing to simplify other components. We contend that starvation-induced mortality, particularly for mature marine animals, represents an overlooked component of natural mortality and should be more frequently considered when developing scientific advice for ecosystem-based fisheries management. To defend this contention, we 1) describe marine animal energy maintenance and when starvation may be important, 2) highlight three case studies where starvation-induced mortality of mature animals may have affected population dynamics, 3) describe methods for measuring and estimating starvation to improve ecosystem-based fisheries management, and 4) describe how starvation risks may increase with climate change. Overall, improving stock assessment modeling requires that we continually reassess whether model simplifications are sufficient to estimate how populations are changing in support of fisheries management.

1. **Introduction**

Marine animal population dynamics models were developed over the last century to understand and inform policy makers about the impacts of harvest on populations (Quinn 2003). These models enable the estimation of fishing mortality on targeted species. However, models are a simplification of real population dynamics. For example, biomass dynamics models assume that population dynamics are not affected by age or size structure, or other characteristics, and these models combine recruitment, growth, and natural mortality into a single parameter (Hilborn and Walters 1992). The simplifications used in these types of single-species population dynamics models produced a variety of unintended management consequences (e.g., Smith et al. 2011) and eventually led to the development of ecosystem-based fisheries management, which seeks to address parameters that were initially overlooked (Goethel et al. 2023). For example, multispecies and ecosystem models have been developed to address the potential for cascading impacts of harvest of one species on other species or on entire ecosystems. However, no model can fully address the complexity of natural ecosystem dynamics (sensu Collie et al., 2016) and there always remains a risk that simplifications may produce consequences for effective management.

The natural mortality rate (*M*) is an important parameter that affects stock assessment results, and this parameter is usually simplified in practice because it is difficult to estimate (e.g., Punt et al. 2021). *M* refers to all components of mortality that are not attributed to harvest, including predation, starvation, disease, and senescence (Figure 1). Historically, single-species population dynamics models did not distinguish between components of *M* and tended to assume that it was constant across animal ages/sizes and years. This assumption was made due to the difficulty of observing deaths of animals that live underwater. However, *M* is known to vary by age/size (Lorenzen 2022) and over time (Johnson et al. 2015) and recent modeling advances have permitted *M* estimation in single-species population dynamics models (see review by Maunder et al. 2023). These modeling advances have primarily been used to estimate fluctuations in predation mortality. For example, diet data are used to inform variability in predation mortality in single-species (Howell et al. 2021), multispecies (Lewy and Vinther 2004; Trijoulet et al. 2019; Adams et al. 2022), and time-dynamic ecosystem models (Christensen and Walters 2004; Reum et al. 2019). Although these advances have benefited management outcomes, predation only represents a single component of *M* and models still tend to simplify other components. This matters because distinguishing among sources of *M* is necessary to identify appropriate indicators of population productivity and for incorporating data that can help inform *M* estimation within population and ecosystem models.

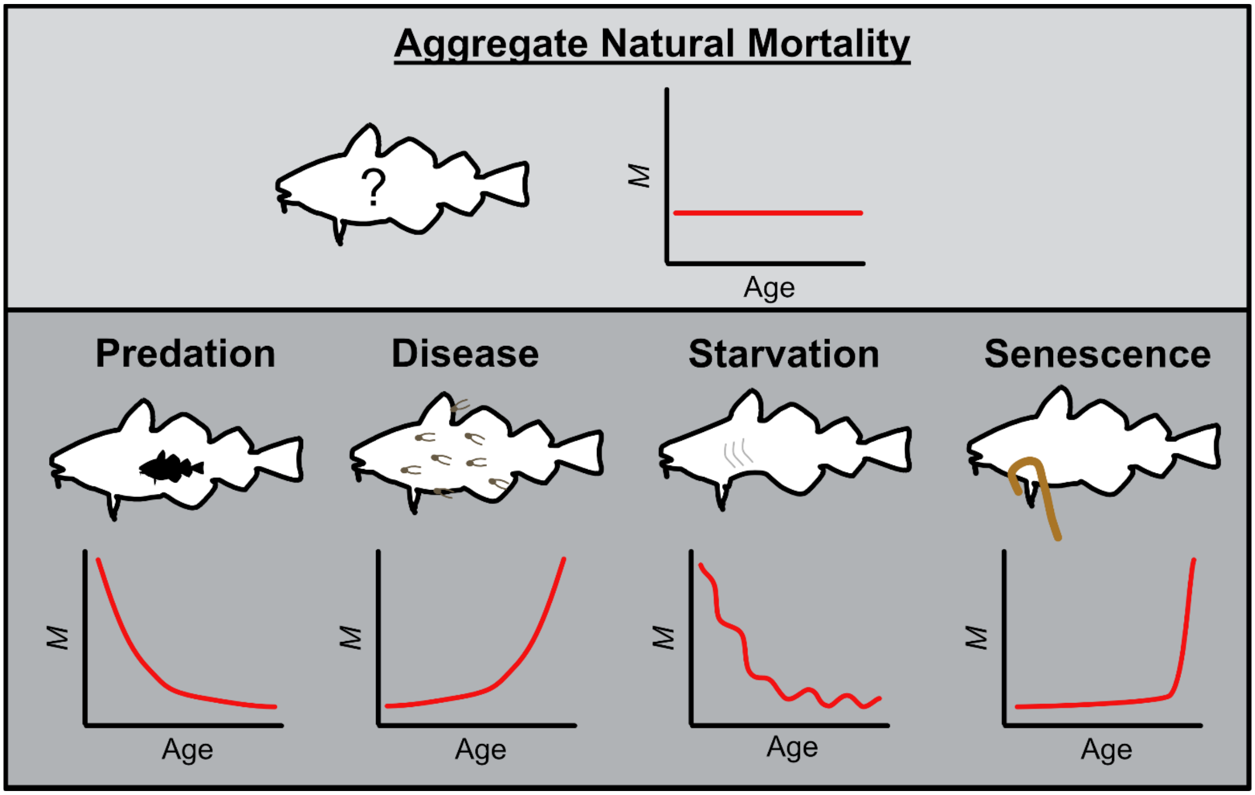

Figure 1. Conceptual diagram of generic age-specific trends from different sources of natural mortality rates (*M*). Fluctuations for the starvation panel represent seasonal fluctuations.

Starvation-induced mortality represents a source of mortality that can play an important role in population dynamics. Starvation refers to an animal that is willing and able to eat but is unable to do so because of some extrinsic limitation on food resources (McCue 2010). Animals may also undergo periods of fasting, which is commonly defined as a lack of feeding due to some endogenous, rather than exogenous control (McCue 2012). We focus on starvation but note that starvation and fasting may not necessarily be mutually exclusive. For example, an animal may initiate fasting during a migration but die from starvation during the migration if energy reserves run out. Further, starvation-induced mortality refers to mortality that is ultimately driven by starvation but that may be proximately caused by increased susceptibility to predation (Verdolin 2006), capture by fishing gear (Steingrund et al. 2009), and disease (Houston et al. 2007).

Marine animals, particularly fishes, are well known for their resilience to prolonged periods of starvation (Bar 2014). Furthermore, given that many marine animals are mobile and generalist consumers, there has been a tendency to assume that these animals may primarily suffer from periods of reduced growth and reproductive success rather than fully succumbing to mortality when confronted with limited prey availability (e.g., Ali et al. 2003; Rideout et al. 2005; Lorenzen 2016). These assumptions are not always borne out in reality, as mounting evidence indicates that periods of starvation have promoted periodic increases in M, including both incidences of mass-mortality and sustained increases in M (Stewart et al. 2021, 2023; Queiros et al. 2021; Regular et al. 2022; Szuwalski et al. 2023; Weerasekera et al. 2024; Robertson et al. 2025).

Here, we contend that starvation-induced mortality, particularly for mature marine animals, represents an overlooked component of M and should be more frequently considered when developing scientific advice for ecosystem-based fisheries management. To defend this contention, we will 1) describe the basics of animal energy maintenance and when starvation may be important, 2) focus on three case studies where starvation-induced mortality of mature animals affected population dynamics, 3) describe how recognition and estimation of starvation may occur and be used to improve ecosystem-based fisheries management and 4) highlight how the risks of starvation may increase under anthropogenic climate change.

2. Energy maintenance: the basics

Animals eat to obtain energy and nutrients. Energy is critical to support basal metabolism and daily activities such as locomotion, competition for mates, and predation escape (Brett 1976). Nutrients consist of the macronutrients (e.g., lipids, proteins, carbohydrates) and micronutrients (e.g., Fe, Mg, Mn) needed for body tissue growth and maintenance. Animals routinely encounter external and internal challenges (e.g., changing temperature, hypoxia, disease), and energy and nutrients support the physiological responses to cope with these challenges (e.g., morphological and biochemical acclimation processes; Hardison and Eliason, 2024). Malnutrition, or insufficient energy and nutrients to sustain life, can have severe consequences on the performance, resilience and survival of animals (McCue 2012).

A mismatch between energy intake and energy use leads to starvation (McCue 2010). This can arise from insufficient energy intake or excessive energy use. Basal metabolic rate (BMR, term used in endotherms) or standard metabolic rate (SMR, term used in ectotherms) is the minimum energy required just to maintain basic body processes (e.g., support cardiac output, ventilation, protein turnover; Chabot et al. 2016). BMR/SMR needs must first be met before energy is available for other activities such as locomotion, reproduction, consuming prey, tissue growth, and energy storage. Insufficient food availability in the environment will result in a reduction in energy intake which can have numerous consequences. Metabolic depression, or a decrease in SMR/BMR, is a common response to resource limitation (Storey and Storey 2004). Additional consequences include reduced energy stores and tissue mass (McCue 2010), lost opportunities for reproduction or feeding (Guillou et al. 2000), altered social behaviours (Frommen et al. 2007), and increased susceptibility to disease and predation (Yin and Blaxter 1987; Killen et al. 2011). Alternatively, animals may burn through their available energy stores by having an excessively elevated BMR/SMR (e.g., SMR increases with warming; Brett 1971) or via excessive activity (e.g., prolonged locomotion searching for food, getting lost during migration; Ware 1975). Disproportionate energy use over a short period may have minimal consequences on an animal; however, prolonged exposure could have phenological consequences (e.g., mistimed arrival at reproductive or feeding grounds; Wilson et al. 2022), physiological consequences (e.g., reduced energy stores and tissue mass, impaired ability to respond to environmental perturbation; Macdonald et al. 2010), and can even lead to death (Leung et al. 2018).

Malnourishment can also result from inadequate nutrient availability. Shifts in diet options (e.g., changes to community structure such that ideal prey are less available; Rose and O'Driscoll 2002) and shifts in diet quality (e.g., changing lipid levels in prey; Hixson and Arts 2016) can impact the available nutrients to animals. These shifts can occur naturally (e.g., geographical, Bird et al. 2018; seasonal changes, Vollenweider et al. 2011) and due to anthropogenic stressors (e.g., marine heat wave, Von Biela et al. 2019; overfishing, González Ortiz et al. 2025). Both macro and micronutrients provide essential components for cellular function (e.g., membrane structure, gene regulation, cell signaling) so deficiencies can profoundly alter physiological performance and plasticity, with deleterious consequences for animal survival (Hardison and Eliason 2024). For example, thiamine deficiency is becoming a major concern across taxa including mammals, fish and bivalves (Harder et al. 2018). Thiamine, a water-soluble vitamin, is exclusively obtained from the diet for fishes and plays a key role in energy metabolism and generating ATP. Deficiencies in thiamine result in impaired neurological function, such as abnormal swimming behaviour and even death (Amcoff et al. 1998; Brown et al. 2005).

The amount of energy that animals require depends on their ontogeny and life history strategy. Fish have generally been expected to be at greatest risk of starvation (up to 99% mortality rates) in the "critical period" following first feeding (Hjort 1914; China and Holzman 2014). The risk of starvation then decreases throughout the juvenile period as animals develop the energy stores required to cope with unfavorable environmental conditions (Byström et al. 2006; Shoup and Wahl 2011; Martin et al. 2017). Adult marine animal energy reserves are then expected to fluctuate seasonally (Figure 1) in response to food availability and dietary changes (Rikardsen et al. 2006), reproduction (Smith et al. 1990), and migration (Braithwaite et al. 2015). For example, animal energy reserves in temperate and Arctic ecosystems can decline over winter due to a reduced resource base (Hurst 2007; Fernandes and McMeans 2019). Further, capital breeders provision reproduction using stored energy resources, resulting in large seasonal fluctuations (e.g., Lambert and Dutil 1997), while income breeders continue to feed during spawning and therefore, tend to maintain more stable, lower amounts of stored energy (Jonsson 1997; McBride et al. 2015).

3. Starvation mortality case-studies

In recent years, there have been several high-profile marine animal populations where evidence for mass-mortality events or sustained increases in mortality have been attributed to starvation. Here, we will highlight case-studies for three marine animal populations with disparate life-history strategies (i.e., a marine mammal, a teleost, and an invertebrate) where there is evidence that starvation-induced mortality had population level-consequences.

3.1 Eastern gray whales

Gray whales (*Eschrichtius robustus*, Eschrichtiidae) that range from the Chukchi and Bering Seas to Baja California, Mexico are considered a single stock (Eastern gray whales) that is separate from the only other gray whale population (Western gray whales) in the Western North Pacific (Lang et al. 2022). Both populations were depleted by commercial whaling by the early 1900s, where Eastern gray whales have since recovered to estimated pre-whaling population sizes (current population size >17,000 whales; Eguchi et al. 2024) while Western gray whales have not recovered and are currently listed as critically endangered (current population size ~ 130 whales; IUCN).

Being large, long-lived, migratory animals, gray whales are capital breeders that rely on energy stored during the feeding season (May–November) to cover their needs during migration and reproduction when they feed very little, if at all (November–April; Villegas-Amtmann et al. 2015). This energy storage strategy is particularly relevant for the Eastern gray whale population, as these whales undergo one of the largest mammalian migrations between their southern breeding grounds and northern feeding grounds (~8,000 km; Pike 1962). During this migration, Eastern gray whales develop their energy stores primarily by suction feeding on infaunal amphipods (Moore et al. 2022). Energy gained in this way is stored in blubber, muscle, and other types of fat (Lockyer 2007). Maintaining a large energy store is necessary for reproductive females given the energy intensive nature of lactation which can occur for most of the year (Gittleman and Thompson 1988).

Twice in the last 25 years (1999–2000 & 2019–2020) “unusual mortality events” have occurred for the Eastern gray whale population, where the number of unexpected die-offs increased dramatically (mean = 41 dead, 1999–2000 = 651 dead, 2019–2020 = 384 dead; Christiansen et al. 2021). These mortality events were also unique in that juveniles and adults underwent similar levels of strandings compared to most other years where the majority of stranded whales were juveniles. Visual observations and post-mortem findings during both periods identified that whales were severely emaciated during their southward migration and on the breeding grounds, providing evidence that starvation was a likely contributor to the increase in mortality (Gulland et al. 2005; Christiansen et al. 2021; Raverty et al. 2024). The mechanism underpinning this starvation remains unresolved, although evidence indicates that it may be due to some combination of upwelling-induced shifts in primary productivity, ice-cover driven shifts in foraging ground access, and prey biomass distribution (Soledade Lemos et al. 2020; Moore et al. 2022; Stewart et al. 2023). Additionally, there is some evidence that vessel strikes, orca predation, and gear entanglement contributed to whale strandings (Raverty et al. 2024), indicating a complex combination of drivers of mortality which may be linked to starvation.

A population dynamics model was developed to account for these Eastern gray whale unusual mortality events. This biomass dynamics model included a time-varying carrying capacity term to represent shifts in feeding success, which was informed by estimates of body condition over time (Stewart et al. 2023). Estimates indicate that although only several hundred dead whales were observed in years with unexpected die-offs, these events likely represented several thousand dead whales, ultimately reducing the population size by 15–25% (Figure 2). By accounting for starvation-induced mortality using a time-varying carrying capacity term, this research indicates that these types of starvation events have only become important as the population has recovered (Moore et al. 2001). However, it is worth noting that the currently assumed drivers of these shifts (e.g., ice-cover, upwelling) are associated with large-scale climate variability and the model estimated substantial shifts in carrying capacity, ranging from 10,000 to >60,000 whales, indicating that similar mortality events could occur at relatively small population sizes.

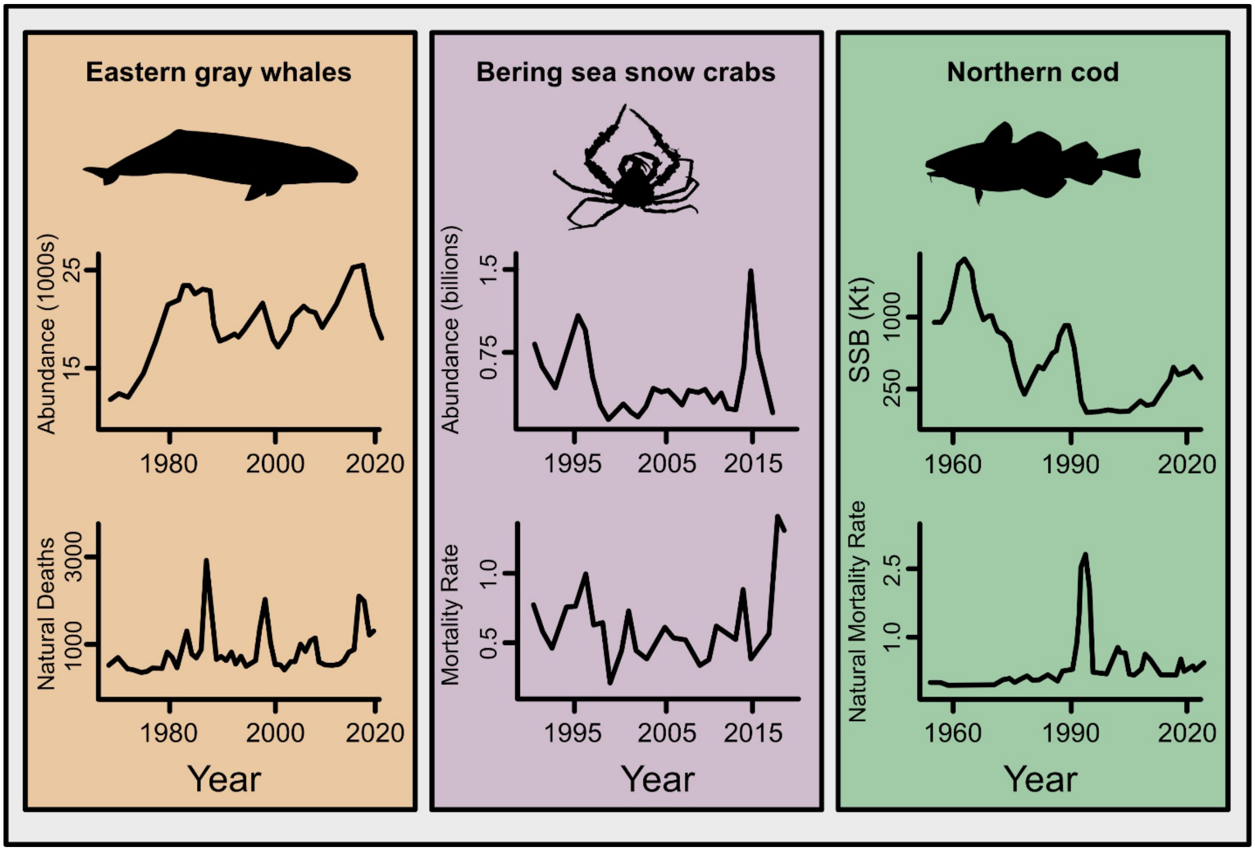

Figure 2. Estimated trends in population size (top row) and mortality (bottom row) for the three case studies. Redrawn from Stewart et al. 2023 (Eastern gray whales; 1968-2022), Szuwalski et al. 2023 (Bering sea snow crabs; 1988-2021), and DFO 2024 (Northern cod; 1954-2024). Axes reflect the metrics used to represent population size and mortality in each study. Abundance and mortality rates for the Bering sea snow crab study reflect estimates for the mature component of the population. Natural mortality rate for Northern cod reflects the average rate for ages 5+. SSB is spawning stock biomass. Kt is kilotons.

3.2 Newfoundland and Labrador Atlantic cod

Three populations of Atlantic cod (*Gadus morhua*, Gadidae) exist along the eastern coast of Newfoundland and Labrador. Northern cod is the infamous cod population which has become a global example of overfishing, while more southerly Newfoundland cod populations (NAFO Divisions 3NO and 3Ps) have historically received less global attention due to their smaller fisheries. However, all three populations underwent population collapses over the past forty years and none of the populations have recovered to historical population sizes (DFO 2020; Cadigan et al. 2022a; DFO 2022). The population collapse, especially of Northern cod, has outstanding questions about how much of the collapse can be attributed to overfishing or environmental change (Rose and Walters 2019; Cyr et al. 2025), since the time-period of collapse coincided with the coldest ocean temperatures ever observed in the region which was followed by an ecosystem regime shift (Pedersen et al. 2017; Dempsey et al. 2018).

The majority of Atlantic cod around Newfoundland and Labrador undergo seasonal migrations from offshore spawning grounds to inshore feeding grounds (Rose and Rowe 2024). Cod in this region tend to mostly feed during the spring, summer, and fall, with a short period of reduced feeding during reproduction in the spring and summer (March–September; Krumsick and Rose 2012), and a prolonged period of very little feeding over winter (Schwalme and Chouinard 1999). In addition to seasonal variability in feeding, Atlantic cod undergo an ontogenetic diet shift. Juvenile fish (<30 cm) predominantly feed on zooplankton, benthos, and shrimp, intermediate-sized fish (30–60 cm) consume more forage fishes, and the largest fish (>60 cm) tend to be generalists (Link and Garrison 2002; Sherwood et al. 2007). Cod store energy gained during feeding in the form of protein in white muscle tissue and as lipids in the liver (Lambert and Dutil 1997). Given the limited degree of feeding over winter, cod body condition has been observed to gradually decrease from fall to spring as their energy stores are depleted (Schwalme and Chouinard 1999; Mello and Rose 2005).

All three cod populations on the east coast of Newfoundland and Labrador have been in a period of reduced population productivity since the 1990s despite reduced levels of fishing mortality. Recent research has indicated that all three stocks have undergone major fluctuations in body condition (Cadigan et al. 2022b; Weerasekera et al. 2024; Soares et al. In Press), where reductions in body condition, specifically during the spring, have been directly related to increased *M* for all three populations (DFO 2020; Regular et al. 2022; Cadigan et al. 2024). The timing of body condition reductions correspond to timing of declines in the abundance of key forage fish prey, namely capelin (*Mallotus villosus*, Osmeridae; Regular et al. 2022) and Northern sand lance (*Ammodytes dubius*, Ammodytidae; Cadigan et al. 2022b). Although estimated starvation-induced mortality rates have been particularly high in some years (e.g., during the collapse of Northern cod), it is notable that estimated starvation-induced mortality rates have been elevated for prolonged periods of time. Recent estimates indicate that starvation-induced mortality has consistently impacted Atlantic cod population dynamics around Newfoundland and Labrador, especially over the last three decades.

The stock assessments for each of these cod populations currently account for shifts in *M*, although the methods implemented to do so differ. The Northern cod stock assessment implements an extensive tagging program which directly informs time-varying *M* in a state-space age-structured stock assessment model (Cadigan 2016; DFO 2022). Additionally, this model incorporates an index of capelin to account for shifts in *M* based on evidence that capelin availability has aligned with shifts in starvation-induced mortality (Regular et al. 2025). Meanwhile both NAFO Divisions 3Ps and 3NO cod stock assessments use integrated state-space assessment models where an index derived from body condition data is used to account for process error in *M* (Ings et al. 2024; Cadigan et al. 2024). In both cases, the condition indices estimate the proportion of cod below a critical condition threshold which was shown to lead to starvation-induced mortality in laboratory settings (Dutil and Lambert 2000; Casini et al. 2016). Despite similar approaches, *M* estimation differs slightly between 3Ps and 3NO cod models. Where the 3Ps cod model uses an aggregate condition index across ages and assumes that all other sources of *M* are not time- or age-varying, while the 3NO cod model uses an age-based condition index and assumes that predation composes the other main source of *M,* and is assumed to vary by time and age based on body weight (e.g., Lorenzen, 1996).

3.3 Bering Sea snow crab

Southeast Bering Sea snow crab (*Chionoecetes opilio*, Oregoniidae) are one of the most economically important fisheries in the United States with a mean ex-vessel revenue >USD$100 million from 2018–2022 (Garber-Yonts and Lee 2024). Given its economic value, this population has received substantial research attention focused on describing how its productivity and spatial distribution are modified by environmental changes (e.g., Fedewa et al. 2020; Szuwalski et al. 2021).

Bering sea snow crabs undergo an ontogenetic migration which may influence their feeding requirements and energy storage. Juvenile Bering Sea snow crabs are associated with cold temperatures, specifically with the cold pool (2°C bottom temperature isotherm; Parada et al. 2010). As snow crabs mature they migrate to warmer, offshore waters and once they reach maturity, they undergo a terminal molt and no longer grow (Parada et al. 2010). Our understanding about the mechanisms underpinning this ontogenetic migration remain somewhat limited, although water temperatures have been found to affect snow crab growth, survival, and molt timing (Dutil et al. 2010; Yamamoto et al. 2015; Siikavuopio et al. 2017). Additionally, although snow crabs are expected to be relatively opportunistic consumers of bivalves, polychaetes, crustaceans, ophiuroids, and gastropods, juvenile crabs tend to be most abundant in locations with an abundance of amphipods and small bivalves (Kolts et al. 2013).

The snow crab molting period and adult male migrations likely also influence seasonal cycles in energy reserves. Snow crabs molt each winter (February–March) prior to their terminal molt (~age 4 for females and age 8–9 for males; Parada et al. 2010; Ernst et al. 2012) and do not feed for 3–6 weeks before and for 3–4 weeks after their molt (O'Halloran and O'Dor 1988). This reduction in feeding, coupled with the energy requirements of molting, have been associated with decreased snow crab body condition, indicating that this is a period when snow crabs have reduced energy reserves (Dutil et al. 2009). Finally, adult male snow crabs in the Bering Sea undergo spawning migrations in the spring (Nichol and Somerton 2015).

In 2018–2019 tens of billions of Bering Sea snow crabs disappeared following a marine heatwave (Szuwalski et al. 2023; Litzow et al. 2024). This disappearance resulted in the population size declining by 90% from a historical high in 2018. Initially, there were questions about whether the fisheries independent survey simply did not observe the crabs due to a potential change in crab spatial distribution, however, it has become more certain that this disappearance reflected a mortality event rather than a distribution shift. A size-structured population dynamics model for snow crabs was used to assess variability in mortality (Szuwalski et al. 2023). This model estimated time-varying *M* and identified that the recent spike in mortality (Figure 2) was best explained by variability in bottom-water temperatures that crabs occupy. The mechanism(s) underpinning this spike in mortality remains disputed, however, the leading hypotheses include starvation, predation, and disease (Szuwalski et al. 2023; Litzow et al. 2024; Fedewa et al. 2025). The hypothesis for starvation-induced mortality posits that increased bottom-water temperatures increased the metabolic demands at a time when foraging areas (i.e., cold-water habitat) and prey availability (i.e., benthic secondary production) were reduced. Given that reduced energy reserves can increase the susceptibility of organisms to predation and disease, it is likely that these effects synergistically contributed to this massive mortality event.

4. How fisheries management can consider starvation mortality

A range of approaches are available for identifying and incorporating starvation mortality into fisheries management, including population indicators, single-species assessment models, ecosystem models, and bioenergetic frameworks (Table 1). The first step towards considering starvation mortality in fisheries management involves monitoring population indicators for when starvation mortality may be more likely to occur. Morphometric body condition indices (i.e., length and weight) are frequently recorded on research surveys, alongside other population indicators, to provide information on major spatial or temporal shifts in population productivity (Link et al. 2021). In instances where body condition appears to have dramatically changed, this could spur increased data collection on other physiological indicators (e.g., Brosset et al. 2021) and diet to more thoroughly assess the likelihood that starvation mortality is widespread. For example, physiological condition can be assessed with limited additional time resources in the field using a range of approaches, including fatmeter measurements (Brosset et al. 2015) and collection of blood (Sadoul and Geffroy 2019), stable isotope (Hatch 2012), proteomics (Raposo De Magalhães et al. 2020), or metabolomics (Roques et al. 2020) samples. Each of these forms of sampling would require additional time and monetary investments after sampling, which may limit the feasibility of regular collection, but they could provide options when additional sampling is desired to evaluate starvation risk more thoroughly.

Table 1. Summary of approaches used in fisheries science to identify, represent, and incorporate starvation mortality into population assessment and management. This table illustrates how each method represents starvation mortality, key data requirements, the relevance of each approach to fisheries management, and references to example applications for illustration.

Method	**Representation of starvation mortality**	**Data needs**	**Management relevance**	**Example applications**
Population indicators and monitoring	Explicit or implicit representation by identifying changes in condition, physiology, and/or diet	Length–weight, physiology, diet	Early warning indicators; motivation for model refinement	Brosset et al. 2015; Regular et al. 2022
Single-species models with time-varying parameters	Implicit representation via temporal, age-, and/or size-varying process error	Abundance, life-history, age/size composition, fisheries catch and effort	Direct stock status estimation and catch advice	Szuwalski et al. 2023
Single-species models with starvation covariates	Explicit representation by starvation indicator and process error correlation	Assessment model data (see above) and condition, prey, or environmental indices	As above with improved interpretation of productivity and uncertainty	Stewart et al. 2023; Cadigan et al. 2024; Robertson et al. 2025
Marine ecosystem models	Explicit or implicit representation via energy limitation or prey dynamics	Abundance, diet composition, growth, fisheries catch, primary production	Evaluates how ecosystem productivity and fishing interact to limit stock growth	Fu et al. 2017
Bioenergetics models	Explicit representation using mechanistic thresholds for starvation based on energy balance	Life history, physiology	Identifies conditions when starvation is likely	Lyons 1997; Chudzińska et al. 2024

Morphometric fish body condition data can also be collected by fisheries observers or other fisheries monitoring programs (Gilman et al. 2017). Fisheries often operate during different times of year and in different areas than research surveys. As a result, fisheries-dependent data may provide a better understanding about how fish body condition varies within a year and across space (e.g., Pecquerie et al. 2004). Given that starvation mortality is often an acute phenomenon that occurs during stressful life-history events (e.g., following reproduction) and after prolonged periods of reduced feeding (e.g., winter) or periods of heightened metabolic rates (e.g., marine heat-waves), having more complete spatial and temporal coverage may increase the likelihood of identifying starvation mortality risks. However, it is worth noting that fish in poor body condition may be less likely to outswim fishing gear (Martínez et al. 2003) and therefore, poor condition fish could be overrepresented in fisheries or research survey trawls. This issue has received limited research attention and would require an evaluation of relative selectivity between fish of different lengths and condition factors to correct for any overrepresentation of poor condition fish.

Single-species population dynamics models are becoming more capable of estimating time, size, and/or age-varying *M* (Maunder et al. 2023). While there is not a single, best method for estimating the impacts of starvation mortality, using a flexible framework in which time-varying *M* represents a minimum level of complexity, is likely most appropriate. As shown in our case-studies, *M* estimates can either be derived from models that have implicit assumptions about the impacts of starvation (e.g., time-varying carrying capacity; Stewart et al. 2023), can be correlated to potential mechanisms/ecosystem drivers after estimation within the model (Szuwalski et al. 2023), or can be explicitly driven by starvation estimates internally (Cadigan et al. 2024; Robertson et al. 2025). Whether these models implicitly or explicitly account for starvation mortality depends primarily on data availability and model structure (Table 1). State-space population dynamics models are considered an essential part of next-generation stock assessment (Punt et al. 2020) and are likely the best framework for estimating the effects of starvation regardless of model structure (e.g., catch-at-age or biomass dynamics models). State-space models are useful because they allow for the estimation of process and observation errors (Aeberhard et al. 2018). As a result, these models can implicitly account for starvation effects by estimating variability in population carrying capacity or *M* process errors (Szuwalski et al. 2023;

Stewart et al. 2023) or explicitly through the inclusion of starvation indicators (e.g., body condition or prey population abundance) as drivers of mortality processes (Cadigan et al. 2024; Robertson et al. 2025).

Marine ecosystem models such as Ecopath with Ecosim (Christensen and Walters 2004), Atlantis (Fulton et al. 2011), OSMOSE (Grüss et al. 2016), and mizer (Scott et al. 2014), represent food web interactions through predator and prey feeding relationships. While the most complex marine ecosystem models can explicitly represent starvation (e.g., Atlantis, OSMOSE; Audzijonyte et al., 2019; Travers et al., 2010), simpler models implicitly account for starvation through feeding interactions. For example, in Ecopath with Ecosim and mizer, declines in prey abundance or competition with other predators can lead to declines in predator population size (Andersen et al. 2016; Vajas et al. 2025). A major benefit of marine ecosystem models in the context of starvation, is that they are energy constrained. In essence, because marine ecosystem models represent primary production inputs to a food web, there are limits to the amount of energy available (Eddy et al. 2021). When primary and/or secondary production decreases, energy flow is limited, leading to resource limitation or starvation. Regardless of the model used, most ecosystem models have not yet been employed to evaluate risks of starvation mortality but have instead been employed to understand how modified fishing scenarios or climate change may have cascading consequences throughout an ecosystem (Worm et al. 2009; Smith et al. 2011; Eddy et al. 2025). Ecosystem models have sometimes been used to inform *M* in single-species models, especially in Europe (ICES 2024), however, they have primarily been used to inform predation rather than starvation or other sources of *M*.

Bioenergetic models such as the Wisconsin Energy Budget (WEB; Kitchell et al. 1974), Dynamic Energy Budget (DEB; Kooijman 2009), and Physiological Energy Budget (PEB; Sibly et al. 2013) can be used to improve mechanistic understanding about the circumstances where starvation may be most likely. Bioenergetic models are related to the balanced energy budget of individual animals (i.e., energy consumed and energy used for growth, metabolism, and waste; Brownscombe et al. 2022). As such, these models can be used to evaluate impacts of changing prey fields and environmental conditions to population dynamics, predator-prey dynamics, and habitat use. Examining the circumstances in which starvation mortality occurs has been the focus of several bioenergetics model applications (Lyons 1997; Jonas and Wahl 1998; Breck 2008; Dambrine et al. 2020; Chudzińska et al. 2024). Bioenergetic models can then be scaled up to assess whether individual processes can lead to population level consequences via the use of individual based models (Rose et al. 2024) or by integrating components of bioenergetics models into single-, multi-species (e.g., Holsman et al. 2016), or ecosystem models (e.g., Punt et al. 2016).

Models that account for starvation mortality need to be cognizant of the spatial, temporal, and demographic extent of its impacts. For example, animals that undergo ontogenetic diet shifts may only have some age/length groups that are impacted by reductions in a prey's population size if that prey is only consumed by smaller/larger animals. Furthermore, as discussed previously, starvation mortality is often an acute phenomenon and therefore, surveys are likely to over/underestimate the extent of starvation mortality depending on their spatial and temporal coverage. Misspecifying M can impact important aspects of models that inform management advice (Punt et al. 2021). This risk of misspecification, however, highlights the importance of conducting further research on the ubiquity of large-scale starvation-induced mortality for marine animal populations given the growing predominance of the length-inverse mortality hypothesis applied to account for predation mortality (Lorenzen 2022). The length-inverse mortality hypothesis assumes that *M* will be relatively low for larger individuals, which may be violated during periods of increased starvation-induced mortality.

Finally, recently developed approaches have proposed methods to modify catch advice using ecosystem indicators (Hill et al. 2020; Howell et al. 2021) which could benefit from starvation indicators for species at greater risk of starvation mortality. For example, the ecosystem-based fishing mortality reference point approach (F_{ECO}) adjusts fishing mortality reference points up or down when ecosystem indicators for a stock vary (Bentley et al. 2021; Howell et al. 2021). This approach represents a means of coupling results from single-species population dynamics models with ecosystem models, where ecosystem productivity or resource availability estimates from an ecosystem model may serve as ecosystem indicators that modify catch advice derived from single-species models.

5. Climate change may increase the risk of starvation

Temperature profoundly impacts chemical and biochemical reactions, and thus physiology and behaviour (Brett 1971). As temperatures rise, SMR increases exponentially, so ectothermic animals must eat more just to sustain their maintenance metabolism (Brett 1976). If resource supply cannot keep pace with rising metabolic demands, this can lead to 'metabolic meltdown' (Huey and Kingsolver 2019). Maximum metabolic rate (MMR) increases with warming up to a point, thereafter, it will typically plateau or decline with continued warming. Aerobic scope (the difference between MMR and SMR) represents the aerobic capacity for an animal to perform any activity above maintenance (e.g., move, compete for mates, digest a meal, escape predation, Brett 1971). The shape of the thermal performance curve (TPC) for aerobic scope varies but typically displays a gradual rise to a peak (termed the optimal temperature, Topt) followed by a steep decline (Schulte 2015). Animals cease feeding entirely at thermal extremes, likely due to insufficient aerobic capacity to digest a meal (Sinclair et al. 2016; Jutfelt et al. 2021). Even if food is abundant, animals may not be able to digest and assimilate it outside their optimal thermal range (Peck et al. 2008; Sinclair et al. 2016). Furthermore, changes in temperature often co-occur with other oceanographic changes, disease prevalence, and parasite burdens which may synergistically modify a species aerobic scope (Pörtner et al. 2005; Hvas et al. 2017). As such, animals are at risk of starvation when temperatures are too cold or too hot, which is becoming increasingly frequent with climate change.

Modifications to an animal's aerobic scope, cardiac output, and muscle development can modify swimming performance and behaviors related to predator-prey interactions (Domenici et al. 2019). In fact, temperature driven changes to metabolic rates were identified as a primary mechanism driving projections of fish biomass decline with climate change (Heneghan et al. 2021). Depending on the level of warming and the predator and prey species, modifications to metabolism and muscle development can alter predator attack success and prey escape performance. Climate warming is also expected to affect fish growth, where fish (and other animals) are generally expected to become smaller (Sheridan and Bickford 2011; Cheung et al. 2013), although some species may get larger (Audzijonyte et al. 2020). Body size is a major structuring force for predator-prey interactions (Persson and De Roos 2006; Andersen et al. 2016) and therefore, changes in predator or prey size could affect the number and strength of predator-prey interactions as well as the amount of energy obtained from consuming a given prey.

Marine species are moving in space and modifying their phenology in response to climate change (Brown et al. 2016; Asch et al. 2019; Pinsky et al. 2020) which can affect overlap between predators and their prey (Durant et al. 2007; Carroll et al. 2024; Bas et al. 2025).

Phenological and spatial shifts may reduce availability of prey at critical life history periods. The importance of prey availability at specific periods has often been discussed in relation to fish larvae (i.e., the critical period hypothesis; Hjort 1914; Houde 2008). However, if predators and prey do not overlap in areas and times historically used as part of a feeding migration (Stewart et al. 2023) or prior to/after energy intensive behaviors (e.g., reproductive periods; Rideout et al. 2006) the predator may be at greater risk of starvation. Most marine animals are not restricted to consuming a single type of prey, and therefore spatial and phenological shifts that alter overlap with favored prey species may simply result in prey switching and in turn may not greatly affect total prey consumption. However, prey switching may lead to consumption of prey that do not have the same quality. For example, Northern cod shifted from consuming primarily capelin (high protein, high lipid) to consuming shrimp (high protein, low lipid) following the collapse of capelin (Rose and O'Driscoll 2002). The shift to consuming more shrimp aligned with a period of reduced population productivity that has been at least partially driven by periods of increased starvation-induced mortality (Regular et al. 2022). Insufficient energy and nutrients can impair animal performance and tolerance, and ultimately impact persistence (Hardison and Eliason 2024).

6. Summary

Marine animals die from a variety of processes that are difficult to observe in the field and that have historically been poorly understood, aggregated, and treated as static assumptions when modeling population dynamics. Although modeling complex biological processes requires the use of simplifying assumptions, generating accurate predictions for how populations will respond to harvest under a changing climate will require re-considering which assumptions are reasonable. This paper discussed how starvation mortality may represent an overlooked component of natural mortality, which may become more relevant with climate change. We described how, despite a historical assumption that starvation is mainly a concern for larval and juvenile marine animals, starvation has resulted in large mortality events for mature animals across life-history strategies. In general, this work has highlighted a key population process that has not often been considered in single-species stock assessment models, and we discuss a variety of data streams and modeling platforms that could be leveraged to inform when populations may be at a greater risk of starvation. Continuously reassessing our assumptions and how we can test their validity will continue to be an important component of progressing ecosystem-based fisheries management.

Acknowledgements

Research funding to M.D.R., N.G.C., and T.D.E. was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC). Research funding to M.D.R. was provided by a start-up grant provided by the Marine Institute of Memorial University of Newfoundland. Research funding to N.G.C. was provided by the Ocean Choice International Industry Research Chair program at the Marine Institute of Memorial University of Newfoundland and by the Ocean Frontier Institute, through an award from the Canada First Research Excellence Fund. Research funding to T.D.E was provided by the Fisheries & Oceans Canada (DFO) Atlantic Fisheries Fund (AFF), the Fisheries and Oceans Canada (DFO) Sustainable Fisheries Science Fund (SFSF), the Canada First Research Excellence Fund (CFREF).

Conflict of Interest Statement

The authors declare no conflicts of interest

References

Adams GD, Holsman KK, Barbeaux SJ, et al (2022) An ensemble approach to understand predation mortality for groundfish in the Gulf of Alaska. Fisheries Research 251:. https://doi.org/10.1016/j.fishres.2022.106303

Aeberhard WH, Flemming JM, Nielsen A (2018) Review of State-Space Models for Fisheries Science. Annual Review of Statistics and Its Application 5:215–235. https://doi.org/10.1146/annurev-statistics-031017-100427

Ali M, Nicieza A, Wootton RJ (2003) Compensatory growth in fishes: a response to growth depression. Fish and Fisheries 4:147–190. https://doi.org/10.1046/j.1467-2979.2003.00120.x

Amcoff P, Börjeson H, Eriksson R, Norrgren L (1998) Effects of Thiamine Treatments on Survival of M74-Affected Feral Baltic Salmon. American Fisheries Society Symposium 21:31–40

Andersen KH, Jacobsen NS, Farnsworth KD (2016) The theoretical foundations for size spectrum models of fish communities. Canadian Journal of Fisheries and Aquatic Sciences 73:575–588. http://dx.doi.org/10.1139/cjfas-2015-0230

Asch RG, Stock CA, Sarmiento JL (2019) Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. Global Change Biology 25:2544–2559. https://doi.org/10.1111/gcb.14650

Audzijonyte A, Pethybridge H, Porobic J, et al (2019) Atlantis: A spatially explicit end-to-end marine ecosystem model with dynamically integrated physics, ecology and socio-economic modules. Methods in Ecology and Evolution 10:1814–1819. https://doi.org/10.1111/2041-210X.13272

Audzijonyte A, Richards SA, Stuart-Smith RD, et al (2020) Fish body sizes change with temperature but not all species shrink with warming. Nat Ecol Evol 4:809–814. https://doi.org/10.1038/s41559-020-1171-0

Bar N (2014) Physiological and hormonal changes during prolonged starvation in fish. Can J Fish Aquat Sci 71:1447–1458. https://doi.org/10.1139/cjfas-2013-0175

Bas M, Ouled-Cheikh J, Fuster-Alonso A, et al (2025) Potential Spatial Mismatches Between Marine Predators and Their Prey in the Southern Hemisphere in Response to Climate Change. Global Change Biology 31:e70080. https://doi.org/10.1111/gcb.70080

Bentley J, Lundy M, Howell D, et al (2021) Refining Fisheries Advice With Stock-Specific Ecosystem Information. Frontiers in Marine Science 8:. https://doi.org/10.3389/fmars.2021.602072

Bird CS, Veríssimo A, Magozzi S, et al (2018) A global perspective on the trophic geography of sharks. Nat Ecol Evol 2:299–305. https://doi.org/10.1038/s41559-017-0432-z

Braithwaite JE, Meeuwig JJ, Hipsey MR (2015) Optimal migration energetics of humpback whales and the implications of disturbance. Conserv Physiol 3:cov001. https://doi.org/10.1093/conphys/cov001

Breck JE (2008) Enhancing Bioenergetics Models to Account for Dynamic Changes in Fish Body Composition and Energy Density. Trans Am Fish Soc 137:340–356. https://doi.org/10.1577/t05-240.1

Brett JR (1976) Scope for Metabolism and Growth of Sockeye Salmon, *Oncorhynchus nerka* , and Some Related Energetics. J Fish Res Bd Can 33:307–313. https://doi.org/10.1139/f76-046

Brett JR (1971) Energetic Responses of Salmon to Temperature. A Study of Some Thermal Relations in the Physiology and Freshwater Ecology of Sockeye Salmon (Oncorhynchus nerkd). American Zoologist 11:99–113. https://doi.org/10.1093/icb/11.1.99

Brosset P, Cooke SJ, Schull Q, et al (2021) Physiological biomarkers and fisheries management. Rev Fish Biol Fisheries 31:797–819. https://doi.org/10.1007/s11160-021-09677-5

Brosset P, Fromentin J-M, Ménard F, et al (2015) Measurement and analysis of small pelagic fish condition: A suitable method for rapid evaluation in the field. Journal of Experimental Marine Biology and Ecology 462:90–97. https://doi.org/10.1016/j.jembe.2014.10.016

Brown CJ, O'Connor MI, Poloczanska ES, et al (2016) Ecological and methodological drivers of species' distribution and phenology responses to climate change. Global Change Biology 22:1548–1560. https://doi.org/10.1111/gcb.13184

Brown SB, Fitzsimons JD, Honeyfield DC, Tillitt DE (2005) Implications of Thiamine Deficiency in Great Lakes Salmonines. Journal of Aquatic Animal Health 17:113–124. https://doi.org/10.1577/H04-015.1

Brownscombe JW, Lawrence MJ, Deslauriers D, et al (2022) Chapter 4 - Applied fish bioenergetics. In: Cooke SJ, Fangue NA, Farrell AP, et al. (eds) Fish Physiology. Academic Press, pp 141–188

Byström P, Andersson J, Kiessling A, Eriksson L-O (2006) Size and temperature dependent foraging capacities and metabolism: consequences for winter starvation mortality in fish. Oikos 115:43–52. https://doi.org/10.1111/j.2006.0030-1299.15014.x

Cadigan NG (2016) A state-space stock assessment model for northern cod, including under-reported catches and variable natural mortality rates. Can J Fish Aquat Sci 73:296–308. https://doi.org/10.1139/cjfas-2015-0047

Cadigan NG, Rideout RM, Regular PM (2022a) A State-Space Assessment Model for 3NO Cod. NAFO SCR Doc 22/039:55

Cadigan NG, Robertson MD, Nirmalkanna K, Zheng N (2022b) The complex relationship between weight and length of Atlantic cod off the south coast of Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 79:1798–1819. https://doi.org/10.1139/cjfas-2021-0325

Cadigan NG, Weerasekera SJWWMMP, Regular PM, Rideout RM (2024) Time varying M with starvation mortality in a state-space stock assessment model: Part 2: Atlantic cod (*Gadus morhua*) on the southern Grand Bank of Newfoundland. Fisheries Research 280:107174. https://doi.org/10.1016/j.fishres.2024.107174

Carroll G, Abrahms B, Brodie S, Cimino MA (2024) Spatial match–mismatch between predators and prey under climate change. Nat Ecol Evol 8:1593–1601. https://doi.org/10.1038/s41559-024-02454-0

Casini M, Eero M, Carlshamre S, Lövgren J (2016) Using alternative biological information in stock assessment: Condition-corrected natural mortality of Eastern Baltic cod. ICES Journal of Marine Science 73:2625–2631. https://doi.org/10.1093/icesjms/fsw117

Chabot D, Steffensen JF, Farrell AP (2016) The determination of standard metabolic rate in fishes. Journal of Fish Biology 88:81–121. https://doi.org/10.1111/jfb.12845

Cheung WWL, Sarmiento JL, Dunne J, et al (2013) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nature Clim Change 3:254–258. https://doi.org/10.1038/nclimate1691

China V, Holzman R (2014) Hydrodynamic starvation in first-feeding larval fishes. Proc Natl Acad Sci USA 111:8083–8088. https://doi.org/10.1073/pnas.1323205111

Christensen V, Walters CJ (2004) Ecopath with Ecosim: Methods, capabilities and limitations. Ecological Modelling 172:109–139. https://doi.org/10.1016/j.ecolmodel.2003.09.003

Christiansen F, Rodríguez-González F, Martínez-Aguilar S, et al (2021) Poor body condition associated with an unusual mortality event in gray whales. Mar Ecol Prog Ser 658:237–252. https://doi.org/10.3354/meps13585

Chudzińska M, Klementisová K, Booth C, Harwood J (2024) Combining bioenergetics and movement models to improve understanding of the population consequences of disturbance. Oikos 2024:e10123. https://doi.org/10.1111/oik.10123

Collie JS, Botsford LW, Hastings A, et al (2016) Ecosystem models for fisheries management: Finding the sweet spot. Fish and Fisheries 17:101–125. https://doi.org/10.1111/faf.12093

Cyr F, Adamack AT, Bélanger D, et al (2025) Environmental control on the productivity of a heavily fished ecosystem. Nat Commun 16:5277. https://doi.org/10.1038/s41467-025-60453-6

Dambrine C, Huret M, Woillez M, et al (2020) Contribution of a bioenergetics model to investigate the growth and survival of European seabass in the Bay of Biscay – English

Channel area. Ecological Modelling 423:109007. https://doi.org/10.1016/j.ecolmodel.2020.109007

Dempsey DP, Gentleman WC, Pepin P, Koen-Alonso M (2018) Explanatory power of human and environmental pressures on the fish community of the Grand Bank before and after the biomass collapse. Frontiers in Marine Science 5:1–16. https://doi.org/10.3389/fmars.2018.00037

DFO (2020) Stock Assessment of NAFO Subdivision 3Ps cod. CSAS Research Document 18:

DFO (2022) Stock assessment of Northern cod (NAFO Divisions 2J3KL) in 2021. Fisheries and Oceans Canada

Domenici P, Allan BJM, Lefrançois C, McCormick MI (2019) The effect of climate change on the escape kinematics and performance of fishes: implications for future predator–prey interactions. Conservation Physiology 7:coz078. https://doi.org/10.1093/conphys/coz078

Durant JM, Hjermann D, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Climate Research 33:271–283. https://doi.org/10.3354/cr033271

Dutil JD, Dion C, Gamache L, et al (2010) Ration and Temperature Effects on the Condition of Male Adolescent Molter and Skip Molter Snow Crab. Journal of Shellfish Research 29:1025–1033. https://doi.org/10.2983/035.029.0404

Dutil JD, Lambert Y (2000) Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 57:826–836. https://doi.org/10.1139/f00-023

Dutil JD, Larocque R, Valois S, et al (2009) Spatial, annual and seasonal patterns in the condition and muscle size of snow crab. Mar Biol 156:1903–1916. https://doi.org/10.1007/s00227-009-1223-0

Eddy TD, Bernhardt JR, Blanchard JL, et al (2021) Energy Flow Through Marine Ecosystems: Confronting Transfer Efficiency. Trends in Ecology & Evolution 36:76–86. https://doi.org/10.1016/j.tree.2020.09.006

Eddy TD, Heneghan RF, Bryndum-Buchholz A, et al (2025) Global and Regional Marine Ecosystem Models Reveal Key Uncertainties in Climate Change Projections. Earth's Future 13:e2024EF005537. https://doi.org/10.1029/2024EF005537

Eguchi T, Lang A, Weller D (2024) Abundance of eastern North Pacific gray whales 2023/2024. U.S. Department of Commerce

Ernst B, Armstrong DA, Burgos J, Orensanz JM (Lobo) (2012) Life history schedule and periodic recruitment of female snow crab (Chionoecetes opilio) in the eastern Bering Sea. Can J Fish Aquat Sci 69:532–550. https://doi.org/10.1139/f2011-173

Fedewa E, Copeman LA, Litzow MA (2025) Energetic limitations and mass mortality of Bering Sea snow crab: Interacting effects of warming and density on collapse and recovery. Can J Fish Aquat Sci cjfas-2025-0099. https://doi.org/10.1139/cjfas-2025-0099

Fedewa EJ, Jackson TM, Richar JI, et al (2020) Recent shifts in northern Bering Sea snow crab (Chionoecetes opilio) size structure and the potential role of climate-mediated range contraction. Deep Sea Research Part II: Topical Studies in Oceanography 181–182:104878. https://doi.org/10.1016/j.dsr2.2020.104878

Fernandes T, McMeans BC (2019) Coping with the cold: energy storage strategies for surviving winter in freshwater fish. Ecography 42:2037–2052. https://doi.org/10.1111/ecog.04386

Frommen JG, Luz C, Bakker TCM (2007) Nutritional state influences shoaling preference for familiars. Zoology 110:369–376. https://doi.org/10.1016/j.zool.2007.06.002

Fu C, Olsen N, Taylor N, et al (2017) Spatial and temporal dynamics of predator-prey species interactions off western Canada. ICES Journal of Marine Science 74:2107–2119. https://doi.org/10.1093/icesjms/fsx056

Fulton EA, Link JS, Kaplan IC, et al (2011) Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries 12:171–188. https://doi.org/10.1111/j.1467-2979.2011.00412.x

Garber-Yonts B, Lee J (2024) Economic status of the BSAI King and Tanner crab fisheries off Alaska. NOAA

Gilman E, Weijerman M, Suuronen P (2017) Ecological data from observer programmes underpin ecosystem-based fisheries management. ICES Journal of Marine Science 74:1481–1495. https://doi.org/10.1093/icesjms/fsx032

Gittleman JL, Thompson SD (1988) Energy Allocation in Mammalian Reproduction. Am Zool 28:863–875. https://doi.org/10.1093/icb/28.3.863

Goethel DR, Omori KL, Punt AE, et al (2023) Oceans of plenty? Challenges, advancements, and future directions for the provision of evidence - based fisheries management advice. Reviews in Fish Biology and Fisheries 33:. https://doi.org/10.1007/s11160-022-09726-7

González Ortiz AA, Walsworth TE, Hammill E, et al (2025) Fisheries disrupt marine nutrient cycles through biomass extraction. Commun Earth Environ 6:277. https://doi.org/10.1038/s43247-025-02218-z

Grüss A, Schirripa MJ, Chagaris D, et al (2016) Estimating natural mortality rates and simulating fishing scenarios for Gulf of Mexico red grouper (Epinephelus morio) using the ecosystem model OSMOSE-WFS. Journal of Marine Systems 154:264–279. https://doi.org/10.1016/j.jmarsys.2015.10.014

Guillou M, Lumingas LJL, Michel C (2000) The effect of feeding or starvation on resource allocation to body components during the reproductive cycle of the sea urchin

Sphaerechinus granularis (Lamarck). Journal of Experimental Marine Biology and Ecology 245:183–196. https://doi.org/10.1016/S0022-0981(99)00162-8

Gulland FMD, Perez-Cortes H, Urban J, et al (2005) Eastern North Pacific gray whale (Eschrichtius robustus) unusual mortality event, 1999-2000. U.S. Department of Commerce

Harder AM, Ardren WR, Evans AN, et al (2018) Thiamine deficiency in fishes: causes, consequences, and potential solutions. Rev Fish Biol Fisheries 28:865–886. https://doi.org/10.1007/s11160-018-9538-x

Hardison EA, Eliason EJ (2024) Diet effects on ectotherm thermal performance. Biological Reviews 99:1537–1555. https://doi.org/10.1111/brv.13081

Hatch KA (2012) The use and application of stable isotope analysis to the study of starvation, fasting, and nutritional stress in animals. In: McCue MD (ed) Comparative Physiology of Fasting, Starvation, and Food Limitation. Springer Berlin Heidelberg, pp 337–364

Heneghan RF, Galbraith E, Blanchard JL, et al (2021) Disentangling diverse responses to climate change among global marine ecosystem models. Progress in Oceanography 198:. https://doi.org/10.1016/j.pocean.2021.102659

Hilborn R, Walters CJ (1992) Biomass dynamic models. In: Quantitative Fisheries Stock Assessment. Chapman & Hall, London, pp 297–329

Hill SL, Hinke J, Bertrand S, et al (2020) Reference points for predators will progress ecosystem-based management of fisheries. Fish and Fisheries 21:368–378. https://doi.org/10.1111/faf.12434

Hixson SM, Arts MT (2016) Climate warming is predicted to reduce omega-3, long-chain, polyunsaturated fatty acid production in phytoplankton. Global Change Biology 22:2744–2755. https://doi.org/10.1111/gcb.13295

Hjort J (1914) Fluctuations in the great fisheries of Northern Europe. 20:228

Holsman KK, Ianelli J, Aydin K, et al (2016) A comparison of fisheries biological reference points estimated from temperature-specific multi-species and single-species climate-enhanced stock assessment models. Deep Sea Research Part II: Topical Studies in Oceanography 134:360–378. https://doi.org/10.1016/j.dsr2.2015.08.001

Houde ED (2008) Emerging from Hjort's shadow. Journal of Northwest Atlantic Fishery Science 41:53–70. https://doi.org/10.2960/J.v41.m634

Houston AI, McNamara JM, Barta Z, Klasing KC (2007) The effect of energy reserves and food availability on optimal immune defence. Proc R Soc B 274:2835–2842. https://doi.org/10.1098/rspb.2007.0934

Howell D, Schueller A, Bentley J, et al (2021) Combining Ecosystem and Single-Species Modeling to Provide Ecosystem-Based Fisheries Management Advice Within Current Management Systems. Frontiers in Marine Science 7:. https://doi.org/10.3389/fmars.2020.607831

Huey RB, Kingsolver JG (2019) Climate Warming, Resource Availability, and the Metabolic Meltdown of Ectotherms. The American Naturalist 194:E140–E150. https://doi.org/10.1086/705679

Hurst TP (2007) Causes and consequences of winter mortality in fishes. Journal of Fish Biology 71:315–345. https://doi.org/10.1111/j.1095-8649.2007.01596.x

Hvas M, Karlsbakk E, Mæhle S, et al (2017) The gill parasite Paramoeba perurans compromises aerobic scope, swimming capacity and ion balance in Atlantic salmon. Conservation Physiology 5:. https://doi.org/10.1093/conphys/cox066

ICES (2024) Working Group on Multispecies Assessment Methods (WGSAM)

Ings DW, Varkey DA, Babyn J, et al (2024) Assessing the Status of the Cod (Gadus morhua) Stock in NAFO Subdivision 3Ps in 2019

Johnson KF, Monnahan CC, Mcgilliard CR, et al (2015) Time-varying natural mortality in fisheries stock assessment models: identifying a default approach. ICES Journal of Marine Science 72:137–150. https://doi.org/10.1094/icesjms/fsu055

Jonas JL, Wahl DH (1998) Relative Importance of Direct and Indirect Effects of Starvation for Young Walleyes. Transactions of the American Fisheries Society 127:192–205. https://doi.org/10.1577/1548-8659(1998)127%253C0192:RIODAI%253E2.0.CO;2

Jonsson KI (1997) Capital and Income Breeding as Alternative Tactics of Resource Use in Reproduction. Oikos 78:57–66. https://doi.org/10.2307/3545800

Jutfelt F, Norin T, Åsheim ER, et al (2021) 'Aerobic scope protection' reduces ectotherm growth under warming. Functional Ecology 35:1397–1407. https://doi.org/10.1111/1365-2435.13811

Killen SS, Marras S, McKenzie DJ (2011) Fuel, fasting, fear: routine metabolic rate and food deprivation exert synergistic effects on risk-taking in individual juvenile European sea bass. Journal of Animal Ecology 80:1024–1033. https://doi.org/10.1111/j.1365-2656.2011.01844.x

Kitchell JF, Koonce JF, Magnuson JJ, et al (1974) Model of Fish Biomass Dynamics. Transactions of the American Fisheries Society 103:786–798. https://doi.org/10.1577/1548-8659(1974)103%253C786:MOFBD%253E2.0.CO;2

Kolts J, Lovvorn J, North C, et al (2013) Effects of body size, gender, and prey availability on diets of snow crabs in the northern Bering Sea. Mar Ecol Prog Ser 483:209–220. https://doi.org/10.3354/meps10292

Kooijman B (2009) Dynamic Energy Budget Theory for Metabolic Organisation, 3rd edn. Cambridge University Press

Krumsick KJ, Rose GA (2012) Atlantic cod (Gadus morhua) feed during spawning off Newfoundland and Labrador. ICES Journal of Marine Science 69:1701–1709. https://doi.org/10.1093/icesjms/fss158

Lambert Y, Dutil J (1997) Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (*Gadus morhua*)? Canadian Journal of Fisheries and Aquatic Science 54:104–112

Lang AR, Weller DW, Burdin AM, et al (2022) Population structure of North Pacific gray whales in light of trans-Pacific movements. Marine Mammal Science 38:433–468. https://doi.org/10.1111/mms.12875

Leung JYS, Nagelkerken I, Russell BD, et al (2018) Boosted nutritional quality of food by CO2 enrichment fails to offset energy demand of herbivores under ocean warming, causing energy depletion and mortality. Science of The Total Environment 639:360–366. https://doi.org/10.1016/j.scitotenv.2018.05.161

Lewy P, Vinther M (2004) A stochastic age-length-structured multispecies model applied to North Sea stocks. ICES CM 33:1–33

Link JS, Garrison LP (2002) Trophic ecology of Atlantic cod Gadus morhua on the northeast US continental shelf. Marine Ecology Progress Series 227:109–123

Link JS, Karp M, Lynch P, et al (2021) Proposed business rules to incorporate climate-induced changes in fisheries management. ICES Journal of Marine Science 78:3562–3580

Litzow MA, Fedewa EJ, Malick MJ, et al (2024) Human-induced borealization leads to the collapse of Bering Sea snow crab. Nat Clim Chang 1–4. https://doi.org/10.1038/s41558-024-02093-0

Lockyer C (2007) All creatures great and smaller: a study in cetacean life history energetics. J Mar Biol Ass 87:1035–1045. https://doi.org/10.1017/S0025315407054720

Lorenzen K (1996) The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. Journal of Fish Biology 49:627–642. https://doi.org/10.1111/j.1095-8649.1996.tb00060.x

Lorenzen K (2022) Size- and age-dependent natural mortality in fish populations: Biology, models, implications, and a generalized length-inverse mortality paradigm. Fisheries Research 255:. https://doi.org/10.1016/j.fishres.2022.106454

Lorenzen K (2016) Toward a new paradigm for growth modeling in fisheries stock assessments: Embracing plasticity and its consequences. Fisheries Research 180:4–22. https://doi.org/10.1016/j.fishres.2016.01.006

Lyons J (1997) Influence of Winter Starvation on the Distribution of Smallmouth Bass among Wisconsin Streams: A Bioenergetics Modeling Assessment. Transactions of the American Fisheries Society 126:157–162. https://doi.org/10.1577/1548-8659(1997)126%253C0157:iowsot%253E2.3.co;2

Macdonald JS, Patterson DA, Hague MJ, Guthrie IC (2010) Modeling the Influence of Environmental Factors on Spawning Migration Mortality for Sockeye Salmon Fisheries Management in the Fraser River, British Columbia. Transactions of the American Fisheries Society 139:768–782. https://doi.org/10.1577/T08-223.1

Martin BT, Heintz R, Danner EM, Nisbet RM (2017) Integrating lipid storage into general representations of fish energetics. Journal of Animal Ecology 86:812–825. https://doi.org/10.1111/1365-2656.12667

Martínez M, Guderley H, Dutil J-D, et al (2003) Condition, prolonged swimming performance and muscle metabolic capacities of cod Gadus morhua. Journal of Experimental Biology 206:503–511. https://doi.org/10.1242/jeb.00098

Maunder MN, Hamel OS, Lee H, et al (2023) A review of estimation methods for natural mortality and their performance in the context of fishery stock assessment. Fisheries Research 257:. https://doi.org/10.1016/j.fishres.2022.106489

McBride RS, Somarakis S, Fitzhugh GR, et al (2015) Energy acquisition and allocation to egg production in relation to fish reproductive strategies. Fish and Fisheries 16:23–57. https://doi.org/10.1111/faf.12043

McCue MD (2010) Starvation physiology: Reviewing the different strategies animals use to survive a common challenge. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 156:1–18. https://doi.org/10.1016/j.cbpa.2010.01.002

McCue MD (ed) (2012) Comparative Physiology of Fasting, Starvation, and Food Limitation. Springer Berlin Heidelberg, Berlin, Heidelberg

Mello LGS, Rose GA (2005) Seasonal cycles in weight and condition in Atlantic cod (Gadus morhua L.) in relation to fisheries. ICES Journal of Marine Science 62:1006–1015. https://doi.org/10.1016/j.icesjms.2005.03.008

Moore SE, Clarke JT, Okkonen SR, et al (2022) Changes in gray whale phenology and distribution related to prey variability and ocean biophysics in the northern Bering and eastern Chukchi seas. PLoS ONE 17:e0265934. https://doi.org/10.1371/journal.pone.0265934

Moore SE, R. JU, Perryman WL, et al (2001) Are Gray Whales Hitting "K" Hard? Marine Mammal Science 17:954–958. https://doi.org/10.1111/j.1748-7692.2001.tb01310.x

Nichol DG, Somerton DA (2015) Seasonal migrations of morphometrically mature male snow crab (Chionoecetes opilio) in the eastern Bering Sea in relation to mating dynamics. FB 113:313–326. https://doi.org/10.7755/FB.113.3.7

O'Halloran MJ, O'Dor RK (1988) Molt Cycle of Male Snow Crabs, Chionoecetes opilio, from Observations of External Features, Setal Changes, and Feeding Behavior. Journal of Crustacean Biology 8:164–176. https://doi.org/10.2307/1548309

Parada C, Armstrong DA, Ernst B, Hinckley S (2010) Spatial dynamics of snow crab (Chinoecetes opilio) in the Eastern Bering Sea - putting together the pieces of the puzzle. Bulletin of Marine Science 86:

Peck L, Webb K, Miller A, et al (2008) Temperature limits to activity, feeding and metabolism in the Antarctic starfish Odontaster validus. Mar Ecol Prog Ser 358:181–189. https://doi.org/10.3354/meps07336

Pecquerie L, Drapeau L, Fréon P, et al (2004) Distribution patterns of key fish species of the southern Benguela ecosystem: an approach combining fishery-dependent and fishery-independent data. African Journal of Marine Science 26:115–139. https://doi.org/10.2989/18142320409504053

Pedersen EJ, Link H, Thompson PL, et al (2017) Signatures of the collapse and incipient recovery of an overexploited marine ecosystem. Royal Society Open Science 4:170215. https://doi.org/10.1098/rsos.170215

Persson L, De Roos AM (2006) Food-dependent individual growth and population dynamics in fishes. Journal of Fish Biology 69:1–20. https://doi.org/10.1111/j.1095-8649.2006.01269.x

Pike GC (1962) Migration and Feeding of the Gray Whale (*Eschrichtius gibbosus*). J Fish Res Bd Can 19:815–838. https://doi.org/10.1139/f62-051

Pinsky ML, Selden RL, Kitchel ZJ (2020) Climate-Driven Shifts in Marine Species Ranges: Scaling from Organisms to Communities. Annual Review of Marine Science 12:153–179. https://doi.org/10.1146/annurev-marine-010419-010916

Pörtner HO, Langenbuch M, Michaelidis B (2005) Synergistic effects of temperature extremes, hypoxia, and increases in CO2 on marine animals: From Earth history to global change. Journal of Geophysical Research: Oceans 110:. https://doi.org/10.1029/2004JC002561

Punt AE, Castillo-Jordan C, Hamel OS, et al (2021) Consequences of error in natural mortality and its estimation in stock assessment models. Fisheries Research 233:105759

Punt AE, Dunn A, Þór Elvarsson B, et al (2020) Essential features of the next-generation integrated fisheries stock assessment package: A perspective. Fisheries Research 229:. https://doi.org/10.1016/j.fishres.2020.105617

Punt AE, Ortiz I, Aydin KY, et al (2016) End-to-end modeling as part of an integrated research program in the Bering Sea. Deep Sea Research Part II: Topical Studies in Oceanography 134:413–423. https://doi.org/10.1016/j.dsr2.2015.04.018

Queiros Q, Saraux C, Dutto G, et al (2021) Is starvation a cause of overmortality of the Mediterranean sardine? Marine Environmental Research 170:105441. https://doi.org/10.1016/j.marenvres.2021.105441

Quinn TJ (2003) Ruminations on the development and future of population dynamics models in fisheries. Natural Resource Modeling 16:341–392. https://doi.org/10.1111/j.1939-7445.2003.tb00119.x

Raposo De Magalhães C, Schrama D, Farinha AP, et al (2020) Protein changes as robust signatures of fish chronic stress: a proteomics approach to fish welfare research. BMC Genomics 21:309. https://doi.org/10.1186/s12864-020-6728-4

Raverty S, Duignan P, Greig D, et al (2024) Gray whale (Eschrichtius robustus) post-mortem findings from December 2018 through 2021 during the Unusual Mortality Event in the Eastern North Pacific. PLOS ONE 19:e0295861. https://doi.org/10.1371/journal.pone.0295861

Regular PM, Buren AD, Dwyer KS, et al (2022) Indexing starvation mortality to assess its role in the population regulation of Northern cod. Fisheries Research 247:106180. https://doi.org/10.1016/j.fishres.2021.106180

Regular PM, Kumar R, Varkey DA, et al (2025) Extending the Northern Cod (Gadus morhua) Assessment Model - Part II: Quantifying the Impact of Capelin and Seals

Reum JCP, Blanchard JL, Holsman KK, et al (2019) Species-specific ontogenetic diet shifts attenuate trophic cascades and lengthen food chains in exploited ecosystems. Oikos 128:1051–1064. https://doi.org/10.1111/oik.05630

Rideout RM, Morgan MJ, Lilly GR (2006) Variation in the frequency of skipped spawning in Atlantic cod (Gadus morhua) off Newfoundland and Labrador. ICES Journal of Marine Science 63:1101–1110. https://doi.org/10.1016/j.icesjms.2006.04.014

Rideout RM, Rose GA, Burton MPM (2005) Skipped spawning in female iteroparous fishes. Fish and Fisheries 6:50–72. https://doi.org/10.1111/j.1467-2679.2005.00174.x

Rikardsen AH, Amundsen P-A, Knudsen R, Sandring S (2006) Seasonal marine feeding and body condition of sea trout (Salmo trutta) at its northern distribution. ICES Journal of Marine Science 63:466–475. https://doi.org/10.1016/j.icesjms.2005.07.013

Robertson MD, Cadigan NG, Nirmalkanna K, Wheeland LJ (2025) Impact of starvation-induced mortality on the collapse and lack of recovery of American plaice on the Newfoundland Grand Banks. Canadian Journal of Fisheries and Aquatic Science 82:1–14. http://dx.doi.org/10.1139/cjfas-2024-0216

Roques S, Deborde C, Richard N, et al (2020) Metabolomics and fish nutrition: a review in the context of sustainable feed development. Reviews in Aquaculture 12:261–282. https://doi.org/10.1111/raq.12316

Rose GA, O'Driscoll RL (2002) Capelin are good for cod: Can the northern stock rebuild without them? ICES Journal of Marine Science 59:1018–1026. https://doi.org/10.1006/jmsc.2002.1252

Rose GA, Rowe S (2024) Northern cod re-establish historical migration patterns linked to capelin: insights from pop-up satellite archival tags. Can J Fish Aquat Sci. https://doi.org/10.1139/cjfas-2023-0172

Rose GA, Walters CJ (2019) The state of Canada's iconic Northern cod: A second opinion. Fisheries Research 219:105314. https://doi.org/10.1016/j.fishres.2019.105314

Rose KA, Holsman K, Nye J, et al (2024) Advancing bioenergetics-based modeling to improve climate change projections of marine ecosystems. Mar Ecol Prog Ser 732:193–221. https://doi.org/10.3354/meps14535

Sadoul B, Geffroy B (2019) Measuring cortisol, the major stress hormone in fishes. Journal of Fish Biology 94:540–555. https://doi.org/10.1111/jfb.13904

Schulte PM (2015) The effects of temperature on aerobic metabolism: towards a mechanistic understanding of the responses of ectotherms to a changing environment. Journal of Experimental Biology 218:1856–1866. https://doi.org/10.1242/jeb.118851

Schwalme K, Chouinard GA (1999) Seasonal dynamics in feeding, organ weights, and reproductive maturation of Atlantic cod (*Gadus morhua*) in the southern Gulf of St Lawrence. ICES Journal of Marine Science 56:303–319. https://doi.org/10.1006/jmsc.1999.0458

Scott F, Blanchard JL, Andersen KH (2014) mizer: an R package for multispecies, trait-based and community size spectrum ecological modelling. Methods in Ecology and Evolution 5:1121–1125. https://doi.org/10.1111/2041-210X.12256

Sheridan JA, Bickford D (2011) Shrinking body size as an ecological response to climate change. Nature Clim Change 1:401–406. https://doi.org/10.1038/nclimate1259

Sherwood GD, Rideout RM, Fudge SB, Rose GA (2007) Influence of diet on growth, condition and reproductive capacity in Newfoundland and Labrador cod (Gadus morhua): Insights from stable carbon isotopes. Deep Sea Research II 54:2794–2809. https://doi.org/10.1016/j.dsr2.2007.08.007

Shoup DE, Wahl DH (2011) Body Size, Food, and Temperature Affect Overwinter Survival of Age-0 Bluegills. Trans Am Fish Soc 140:1298–1304. https://doi.org/10.1080/00028487.2011.621812

Sibly RM, Grimm V, Martin BT, et al (2013) Representing the acquisition and use of energy by individuals in agent-based models of animal populations. Methods in Ecology and Evolution 4:151–161. https://doi.org/10.1111/2041-210x.12002

Siikavuopio SI, Whitaker RD, Sæther BS, et al (2017) First observations of temperature tolerances of adult male snow crab (*Chionoecetes opilio*) from the Barents Sea population and the effects on the fisheries strategy. Marine Biology Research 13:744–750. https://doi.org/10.1080/17451000.2017.1313989

Sinclair BJ, Marshall KE, Sewell MA, et al (2016) Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? Ecology Letters 19:1372–1385. https://doi.org/10.1111/ele.12686

Smith ADM, Brown C, Bulman C, et al (2011) Impacts of fishing low-trophic level species on marine ecosystems. Science 333:1147–1150

Smith RL, Paul AJ, Paul JM (1990) Seasonal changes in energy and the energy cost of spawning in Gulf of Alaska Pacific cod. Journal of Fish Biology 36:307–316. https://doi.org/10.1111/j.1095-8649.1990.tb05611.x

Soares M, Regular PM, Cadigan NG, Robertson MD (In Press) Assessing ecosystem-scale synchrony in Atlantic cod body condition. Canadian Journal of Fisheries and Aquatic Science. https://doi.org/10.1139/cjfas-2025-0171

Soledade Lemos L, Burnett JD, Chandler TE, et al (2020) Intra- and inter-annual variation in gray whale body condition on a foraging ground. Ecosphere 11:e03094. https://doi.org/10.1002/ecs2.3094

Steingrund P, Clementsen DH, Mouritsen R (2009) Higher food abundance reduces the catchability of cod (*Gadus morhua*) to longlines on the Faroe Plateau. Fisheries Research 100:230–239. https://doi.org/10.1016/j.fishres.2009.08.002

Stewart JD, Durban JW, Fearnbach H, et al (2021) Survival of the fattest: linking body condition to prey availability and survivorship of killer whales. Ecosphere 12:e03660. https://doi.org/10.1002/ecs2.3660

Stewart JD, Joyce TW, Durban JW, et al (2023) Boom-bust cycles in gray whales associated with dynamic and changing Arctic conditions. Science 382:207–211. https://doi.org/10.1126/science.adi1847

Storey KB, Storey JM (2004) Metabolic rate depression in animals: transcriptional and translational controls. Biological Reviews 79:207–233. https://doi.org/10.1017/S1464793103006195

Szuwalski CS, Aydin KY, Fedewa E, et al (2023) The collapse of eastern Bering Sea snow crab. Science 382:306–310. https://doi.org/10.1126/science.adf6035

Szuwalski CS, Cheng W, Foy R, et al (2021) Climate change and the future productivity and distribution of crab in the Bering Sea. ICES Journal of Marine Science 78:502–515. https://doi.org/10.1093/icesjms/fsaa140

Travers M, Watermeyer K, Shannon LJ, Shin Y-J (2010) Changes in food web structure under scenarios of overfishing in the southern Benguela: Comparison of the Ecosim and OSMOSE modelling approaches. Journal of Marine Systems 79:101–111. https://doi.org/10.1016/j.jmarsys.2009.07.005

Trijoulet V, Fay G, Curti KL, et al (2019) Performance of multispecies assessment models: insights on the influence of diet data. ICES Journal of Marine Science. https://doi.org/10.1093/icesjms/fsz112

Vajas P, Wudrick A, West H, Eddy TD (2025) Increase in Harp Seal Ecosystem Role After the Cod Collapse in Newfoundland & Labrador. Fish and Fisheries 26:878–894. https://doi.org/10.1111/faf.70005

Verdolin JL (2006) Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behav Ecol Sociobiol 60:457–464. https://doi.org/10.1007/s00265-006-0172-6

Villegas-Amtmann S, Schwarz LK, Sumich JL, Costa DP (2015) A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. Ecosphere 6:art183. https://doi.org/10.1890/ES15-00146.1

Vollenweider JJ, Heintz RA, Schaufler L, Bradshaw R (2011) Seasonal cycles in whole-body proximate composition and energy content of forage fish vary with water depth. Mar Biol 158:413–427. https://doi.org/10.1007/s00227-010-1569-3

Von Biela V, Arimitsu M, Piatt J, et al (2019) Extreme reduction in nutritional value of a key forage fish during the Pacific marine heatwave of 2014-2016. Mar Ecol Prog Ser 613:171–182. https://doi.org/10.3354/meps12891

Ware DM (1975) Growth, Metabolism, and Optimal Swimming Speed of a Pelagic Fish. J Fish Res Bd Can 32:33–41. https://doi.org/10.1139/f75-005

Weerasekera SJWWMMP, Cadigan NG, Nirmalkanna K, et al (2024) Trends in population starvation mortality based on a spatiotemporal model of condition: Part 1: A case study of Atlantic cod on the Southern Grand Bank. Fisheries Research 278:107113. https://doi.org/10.1016/j.fishres.2024.107113

Wilson S, Patterson D, Moore J (2022) Intra- and inter-population variation in sensitivity of migratory sockeye salmon smolts to phenological mismatch. Mar Ecol Prog Ser 692:119–136. https://doi.org/10.3354/meps14070

Worm B, Hilborn R, Baum JK, et al (2009) Rebuilding Global Fisheries. Science 325:578–585. https://doi.org/10.1126/science.1173146

Yamamoto T, Yamada T, Kinoshita T, et al (2015) Effects of temperature on growth of juvenile snow crabs, (*Chionoecetes opilio*), in the laboratory. Journal of Crustacean Biology 35:140–148. https://doi.org/10.1163/1937240X-00002309

Yin MC, Blaxter JHS (1987) Escape speeds of marine fish larvae during early development and starvation. Mar Biol 96:459–468. https://doi.org/10.1007/BF00397963