PH.D. DISSERTATION PROPOSAL

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This is to certify that this student's PhD Supervisory Committee had read and approved the Ph.D. Dissertation Proposal titled: Quantifying and sustaining ecosystem services of mesopelagic fishes

Approval of Supervisory Committee:

POSITION	PRINTED NAME	SIGNATURE	DATE
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Re: (External) Re: General exam scheduling for June 7

Gordon Holtgrieve <gholt@uw.edu> Mon, May 22, 2023 at 4:38 PM
To: Amy Maas <amy.maas@bios.edu>
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It seems I am unable to modify the .pdf. Please use this email as my approval. Gordon

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Quantifying and sustaining ecosystem services of mesopelagic fishes

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Doctoral proposal

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Background and motivation

Ecosystem services are the traits, processes and functions provided by the non-human natural world that support human wellbeing (Costanza et al. 2017). Some processes and functions in ecosystems exist regardless of their impact on humans, but the processes defined as ecosystem services are specifically those that directly or indirectly relate to and benefit humans. Given that the oceans cover roughly 70% of the planet's surface and constitute the vast majority of livable habitat on earth, marine ecosystems contribute greatly to global ecosystem services (Millennium Ecosystem Assessment, 2005).

The most abundant fishes in the world ocean, mesopelagic fishes, contribute to all major categories of marine ecosystem services: provisioning, regulating, supporting and cultural services (Millennium Ecosystem Assessment, 2005). Provisioning services are the direct benefits that nature provides to humans in the form of products that can be easily traded in our markets, such as mesopelagic fish that can be caught and sold on the market for use in fishmeal or nutritional supplements (Institute of Marine Research, 2017). Regulating services are the benefits humans obtain from the regulation of ecosystem processes such carbon transport by mesopelagic fishes, which are claimed to contribute to carbon sequestration and thus potentially provide some climate mitigation benefit (Saba et al. 2021). Supporting services include energy transfer from lower to upper trophic levels such as by mesopelagics and other forage fish (Iglesias et al. *in prep*, Essington and Munch 2014). Cultural services are the spiritual, recreational, aesthetic, and mental health benefits of nature to humans, which can be the most challenging to assign a specific value to in economic valuation (Kadykalo et al. 2019). Deep sea fishes have cultural value as evidenced by the fascination associated with these seemingly alien life forms, and their memorable appearance in nature documentaries and films.

Mesopelagic fish are among the few highly abundant fishes not yet commercially exploited (Hidalgo & Browman 2019), but there is a potential trade-off between their potential provisioning services and their regulating and supporting ecosystem services. Past attempts to commercially harvest mesopelagic fish have been unsuccessful due to low profit margins (Prellezo 2019, Standal & Grimaldo 2020). Recently, there has been renewed interest in commercially harvesting them for fishmeal and other products due to technological advancements and increased demand for seafood-derived products (Institute of Marine Research, 2017, Hidalgo and Browman, 2019, Standal and Grimaldo 2020). Meanwhile, there are concerns that large-scale commercial fishing could threaten the ecosystem services these fish provide. Because total high seas carbon capture and storage has been valued at $74–222 billion per year (Rogers et al. 2014), even a small contribution by mesopelagic fish would equate to substantial economic value to their regulating service. Additionally, mesopelagic fishes provide valuable supporting services as prey for larger harvested species (Beamish et al. 1999, Potier et al. 2007), marine mammals (Pusineri et al. 2007, Rivière et al. 2019) and seabirds (Watanuki & Thiebot 2018).

The potential impacts of mesopelagic fisheries on these ecosystem services are not well known. Preliminary efforts to consider implications before harvest begins have recommended a precautionary approach (Glover et al. 2018, Cavan & Hill 2022, Wright et al. 2020), but this approach may not provide the justification and funding to collect information needed to judge impacts. In the long-term, ecologically precautionary approaches can avoid exploitation that may be unsustainable, and allow time for scientific research and impact assessments to identify potential impacts before those impacts occur. However, in the short-term, precautionary approaches may also carry high opportunity costs for other human benefits, such improved food security from going forward with fishing. Management strategies to steward this vast marine resource have not yet been evaluated, as experimental fisheries are relatively new (Hidalgo & Browman 2019, Standal & Grimaldo 2020). Therefore, management guidance to support the potential growth of these future large-scale fisheries will be timely.

This dissertation aims to provide a better understanding of the ecosystem services that these fishes provide, as a proactive effort to consider the implications of harvest is needed to inform cost-benefit analyses of their future exploitation. Specifically, I will quantitatively evaluate the role of mesopelagic fish in providing two ecosystem services: their regulating services as transporters of carbon from surface waters into the deep sea, and their supporting services as prey for other marine species. I will also investigate the potential pathways for development of mesopelagic fisheries, a potential provisioning service as an input to human food systems.

Chapter 1: Quantifying sources of uncertainty in fish-mediated carbon transport estimates

Introduction

The ocean absorbs about a quarter of anthropogenic carbon dioxide emissions (Friedlingstein et al. 2021). The ocean's solubility pump is responsible for roughly two thirds of this absorption (Volk and Hoffert, 1985), in which carbon dioxide is chemically dissolved as dissolved inorganic carbon (DIC) and then the large ocean circulation system physically transports some of that DIC into the ocean's interior. The biological carbon pump is thought to be responsible for the remaining carbon transport from surface waters into the deep sea (Volk & Hoffert 1985). Active carbon transport is known to be an important mechanism within the biological carbon pump, but the magnitude of active transport and its drivers are uncertain. Active transport is largely driven by diel vertical migration (Davison et al. 2013, Boyd et al. 2019). Every night, billions of organisms swim up to the productive epipelagic zone (0–200 m) to feed. During the day, they dive back down to the mesopelagic zone (200–1000 m) to hide from visual predators (Klevjer et al. 2016). At depth, these migrating organisms release carbon through respiration, egestion, excretion, and mortality (Steinberg et al. 2000, Davison et al. 2013). While the contribution of zooplankton to active transport is fairly well understood (Ducklow et al. 2001), the contribution of fish, the dominant migrating nekton (Catul et al. 2011), is widely overlooked and a priority for biogeochemical cycling research (St. John et al. 2016).

We currently do not precisely know how mesopelagic fish contribute to regional carbon transport, which makes it difficult to evaluate ecosystem consequences of future mesopelagic fisheries. Mesopelagic fish may transport 10%-50% as much carbon as passive carbon transport (Williams & Koslow 1997, Hidaka et al. 2001, Davison et al. 2013, Ariza et al. 2015, Belcher et al. 2019, Hernández-León et al. 2019), but enormous uncertainties in fish-mediated transport impede our ability compare the value of different ecosystem services with any level of precision (Saba et al. 2021). St. John et al. (2016) therefore argue that a precautionary approach should be applied, limiting fisheries development until key uncertainties can be resolved. However, it is not clear which uncertainties are most important, and which can be easily resolved with current methods of measuring individual physiology, behavior, and metabolism.

Most studies of mesopelagic fish-mediated carbon transport (e.g., Davison et al. 2013) include a basic sensitivity analysis that varies parameters by some arbitrary factor higher or lower than the nominal parameter value, then re-calculates the final carbon transport estimate. However, this basic sensitivity analysis method does not formally propagate error for each parameter, and ignores the compounding uncertainty in the final estimate. There is also a need to better characterize sources of uncertainty in estimates to prioritize future empirical research efforts to constrain model estimates (Saba et al. 2021).

In this chapter, I used a fish bioenergetics and movement model to characterize the parameter uncertainty in estimates of fish-mediated carbon transport. Structural uncertainty (error associated with the underlying structure of the carbon transport model) is outside the study scope. Parameter uncertainty is defined as imprecision in the model output as a consequence of imprecise parameter inputs. If the output is fish-mediated carbon transport (indicated by the red arrow in Figure 1), then parameter uncertainty is caused by imprecise values describing the metabolic and ecological processes (indicated by the black arrows) used to calculate that transport. This analysis revealed the parameters to which the final estimate is most sensitive.

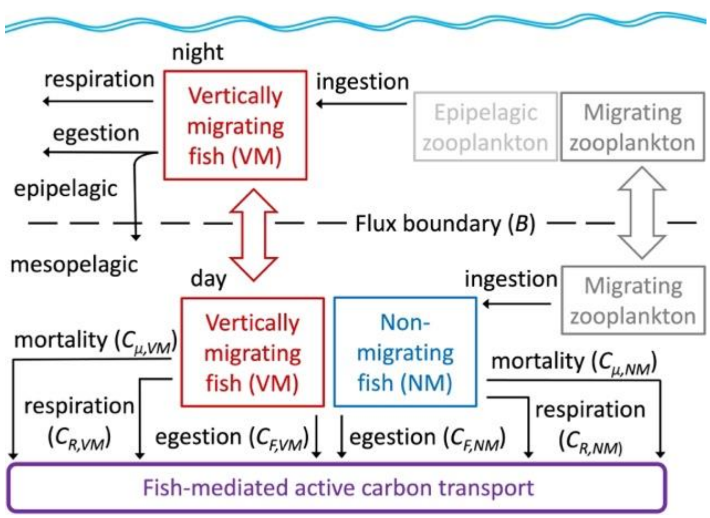

Figure. 1. Conceptual model of fish-mediated carbon transport. Black arrows indicate metabolic and ecological processes used to calculate carbon transport. Red and grey arrows represent vertical movement patterns. Boxes indicate carbon stores. Parameter descriptions are provided in Table S1. Excretion and specific dynamic action fluxes are not shown for simplicity. Carbon passing through non-migrating fish that originated from zooplankton of non-detrital origin is the only portion of non-migrating fish-mediated carbon transport that contributes toward total fish-

mediated carbon transport. Zooplankton are implicitly represented in the model in ingestion rates but shown here for clarity.

Objectives

The objective of my first chapter was to identify and quantify uncertainties associated with estimates of fish-mediated carbon transport. To address this objective, I (1) characterized precision and uncertainty in parameters used to calculated fish-mediated carbon transport, (2) propagated that parameter uncertainty to describe the uncertainty in carbon transport probabilistically, and (3) identified which parameter contributes most to the variance of estimated carbon transport.

Methods

To address the research questions for this objective, I first created a model of fish-mediated carbon transport using a basic bioenergetics model for individual fish. This individual fish model can be scaled up to the ecosystem level by multiplying carbon transported per individual of a given size by size-structured fish abundance estimates. This model was based on one of the most comprehensive estimates of fish-mediated carbon transport available (Davison et al. 2013). Davison et al. (2013) assume that carbon flow is governed by the metabolism, movement, release of fecal waste (egestion), and mortality by predation in the mesopelagic zone. Carbon transport was calculated based on allometric and temperature-dependent relationships with metabolic rate, along with estimated consumption, egestion, and excretion rates. Carbon transport was defined as the amount of carbon transported past a 150 m flux boundary via mortality, respiration, and release of waste that originated from near-surface primary production. The resulting model estimated milligrams of carbon transported by mesopelagic fish per meter squared per day from the epipelagic zone past the pre-determined flux boundary (Figure 1).

I explored uncertainty in the per capita rates, i.e., the carbon transported per individual, 1-gram mesopelagic fish. Models of fish-mediated carbon transport can be scaled to the ecosystem level by calculating the carbon flux per individual fish, and multiplying that flux by the total number of fish in each size bin. I calculated fish-mediated carbon transport using equations that trace carbon flow through these fish from the ingestion to either respiration, egestion, specific dynamic action, excretion, or mortality. Therefore, estimates were model-derived and not empirically measured, as direct measurements *in situ* of fish-mediated carbon transport have not been performed to date. Examining uncertainty of estimates on a per-capita basis allowed me to address the question of parameter uncertainty beyond known uncertainties of fish biomass (Proud et al. 2019).

We evaluated the uncertainty of each carbon transport parameter using a framework that systematically assigns an uncertainty level to each parameter based on previous knowledge (roughly similar to "Ecosense" routines in Aydin et al. 2007). Where there was little information in the literature about the feasible range of parameter values, nominal parameter values were given a coefficient of variation (CV) according to their assumed level of uncertainty. Where possible, an empirically determined CV or parameter range was assigned. After assigning appropriate probability distributions for each parameter, we propagated parameter uncertainty in the carbon transport using Monte Carlo simulations. In these simulations, we randomly sampled the plausible parameter space and calculated carbon flux for each sampled vector of model parameters. Finally, we partitioned the variance in the final estimate caused by each parameter, and determined the carbon transported via different bioenergetic pathways (specific dynamic action, respiration unrelated to digestion, mortality, excretion and egestion).

Results

Per capita fish carbon flux estimates varied over six-fold for both migrating and non-migrating fish. The parameters that carbon flux estimates were most sensitive to were the coefficients of the respiration rate regression and other respiratory parameters (e.g., respiratory quotient), and certain parameters related to the egestion flux of fecal waste (e.g., energy density of fecal pellets). The dominant carbon flux pathways for migrating fish were respiration and egestion, and the dominant carbon flux pathway for non-migrating fish was respiration. Scaling fish-mediated carbon flux estimates up to an ecosystem-level estimate requires biomass estimation, which could increase uncertainty by one to three orders of magnitude. We conclude that it is not currently possible to estimate fish-mediated carbon flux precisely, but that these estimates may be incrementally constrained in the future through dedicated empirical work on the most influential parameters.

Discussion

Results revealed that uncertainty is extremely high given current knowledge gaps in physiological and movement parameters of mesopelagic fishes. Certain parameters are conducive to further empirical work (e.g., energy density of fecal pellets), while other parameters would require technological advances for much more precise measurement (e.g., *in situ* respirometry for more precise respiration rate measurements). Though fish carbon flux cannot yet be estimated precisely, these estimates may be incrementally constrained in the future through dedicated empirical work on the most influential parameters to improve marine carbon cycle modelling.

Chapter 2: Carbon export by mesopelagic fishes during the North Atlantic spring bloom

Introduction

The relative contribution of mesopelagic fishes to the absorption, vertical transport and sequestration of carbon is highly uncertain both among and within regions (Saba et al. 2021). For instance, fish-mediated carbon transport rates vary by a factor of five within studies (Belcher et al. 2019, Hudson et al. 2014). Between studies, estimates of fish carbon transport vary from less than 0.1% to over 40% of gravitational carbon flux (Belcher et al. 2019, Hudson et al. 2014). This variation likely stems from fish biomass uncertainty, differences in sampling method, variation in how fish carbon transport is compared to other passive and active carbon transport mechanisms, and variation in bioenergetic and movement parameters.

Data from a recent cruise can offer unique insights into the relative importance of fish to the biological carbon pump. Mesopelagic fish abundance data is rarely collected alongside passive flux measurements. But in May 2021, the NASA EXPORTS project conducted a three-ship investigation of multiple passive and active carbon flux mechanisms. This chapter will take advantage of an opportunity to estimate the relative contribution of fish to carbon export in the North Atlantic. We will also demonstrate how feasible it currently is to reduce uncertainty in fish carbon flux rates by collecting additional measurements of their respiration rates via direct respirometry or electron transport system assays (a proxy for respiration rate measurements when direct respirometry is not feasible). Respiration rate regression coefficients were identified as the most influential parameters in per capita estimates of fish carbon flux (McMonagle et al., *in revision*). However, the impact of additional costly and time-intensive respiration rate measurements is unknown. Results will either reveal the extent to which fish contribute to carbon sequestration on climate-relevant time scales, or the barriers to converting from carbon transport rates to carbon sequestration rates using available physical oceanographic data outputs.

Findings from this chapter could have applications both in biogeochemical modeling and fisheries management. Marine biogeochemistry models often find a deficit of carbon in the mesopelagic zone given known carbon sources from surface waters (Burd et al. 2010), which may be due to the exclusion of fish and zooplankton from many of these models. The marginal contribution of fish to carbon flux beyond that of their zooplankton prey can be used to inform trade-off analysis between harvest and carbon transport. This study will also inform future research on the impact of additional respiration rate measurements on constraining uncertainty in fish carbon flux, which is relevant to improving carbon cycling models. Our analysis of carbon sequestration times will be relevant to fisheries management and to biogeochemical and climate modeling; concerns about the impacts of fishing to carbon sequestration are raised in debates and articles on harvesting mesopelagic fishes, but these claims have not yet been quantitatively assessed. This study site is near where some experimental mesopelagic fisheries have been proposed in the Northeast Atlantic (Standal & Grimaldo 2020, Schadeberg et al. 2021), so it may be a higher priority area in which to study the contribution of fish to carbon transport in case this ecosystem service should be impacted by a larger-scale commercial fishery.

Objectives

Utilizing a fish-mediated carbon transport model (Chapter 1), the goals of Chapter 2 are to 1) put fish-mediated carbon transport into context of other carbon transport mechanisms, 2) estimate the marginal contribution of fish beyond that of their zooplankton prey, 3) determine the impact of new empirical measurements on fish carbon transport estimates, and 4) examine how long carbon transported by fish is stored from the atmosphere.

Methods

To estimate mesopelagic fish-mediated carbon transport from the North Atlantic cruise data, we will pair fish abundance estimates from the cruise with a fish carbon transport model (Chapter 1). We utilized MOCNESS-10 and MOCNESS-1 net tows aboard the *R/V Sarmiento de Gamboa* and *R/V James Cook* to collect depth-stratified fish abundance and size distribution data, which will be scaled by estimated capture efficiency rates for these nets to estimate fish abundance. Acoustic data collected during this cruise will be used to constrain maximum depth of the fish vertical migration for use in the carbon transport model. We will propagate uncertainty in both the per capita fish carbon flux model and fish biomass data.

Leveraging results from other EXPORTS labs, we will place fish carbon flux estimates into context of total export via the biological pump. We will also estimate the marginal transport by fish beyond that of their zooplankton prey by considering the difference between per capita, daily fish carbon transport past a flux boundary to that which would otherwise be transported daily by the zooplankton that fish ingest each day. Zooplankton carbon flux studies are led by Dr. Deborah Steinberg and Dr. Amy Maas, and many others are estimating passive flux pathways.

To examine the impact of additional empirical measurements of fish carbon flux rates, we will incorporate new empirical data on fish respiration rates into the fish carbon flux model. We collected mesopelagic fish respirometry data at sea, and then back on shore we measured a proxy of respiration rate. This proxy method measures the maximum respiratory capacity of the electron transport system (ETS) in fish tissue. We will use Bayesian statistical methods to explore how additional data affects expected respiration rates and ultimately carbon flux rates.

To estimate carbon sequestration times of carbon transported by fish, we will estimate how much carbon is released at specific depths and in various forms (e.g. respired inorganic carbon or egested particulate organic carbon) and consider storage times for each carbon pool. We will use estimates of physical mixing in the eastern North Atlantic to estimate sequestration times for each carbon pool. Physical mixing model outputs could come from the literature (e.g., Siegel et al. 2021), or from cruise-specific data outputs from other EXPORTS labs (Working Group 4).

Application of results

Results of this chapter will inform our understanding of the role that fish play in the carbon cycle and how fish carbon transport estimates can be better constrained. This chapter will put fish-mediated carbon transport into context of other carbon transport pathways (e.g., zooplankton carbon transport and gravitational sinking of detritus) in a specific place and time, in terms of the magnitude of carbon transport at various flux boundary depths. For the first time, this fish carbon pathway will be discussed not only in terms of carbon transport but also in terms of carbon sequestration by considering sequestration time horizons at various depths at this study site. This chapter will also compare sources of uncertainty related to fish bioenergetics and movement (Chapter 1) with uncertainty related to fish biomass estimation, facilitating prioritization for empirical studies to further constrain estimates of fish carbon transport. Results from the respirometry experiments can be used to determine the impact of additional respiration rate measurements on constraining fish carbon transport estimates. Knowing the impact of these measurements can inform cost-benefit analysis of pursuing challenging measurements of highly influential parameters.

Chapter 3: A meta-analysis of the importance of mesopelagic prey fish in provisioning services for marine predators

Introduction

Mesopelagic prey fish are extremely abundant and highly nutritious (Alvheim et al. 2020), attracting scientific interest in the role that they play in supporting services for marine life and attracting commercial interest as potential fisheries. Median estimates of mesopelagic fish biomass range from about 1-16 billion metric tons (Kaartvedt et al. 2012, Irigoien et al. 2014, Proud et al. 2019), meaning they could make up 50% to 94% of total marine fish biomass if all other fish make up about one billion metric ton (Jennings et al. 2008; Wilson et al. 2009; Bianchi et al. 2021; Gjøsaeter , and Kawaguchi, 1980). Although mesopelagic fishes may generally have lower levels of proteins and digestible lipids than their epipelagic counterparts (Fernandez et al. 2014), some have been found to have similar energy densities than other epipelagic forage fish (Van Pelt et al. 1997, Fernandez et al. 2014). In any case, mesopelagic fishes contribute substantially to energy budgets of epipelagic fish, marine mammals and seabirds and have attracted interest as commercial fisheries for indirect human consumption (Connan et al. 2007, Cherel et al. 2010, Saunders et al. 2019, Standal & Grimaldo 2020).

Although mesopelagic fishes are abundant and attractive prey, there has been no synthesis to ask where and in which taxa do mesopelagic fish play large roles in feeding habits of epipelagic predators. One concern related to harvesting mesopelagic fishes is that they play an important role in marine food webs as forage fish, but currently these claims only cite individual studies on specific mesopelagic fish species or specific predator species in specific study sites. Little work has been done to synthesize these individual studies to draw quantitative conclusions about the role of mesopelagic fish as prey in marine food webs at large. This study will synthesize the role of these fishes in the food web of the study regions selected, reveal known predators of mesopelagic fishes, and demonstrate the prey fish species that those predators most rely on.

The collated data products that I create and the methods I use for this chapter could provide a useful resource for future studies on supporting services of mesopelagic fishes. A better understanding of mesopelagic fish supporting services will be important when determining the role that these fishes play in the supporting service of transferring energy from the base of the food web into upper trophic levels. Results can also be used in future research estimating the impacts of prey harvest on the harvest of their predators (Essington & Munch 2014).

Many have claimed that mesopelagic fish play important roles in food webs, but those claims often lack quantitative analysis at the entire food web scale (Silva et al. 2022). Understanding the extent that marine predators rely on mesopelagic species could help predict shifts in predator abundance and distribution as the abundance and distribution of mesopelagic fish prey changes due to climate-driven changes like deoxygenation (Koslow et al. 2011). Results will also be useful for future efforts to quantify the value of supporting services for these species in environmental economics frameworks. Ultimately, identifying trade-offs between utilizing mesopelagic prey fish for food production (for use in fishmeal, nutritional supplements, and other seafood-derived products) versus conserving them for supporting other top predators could be useful for policy decision-making processes that must consider different and sometimes competing environmental and economic goals. Federal protections for mesopelagic prey fish are currently being debated under the U.S. Magnuson-Stevens Act reauthorization; a better understanding of the role that specific forage fish groups play in supporting upper trophic levels is directly relevant to ongoing marine policymaking.

Objectives

The objectives of this chapter are to 1) assess the contribution of mesopelagic fish to marine predator diet by synthesizing information in existing marine food web models and regional-scale diet databases; and 2) use this meta-analysis to evaluate the hypothesis that mesopelagic fish are generally important components to predator diets, against the alternative hypothesis that their contribution varies substantially by geographic regions and predator type. . Using the greatest taxonomic resolution available in diet content data, this analysis will also 3) reveal which mesopelagic prey fish taxa are most prevalent in these predator diets.

Methods

I will review the literature and publicly available survey data, clean the data into a format that allows for cross comparison, and determine the predators that are most reliant on mesopelagic fishes and the prey species that are most prevalent in predator diets. Mesopelagic prey fish species will be defined as those that are generally small (less than 10 cm in total length), spend at least part of the day between 200-1000m, and primarily consume zooplankton as adults. The literature review will identify studies and datasets in which these mesopelagic prey fish are found in the diets of marine predators either by genetic or morphological identification. I will code prey data using the highest taxonomic resolution possible without sacrificing sample size. Different methods of prey identification can misrepresent the relative abundance of different prey taxa; for example, genetic identification may identify gelatinous, soft-bodied prey where morphological identification of hard parts (e.g., carapaces or otoliths) may underrepresent gelatinous prey species (Urban et al. 2021). In other cases, these seemingly disparate data streams have been combined for stomach content analysis and have in other cases been found to provide similar diet content results (Jargowsky et al. 2019). Potential error from multiple diet composition methods will be an unavoidable limitation of data collation. By comparing across available data, I will identify the most prevalent mesopelagic prey fish species in diets of marine predators and the predators that are most reliant on mesopelagic prey fishes in the regions with sufficient data coverage.

I will focus on regions where data is most available. Data sources I will consider include the NOAA Northwest Fisheries Science Center (NWFSC) trawl survey and two NOAA trawl surveys in 2006 and 2007 that specifically targeted mesopelagic fishes and squid in the Gulf of Alaska, the California Current Predator Diet Database (Szoboszlai et al. 2015), the NWFSC trawl survey, seabird diet data collated by Tim Jones (SAFS postdoctoral researcher) that includes over 40 data sources of mesopelagic fishes in the diets of over 60 seabirds, the MesopTroph database (Silva et al. 2022) and fish biomass and diet data from Ocean Twilight

Zone project cruises led by collaborators at WHOI. There are also many other individual publications from the literature that report on mesopelagic fishes in the diets of top predators like cetaceans and pinnipeds, some of which may contain sufficient diet composition data in the chosen region of interest (e.g., Potier et al. 2007, Beamish et al. 1999, Pusineri et al. 2006, and Rivière et al. 2019). Diet data will need to include some estimate of percent diet composition of mesopelagic prey fishes.

There are some inherent limitations of available diet content analysis data; for example, diet data is generally only a snapshot of the predator's feeding habits and may not be representative of their diets on longer time scales, or among conspecific predators with different prey preferences. Additionally, if predators feed selectively on specific types of prey, then the relative prey abundances assumed from the diets of top predators may be hyperstable. Other limitations include the challenges of determining prey taxa in partially digested stomach contents, which may cause overrepresentation of certain species over others for species that digest (or at least become unidentifiable) more quickly. Using genetically identified diet content data will help with this limitation of morphologically identified diet content data, but current datasets remain sparse.

Application of results

This study will produce a synthesis of all documented predator species of mesopelagic fishes in the chosen regions. This synthesis will be useful for future studies on the effects of changing mesopelagic fish abundance and distribution on other ecologically and commercially important species that rely on mesopelagic fishes.

Chapter 4: Potential challenges to developing mesopelagic fisheries and evaluating the performance of potential management strategies

Introduction

There has been growing interest over the past several decades to harvest mesopelagic prey fish for fishmeal and other products, but policy protections on these prey fish are limited, especially where they occur in the high seas. Norway and Pakistan have issued licenses to fish in the mesopelagic (The Economist, 2017), and recent studies have been published on the biological and economic viability of mesopelagic fisheries in the Bay of Biscay (Prellezo 2019) and in the waters of Denmark (Paoletti et al. 2021) and Norway (Standal & Grimaldo 2020). Experimental fisheries have operated in additional regions including India, South Africa, Iceland, and near Antarctica (Pauly et al. 2021). In U.S. waters in the Pacific, NOAA recently placed a moratorium on fishing mesopelagic fishes until further research has been conducted on the implications of commercial mesopelagic fisheries (Pacific Fisheries Management Council, 2019). In European waters, the European Commission's "Blue Growth Strategy" encourages future exploitation of mesopelagic resources (Hidalgo & Browman 2019).

Appropriate management of mesopelagic fisheries has not yet been established (Standal & Grimaldo 2020). Mesopelagic fisheries would have different challenges to developing a sustainable fishery compared to previous fisheries owing to their diel migratory behavior. Because they inhabit deep waters during daylight, mesopelagic fish are exposed to different threats than pelagic fisheries, including deoxygenation of midwaters, expanding oxygen minimum zones and pollution from future deep sea mining waste plumes. Furthermore, mesopelagic fish species aggregate together in deep scattering layers, which is distinct from the more structured, homogenous schools of some epipelagic forage fish. Mesopelagic fisheries would therefore be multi-species, with limited ability to select for productive stocks or avoid sensitive ones. To fill gaps in our understanding of the implications of various management options for harvesting mesopelagic fishes, I propose a data-limited management strategy evaluation for mesopelagic fishes. A data-limited management strategy evaluation for these understudied species can be used to shed light on the strengths and limitations of a spectrum of management options from a near moratorium on fishing to open access fisheries that are only self-regulated.

Objectives

One way to evaluate how these threats and uncertainties could be managed proactively is to consider the likely performance of alternative management strategies, trade-offs that each produces, and their robustness to key and unique threats to sustainable outcomes (Schindler & Hilborn 2015). The objectives of this chapter will be to 1) summarize unique challenges to developing sustainable mesopelagic fisheries, 2) evaluate the range of outcomes that might ensue as novel, data-limited fisheries develop under different regulatory frameworks, and 3) identify the regulatory and ecological contexts where each framework might be best or least well-suited.

Methods

To achieve these objectives, I will 1) gather information about the unique challenges for mesopelagic fisheries, 2) investigate the implications of an open access fishery, a spatially-managed fishery (with open and closed areas), an effort controlled fishery, or a moratorium on fishing, 3) identify the performance metrics used to evaluate performance of each harvest strategy, and 4) determine the conditions under which each of these harvest strategies leads to collapse of mesopelagic fisheries. The first task will be addressed using literature review and informal interviews with experts on mesopelagic fisheries (e.g., researchers within the ongoing EU-funded research projects MEESO and SUMMER). The second and third tasks will be addressed by creating a management scenario model that emulates those used for management strategy evaluation in data-limited fisheries and examining the results of various simulations.

The methods used for evaluating fishery development pathways will emulate a simplified management strategy evaluation framework. This includes an operating model, observation model, and management model. I will look to other data-limited management strategy evaluation models for inspiration, such as Data Limited Methods Toolkit (DLMtool), and then create a customized model designed specifically for evaluating mesopelagic fisheries development.

I will first establish an operating model that includes population dynamics of mesopelagic prey fish based on available life history data (including data collected by the WHOI OTZ project), fleet dynamics, and spatial structure of fish populations and management areas. The operating model would have only basic taxonomic detail and general spatial detail. The general, representative mesopelagic prey fish modeled would emulate the traits of the species that have attracted the most attention for commercial fisheries: abundant and lipid-rich myctophids (e.g., *Benthosema glaciale*) and sternoptychids (e.g., *Maurolicus muelleri*). The operating model will incorporate discrete, spatial management areas. The extent of spatial resolution would be areas such as “fjord” or “coastal upwelling regions”. Various management scenarios will be considered. For example, under a spatial management scenario, areas with similar biological and economic parameters to another could be used as a control, in which fishing is prohibited. This would allow comparison between the control areas and fished areas for distinguishing between fishing and other environmental impacts on fish abundance (e.g., changes over time in sea surface temperature, midwater oxygen concentrations, or predation). I will consider movement of the mesopelagic fishes between management areas to avoid misattribution of changes in abundance between the control areas and fished areas to either fishing or environmental drivers of mortality. Economic aspects in the operating model would include the price of the targeted mesopelagic fish per unit weight and the cost of fishing. The cost of fishing could change for many reasons including changes in fuel prices or changes in the efficiency of fishing technology due to future innovation.

I will then build an observation model that produces an index of abundance from annual survey data or catch per unit effort. Any abundance index would need to incorporate realistically high error in biomass estimation. I will consider hyperstability in the observation model, i.e., catch per unit effort may not reflect fluctuations in the population size. I will incorporate stochastic variation in fish populations over time that could be due to external drivers such as those related to climate change or predation. The management model would then work with the observation model to implement harvest control rules based on the index of abundance.

Application of results

This chapter will summarize challenges to fisheries management that are unique to mesopelagic fish, and the management strategy simulations will reveal the performance expected of each strategy as measured by biological and economic metrics. For example, unlike many epipelagic forage fish species, many mesopelagic fishes aggregate in low density, highly biodiverse deep scattering layers, which could lead to highly mixed stock fisheries or high bycatch. This poses sustainability issues because fishing could overexploit certain species that have greater vulnerability to fishing within that multi-species catch. Results of the development pathway simulations will reveal what biological and economic conditions or scenarios could lead to an overfished state for mesopelagic fisheries, based on assumptions made in the model.

Results related to specific challenges for sustainable mesopelagic fisheries would summarize threats to sustainable development, and results of the data-limited, management strategy evaluation model would reveal the conditions under which each management strategy would not be robust to preventing overfishing. For example, if mesopelagic fishes can easily become overfished under higher fishing efficiency, this could be of concern; technological innovation for capturing mesopelagic fishes or increased knowledge of hotspots (e.g., spawning aggregations) is likely to occur in early stages of exploration and can drastically change profitability. These management results would be dependent on the assumptions made. However, I will report results under a range of assumptions to examine how these management strategies perform under existing biological and economic uncertainty.

Timeline

Chapter or milestone	**Task**	**2019-2020**	**2020-2021**	**2021-2022**	**2022-2023**	**2023-2024**
Coursework	MS and PhD courses					
Ch 1: Uncertainty in fish-mediated carbon transport	Literature review, build model, sensitivity analysis, write paper					
Ch 2: Fish flux in N Atlantic	Field work, lab work, analysis, write paper					
Bypass	Prepare chapter 1 for submission, write bypass proposal					
Qualifying exam						
General exam						
Dissertation proposal	Write and submit dissertation proposal					
Ch 3: Supporting services of mesopelagic fish	Literature review, build model, write paper					
Ch 4: Harvest strategies for mesopelagic fish	Literature review, build model, write paper					
Dissertation defense						

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