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The Southern Gulf of St. Lawrence as Foraging Habitat for the North Atlantic Right Whale

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The spatial distribution of North Atlantic Right Whales (NARW, *Eubalaena glacialis*) on northwest Atlantic foraging grounds shifted in the early 2010s, with the southern Gulf of St. Lawrence (sGSL) becoming especially important for NARW since 2015. Recent DFO field- and model-based research is synthesized within this document to assess the sGSL as important habitat for the NARW, focusing on the foraging function. Three species of *Calanus* spp. copepods, the preferred prey for NARW, are seasonally abundant in the sGSL. During late fall and winter, when *Calanus* spp. are in diapause in deep water, *Calanus* spp. abundances are low in the sGSL. Transport from the adjacent Laurentian Channel, mainly via the Gaspé Current, resupplies the sGSL when *Calanus* spp. emerge from diapause and return to the surface layer in an active state. *Calanus hyperboreus* and *C. glacialis* are transported into the sGSL in circa March-July, and both transport and local production supply *C. finmarchicus* to the sGSL from circa March through summer and early fall. The magnitude of resupply depends on upstream concentrations and circulation patterns during the *Calanus* spp. active periods. Aggregation of copepods to high concentrations required for NARW feeding (i.e., on the order of 1000 individuals m⁻³ or greater) can occur through interactions of vertical movements and local circulation features or barriers (e.g., the seafloor). Dense near-bottom layers composed mainly of *C. hyperboreus*, with energy levels around the threshold for profitable NARW foraging, have been observed in the sGSL as early as mid-May, and dense mixed-species layers have been observed locally in the sGSL in summer. These observations and simulations indicate that the environmental, oceanographic, and bathymetric conditions of the sGSL can support and aggregate high concentrations of prey for NARW. Characterizing the processes driving distribution and dynamics of *Calanus* spp. in the sGSL provides a basis for assessing foraging habitat and its vulnerability to future environmental and circulation changes.

INTRODUCTION

The endangered North Atlantic Right Whale (NARW), *Eubalaena glacialis*, has been frequently observed in the southern Gulf of St. Lawrence (sGSL) since the mid-2010s (Meyer-Gutbrod et al. 2018, Crowe et al. 2021). Increases in sightings near Anticosti Island and acoustic detections in the western sGSL, off the Gaspé peninsula, have been observed since circa 2015 (Simard et al. 2019, Meyer-Gutbrod et al. 2023). This increase in usage of the GSL by the NARW is part of a large-scale shift in the distribution of this species in the 2010s (Davis et al. 2017, Meyer-Gutbrod et al. 2023) that has been linked to declines in abundance of its key prey, late stages of the copepod *Calanus finmarchicus*, in the Gulf of Maine (GOM), Bay of Fundy, and on the western Scotian Shelf during summer and fall (Record et al. 2019, Meyer-Gutbrod et al. 2021, 2023). From 2015 through 2019, Crowe et al. (2021) estimated that approximately 40% of the NARW population visited the GSL with a high degree of fidelity to the region. Most individuals in the GSL have been sighted in the southern GSL (Crowe et al. 2021).

Calanus spp. copepods are a crucial source of food for the NARW, which feed on their large, energy-rich late copepodite stages (e.g., Meyer-Gutbrod et al. 2015, Lehoux et al. 2020). Three species of *Calanus* occur on the western North Atlantic continental shelves, where the NARW is known to feed, including *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* (Conover 1988). On the northwest Atlantic shelves, the reproductive range of the boreal species, *C. finmarchicus*, extends to the Gulf of Maine in the south, whereas the reproductive range of arctic species *C. hyperboreus* and *C. glacialis* extends to the Gulf of St. Lawrence (Conover 1988, Sorochan et al. 2019). Individuals that occur downstream of these areas are considered expatriates (e.g., Sameoto and Herman 1992). *Calanus* spp. are collectively abundant relative to most other copepod taxa in the Northwest Atlantic (e.g., Pepin et al. 2015, Morse et al. 2017, Blais et al. 2023, Casault et al. 2023), and their large body size, compared to other abundant copepods, and capacity to accumulate storage lipid in their oil sacs (Lee et al. 2006) contribute to their biomass dominance in the mesozooplankton community (e.g., Head et al. 2003, Lehoux et al. 2020).

The NARW uses ram filtration to obtain food. Zooplankton enter the mouth and are filtered on baleen plates while the whale swims forward at a relatively constant speed of approximately 1 m s^{-1} (Werth 2004, van der Hoop et al. 2019). Zooplankton sampling near feeding NARW has indicated that NARW target layers of concentrated zooplankton including copepods (e.g., *C. finmarchicus*, *Pseudocalanus* spp., *Centropages typicus*) and juvenile krill in Cape Cod Bay in late winter and spring (Watkins and Shevill 1976, Mayo and Marx 1990), and primarily late-stage *C. finmarchicus* in Grand Manan Basin, the Great South Channel, and Roseway Basin in summer (e.g., Wishner et al. 1988, Beardsley et al. 1996, Baumgartner and Mate 2003). Foraging has been observed at the surface interface (e.g., Mayo and Marx 1990) and documented using archival tags throughout the water column, including near bottom (Baumgartner et al. 2017).

The NARW must consume massive quantities of copepods to satisfy its energy demands. Estimates of NARW energy consumption (approximately $1,500 \text{ MJ day}^{-1}$; Gavrilchuk et al. 2021) and late-stage *Calanus* energy content (approximately $10 \text{ J copepod}^{-1}$; Davies et al. 2012) indicate that a resting adult female NARW would need to consume approximately 150 million copepods each day. The energy demands of lactating females are approximately double that of resting females (Fortune et al. 2013, Gavrilchuk et al. 2021). In addition to NARW energy demand and prey energy content, conversion to a prey concentration threshold is dependent on clearance rate (i.e., volume of seawater filtered by the NARW per day). When these factors are considered together, it has been predicted that NARWs require sustained minimum *Calanus* spp. concentrations $> 1,000 \text{ m}^{-3}$ (10 kJ m^{-3}) and, in some scenarios, $> 10,000 \text{ m}^{-3}$ (100 kJ m^{-3} ;

Kenney et al. 1986, Fortune et al. 2013, Gavrilchuk et al. 2021). The spatial scale over which these concentrations are measured is important for appropriate interpretation of foraging conditions. Since NARWs use ram filtration to feed, an appropriate scale should be similar to that of the NARW head (e.g., approximately 2 m width; van der Hoop et al. 2019). Measurements of late-stage *Calanus* concentrations $> 1,000 \text{ m}^{-3}$ are rare in the ocean but are commonly made near feeding NARWs. Concentrations of *Calanus* spp. $> 10,000 \text{ m}^{-3}$ are exceptionally rare in the ocean, but occasionally observed near feeding NARWs (Wishner et al. 1988, Mayo and Marx 1990, Wishner et al. 1995, Beardsley et al. 1996, Baumgartner and Mate, 2003). A summary of concentrations of *C. finmarchicus* observed near feeding NARW was provided by Ross et al. (2023).

The formation of high concentrations of prey suitable for NARW foraging requires alignment of prey supply and aggregation at depths where they are available (i.e., prey layers occur at depths that are accessible to the NARW; Baumgartner et al. 2007, Sorochan et al. 2021a). Supply of prey is driven by a complex interaction of population dynamics and transport (e.g., Brennan et al. 2021, Le Corre et al. 2023). Local prey aggregations are formed from biophysical zooplankton accumulation mechanisms (e.g., Genin 2004). A Supply-Aggregation-Availability conceptual framework was established to improve the ability to predict where and when suitable NARW foraging habitat is likely to form on NARW foraging grounds (Figure 1; Sorochan et al. 2021a). This framework provides a conceptual model for understanding the multi-scale processes controlling NARW foraging habitat dynamics.

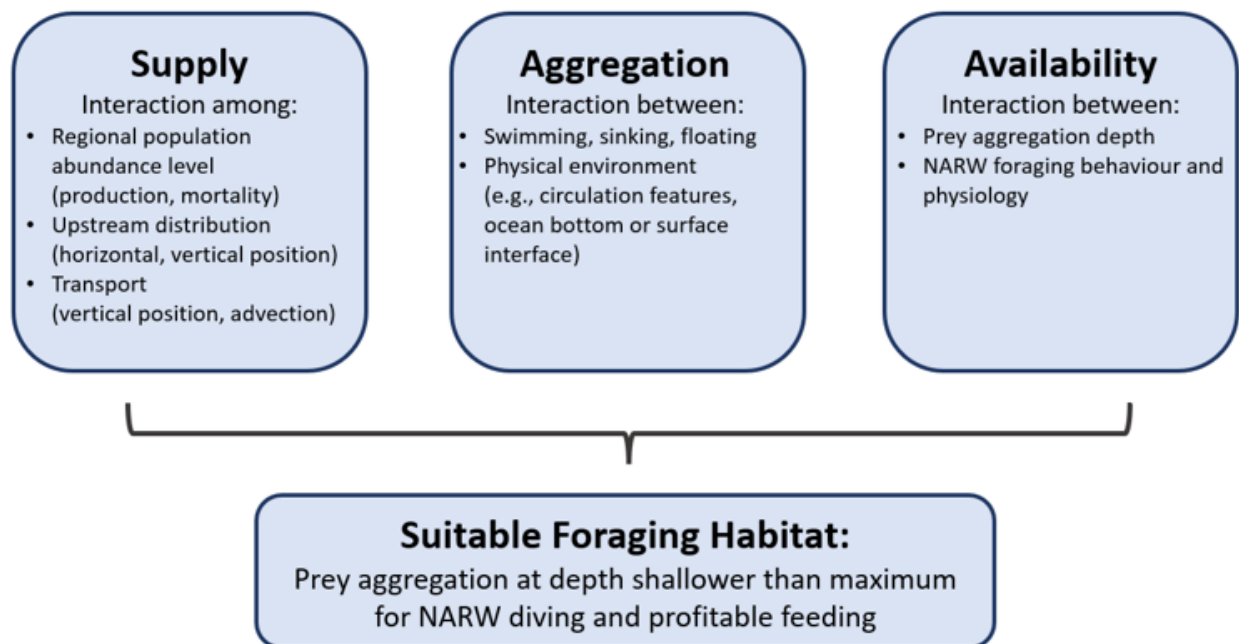


Figure 1. Schematic of the Supply-Aggregation-Availability conceptual model indicating that adequate supply and aggregation processes must align in locations where prey are available at depths that allow for profitable feeding (Sorochan et al. 2021a).

The objective of this document is to synthesize research and observations on the characteristics of NARW foraging habitat and the processes that drive its development and variability in the sGSL, where a 3-D climatology of historical *Calanus* spp. data indicates a high probability that suitable foraging habitat will form (Plourde et al. 2019). This information is needed to define important habitat for NARW in the sGSL, focusing on the foraging function, i.e., “Adult foraging and feeding,” and its primary feature, “Quantity and quality of prey” as identified in the DFO

NARW Action Plan (DFO 2021). The key attributes of the sGSL foraging habitat identified in the Action Plan include “Presence of sufficient quantities and quality CV [i.e., fifth copepodite stage] *Calanus finmarchicus* copepodites to support the population” and “Environmental, oceanographic and bathymetric conditions that support and aggregate concentrations of prey.” Prey composition, abundance, distribution, and quality of *Calanus* spp. in the sGSL is provided in this document. These characteristics are interpreted in the context of interactions between the life histories and annual production cycles of *Calanus* spp. and the environment in the GSL, including regional circulation and bathymetric features of the sGSL and adjacent areas. The uncertainties and risks to foraging habitat in the sGSL based on current understanding of *Calanus* spp. dynamics in the region are also identified.

SOUTHERN GULF OF ST. LAWRENCE

The sGSL is an expansive and relatively shallow shelf area bounded by the coasts of Québec, New Brunswick, Nova Scotia and the deep Laurentian Channel (Figure 2). Bottom depths are generally < 100 m, and bathymetry is characterized by shallow banks and multiple elongated troughs originating from the Laurentian Channel (Loring and Nota 1973). The majority of sGSL NARW detections have occurred in areas north of Prince Edward Island and west or south of the Magdalen Islands (Crowe et al. 2021). Passive acoustic monitoring from 2011-2018 has detected NARW upcalls from late April through mid-January (Simard et al. 2019), and discovery curves have indicated the presence of at least 50 individuals as early as June in 2018 and 2019 (Crowe et al. 2021).

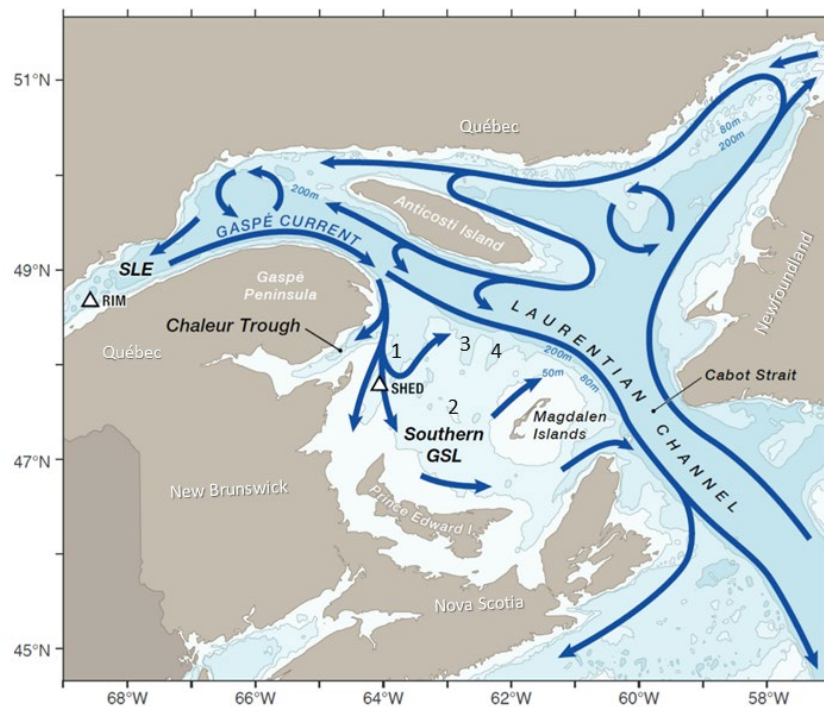


Figure 2. Map of the Gulf of St. Lawrence with schematic general patterns in ocean circulation. Time series stations sampled by the Atlantic Zone Monitoring Program are indicated as triangles (RIM – Rimouski time series station; SHED – Shediac Valley time series station; 1 – Shediac Valley; 2 Bradelle Bank; 3 – W. Bradelle Trough; 4 E. Bradelle Trough). SLE – St. Lawrence Estuary. Adapted from Sorochan et al. 2021a.

Flow fields in the sGSL are influenced by local forcing and circulation variability within the greater GSL, which is primarily driven by variations in freshwater input and wind (Lavoie et al. 2016, Brennan et al. 2021). Circulation in the sGSL is variable and generally characterized by inflow on the western side via the Gaspé Current, relatively weak and variable flows in the central region near Bradelle Bank, and outflow on the eastern side (e.g., El-Sabh 1976, Han et al. 1999, Lavoie et al. 2016). Inflow can also occur in the vicinity of the western and eastern Bradelle troughs, just west of the Magdalen Islands (e.g., El-Sabh 1976, Le Corre et al. 2023). Water properties and stratification are influenced by inputs from the northern GSL, especially the Gaspé Current, and local forcing including wind and tidal mixing, freshwater fluxes, and air-surface heat exchange (Koutitonsky and Bugden 1991). The sGSL is generally characterized by high near-surface temperatures relative to other areas in the GSL and spatial gradients in near-surface temperature and salinity that vary seasonally (Koutitonsky and Bugden 1991, Doyon and Ingram 2000). The Cold Intermediate Layer (i.e., the remainder of the winter surface mixed layer) occurs near the bottom in much of the sGSL in summer (Galbraith et al. 2023), and sea ice typically forms in winter (circa December through February) and persists until spring, receding in March and April (Galbraith et al. 2023). A phytoplankton bloom, dominated by diatoms, occurs in April (de Lafontaine et al. 1991, Blais et al. 2023, Laliberté and Larouche 2023). Analyses of surface chlorophyll concentration in the GSL indicate a maximum during the spring bloom in April, lower chlorophyll levels in spring and summer, and a smaller fall bloom in September (Blais et al. 2023). In the sGSL, elevated surface chlorophyll is typically widespread in April and highest on the western side in May through September (Doyon and Ingram 2000, Laliberté and Larouche 2023).

The zooplankton community in the sGSL varies seasonally and includes taxa derived from coastal and deepwater origins (e.g., Pepin et al. 2015, Debertain et al. 2018). Abundant copepods include *C. finmarchicus*, *C. hyperboreus*, *Pseudocalanus* spp., *Temora longicornis* and *Oithona* spp. (de Lafontaine et al. 1991, Runge et al. 1999, Paradis et al. 2012, Lehoux et al. 2020, Sorochan et al. 2021b, Blais et al. 2023). Euphausiids and meroplankton can be abundant at certain times of the year (de Lafontaine et al. 1991, McQuinn et al. 2015, Plourde et al. 2016). An analysis of the vertical distribution of biomass of dominant zooplankton in the sGSL indicated that variation in suitability of NARW foraging habitat in the sGSL is primarily governed by *Calanus* spp. (Lehoux et al. 2020). Other abundant zooplankton (e.g., *T. longicornis*, *Pseudocalanus* spp., euphausiids) may supplement the NARW diet, but their inferred biomass and energy contributions appear to be minimal relative to *Calanus* spp. (Lehoux et al. 2020). The importance of euphausiids as NARW prey is debatable since it is difficult to assess the abundance of this taxon using routine zooplankton sampling methods (i.e., vertical net tows and other net samplers without strobe lights). Euphausiid adult stages are strong swimmers that can avoid capture in plankton nets (Sameoto et al. 1993, Wiebe et al. 2004), and the extent to which euphausiids can avoid capture by the NARW during ram filtration feeding is uncertain.

Calanus spp. develop through thirteen stages, including the egg, six naupliar stages, and six copepodite stages (CI-CVI), the last of which (CVI) is the adult stage. The presence of interannually-predictable sufficient quantities of lipid-rich stage CV *C. finmarchicus* is a key attribute of the defined Canadian NARW critical habitats in the Bay of Fundy and on the western Scotian Shelf (DFO 2014). The *C. finmarchicus* CV stage is the diapausing stage for this species. Diapause is a state of suspended feeding, activity, development, and growth during which individuals migrate to deep water for a period of several months before resumption of development (Figure 3; Hirche 1998). If the water column is sufficiently deep, diapause allows copepods to temporarily escape unfavorable conditions in the upper water column and synchronize growth and development with periods of food availability (Hirche 1998). Most significantly for NARW foraging, *Calanus* spp. diapause stages are high in energy, because

individuals accumulate substantial quantities of lipids in their oil sacs prior to entering diapause (Figure 4). In the GSL, the *Calanus* spp. complex as a whole can be considered a key attribute in supporting the NARW population. In many parts of the GSL, *C. finmarchicus* is the most abundant of the three species on average (Blais et al. 2023). However, the relatively large body size of *C. hyperboreus* contributes substantially to biomass of *Calanus* spp. (e.g., Plourde et al. 2019), and *C. hyperboreus* is dominant in terms of biomass in deep areas (Sorochan et al. 2019). *Calanus glacialis*, which is slightly larger but morphologically similar to *C. finmarchicus* (Grainger 1961), is the least abundant of the three species throughout the GSL (Sorochan et al. 2019).

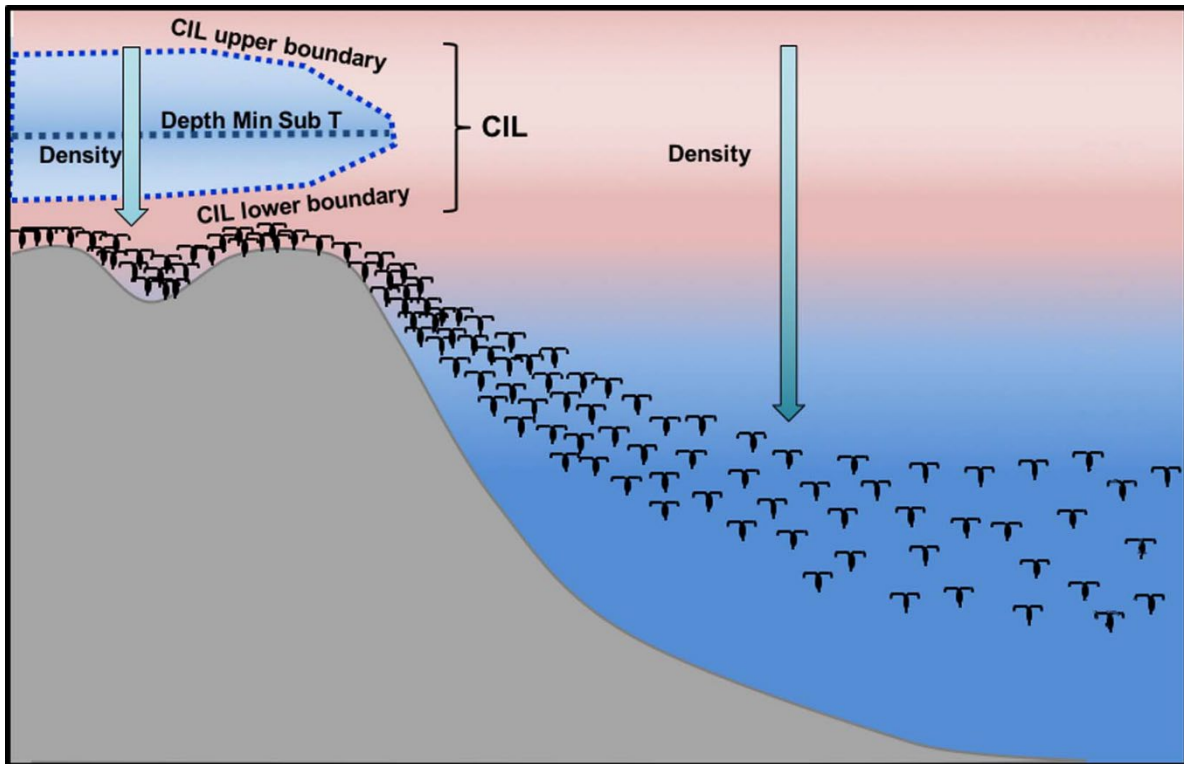


Figure 3. Schematic illustrating the vertical distribution of *Calanus* spp. in diapause on the shelf and slope in summer and fall and associated environmental variables and processes (from Krumhansl et al. 2018). *Calanus* spp. are adapted to enter diapause in relatively deep environments (hundreds of metres of water) as depicted on the right side of this schematic. CIL: Cold Intermediate Layer; Depth Min Sub T: Depth of minimum subsurface temperature.

All three species of *Calanus* have life cycles that include diapause, but the expression of diapause in their life histories differs among the species. *Calanus finmarchicus* have a mainly “income-breeding” reproductive strategy in which egg production is fueled by recent feeding following emergence from diapause, development from the CV to adult (CVI) stage, and migration to the surface layer (Diel and Tande 1992, Plourde and Runge 1993, Irigoien et al. 1998, Harris et al. 2000). In the GSL, *C. finmarchicus* produces eggs primarily during the spring bloom, but it can also continue development and produce multiple generations in a year (Ohman and Runge 1994, Plourde et al. 2001). In contrast, *C. hyperboreus* egg production occurs in deep water at the end of the diapause period, fueled by the lipid reserve built up by feeding in the previous year, known as a “capital-breeding” strategy (Lee 1974, Conover 1988, Smith 1990, Hirche and Niehoff 1996, Hirche 1997, 1998, Plourde et al. 2003). During the multi-year life cycle of *C. hyperboreus* in the GSL, diapause can occur at the fourth and fifth

copepodite and adult female stages (CIV, CV, and CVIf; CVI is the adult stage; Plourde et al. 2003). *Calanus glacialis* performs a hybrid of capital and income breeding, based on location and environmental conditions, with production fueled by stored lipid at the end of the diapause period or from ingestion (Hirche and Kattner 1993, Ringuette et al. 2002, Daase et al. 2013). A two-year life cycle is typical for *C. glacialis*, and diapause in the GSL likely occurs at the CIV and CV stages (Conover 1988, Falk-Peterson et al. 2009). All three *Calanus* spp. have the potential for plasticity in their life cycles across their broad geographical ranges, expressing different life cycle patterns in response to large scale environmental differences (e.g., Conover et al. 1988, Falk-Peterson et al. 2009). Life cycle plasticity means that their generation times can vary, with additional diapause stages added for longer multi-year generation times. Generation times tend to be longer in higher latitude environments for all three species (Conover et al. 1988, Falk-Peterson et al. 2009).

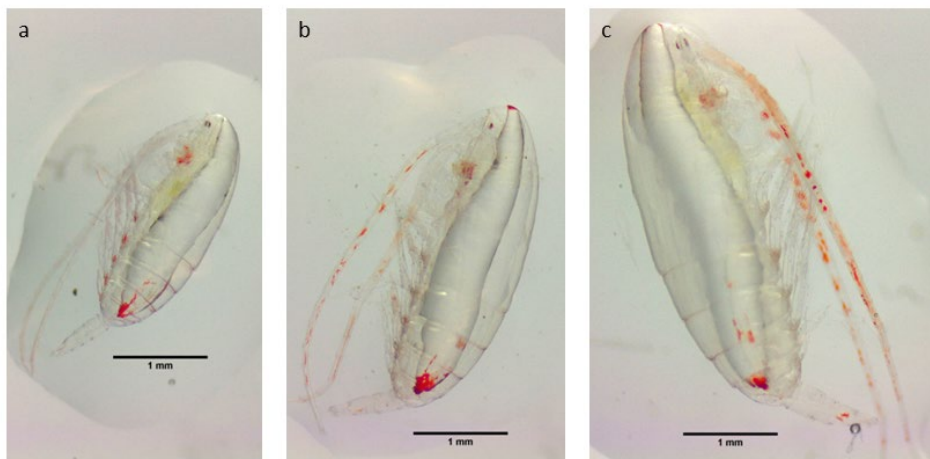


Figure 4. Primary diapausing stages of *Calanus* spp. in the southern Gulf of St. Lawrence, with lipid-filled oil sacs visible within the prosome — a. *Calanus finmarchicus* CV; b. *Calanus hyperboreus* CIV; c. *Calanus hyperboreus* CV. *Calanus glacialis* is morphologically similar to *C. finmarchicus* but slightly larger. (Images: DFO Science.)

The interaction between the timing of annual events in the life cycle of *Calanus* spp. (i.e., phenology) and environmental forcing (e.g., timing of phytoplankton bloom, temperature, ocean circulation) is a key element, along with upstream population level, that governs spatial and temporal variation in supply of these copepods to the sGSL and influences seasonal and horizontal variation in abundance (e.g., Brennan et al. 2021, Le Corre et al. 2023). Diapausing stages of the three *Calanus* spp. are adapted to overwinter at depths of hundreds of meters (Hirche 1998). In deep oceanic waters, vertical distributions can spread over a broad depth range from approximately 100 m to more than 1,000 m (e.g., Head and Pepin 2008). In shallower shelf waters, vertical distributions of diapausing *Calanus* spp. are shallower, more compact, and typically confined to deep basins and channels (Figure 3, Krumhansl et al. 2018, Melle et al. 2014). In both environments, diapausing *Calanus* spp., are typically distributed below the Cold Intermediate Layer (Krumhansl et al. 2018).

In shallow shelf environments like the sGSL, copepods attempting to diapause typically cannot survive through the overwintering period due to high mortality and physical losses (Slagstad and Tande 1996, Melle et al. 2004). Resupply of the shallow shelf with *Calanus* spp. in late fall and winter is inhibited by the deep distribution of *Calanus* spp. in upstream regions. When *Calanus* spp. emerge from diapause and return to the surface layer in spring, they may be transported into the sGSL from upstream sources, mainly located in the northwest and central GSL (e.g.,

Brennan et al. 2019, Le Corre et al. 2023). At the Shediac station in the sGSL, the depletion of *C. finmarchicus*, *C. hyperboreus*, and *C. glacialis* abundance in fall and winter and re-colonization in spring is apparent in changes in total copepodite abundance (Figure 5; Blais et al. 2023). However, there can be considerable interannual variation in abundance and biomass of *Calanus* spp. in the sGSL (Sorochan et al. 2019, Gavrilchuk et al. 2021).

The timing of active growth periods was estimated from annual changes in *Calanus* spp. stage proportions at the Rimouski and Shediac stations and vertical distribution of late-stage *Calanus* spp. copepodites at the Rimouski station. The timing of diapause onset at the Shediac station is evident in shifts of stage dominance from early copepodites (i.e., CI to CIV for *C. finmarchicus*, or CI to CIII for the arctic *Calanus* spp.) to diapausing stages (Figure 5). These metrics indicate that the estimated timing of active growth periods is circa March and July for *C. hyperboreus* and between circa March and September for *C. finmarchicus* (Johnson et al. 2008, Plourde et al. 2003, 2019, Brennan et al. 2019).

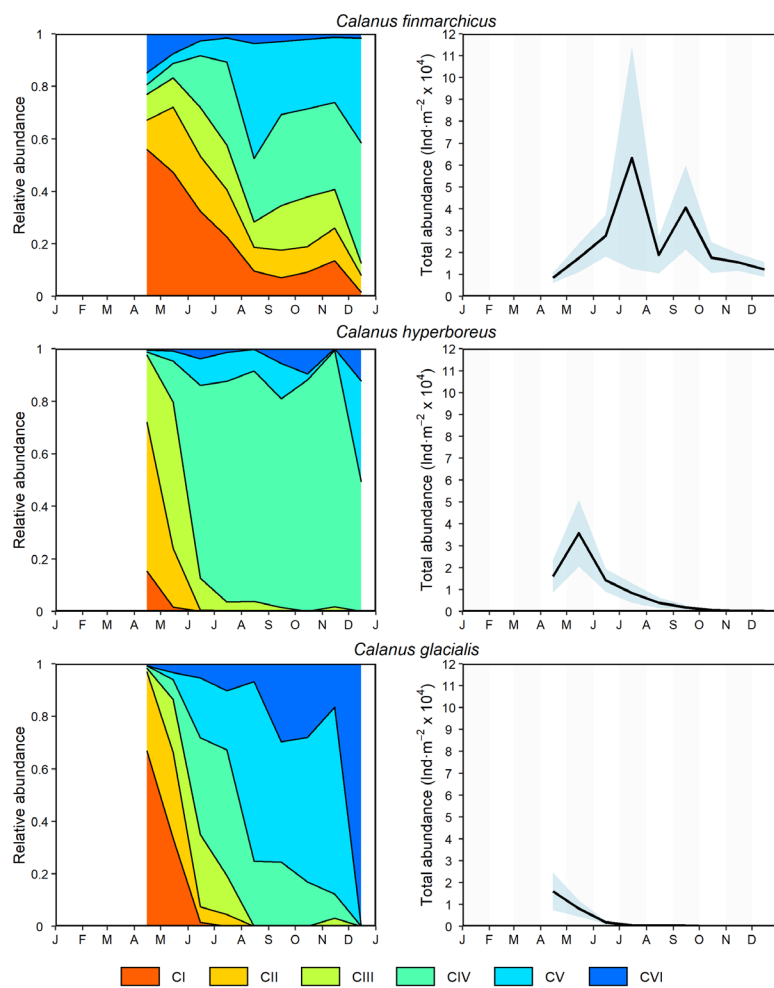


Figure 5. Climatological relative abundance of *Calanus* spp. copepodite stages CI-CVI at Shediac Valley station, based on Atlantic Zone Monitoring Program sampling during the years 1999-2020. Left column: relative proportions of copepodite stages I-VI; right column: annual variation in total abundance of copepodite stages I-VI, with 90% confidence interval indicated in blue shading.

SYNTHESIS

APPROACH

DFO Science has taken a multidisciplinary approach to examining characteristics of NARW foraging habitat in the sGSL and the multi-scale processes driving its development and variability. This paper reviews evidence from several DFO studies, in the context of published literature relevant to NARW foraging habitat, to develop a more comprehensive perspective on how supply and aggregation of *Calanus* spp. contribute to suitable foraging habitat in the shallow waters of the sGSL. This synthesis forms the basis to identify uncertainties and risks related to foraging habitat dynamics in the sGSL. Research has focused on the two most dominant *Calanus* spp., *C. finmarchicus* and *C. hyperboreus*, and this analysis will follow that approach as well. The synthesis presented in this document mainly reviews published DFO research, but a limited set of previously unpublished data analyses on prey layer concentration and energy density is also included. A brief overview of the main sources of information reviewed is provided below, with additional details provided in the subsequent sections.

Ocean observing by the DFO Atlantic Zone Monitoring Program (AZMP) provides data required to characterize annual-scale *Calanus* spp. population development and phenology, long-term variability in *Calanus* spp. regional population levels, and associated environmental conditions (Blais et al. 2023, Galbraith et al. 2023). High frequency time series stations provide data to assess annual variability patterns in the sGSL (Shediac Valley station, circa monthly sampling) and in upstream waters in the Lower St. Lawrence Estuary (Rimouski station, circa weekly sampling). Long-term interannual variability in zooplankton and environmental conditions is assessed using AZMP broadscale sampling across the GSL two times per year, in early summer and fall (Blais et al. 2023, Galbraith et al. 2023).

Temporal and spatial patterns of *Calanus* spp. and environmental variability from ocean observations provide clues for identifying and interpreting the processes that influence population dynamics and transport. These hypotheses can be tested using coupled 3-D *Calanus* spp. population models that combine *Calanus* spp. individual-based models (IBMs) with 3-D circulation models, and sometimes also incorporate biogeochemical models. Hypotheses about supply of *Calanus* spp. to the sGSL have been examined using coupled hindcast models (Brennan et al. 2019, 2021, Le Corre et al. 2023); details are provided below in the supply section.

Since ocean observing programs do not provide data at small spatial scales relevant to NARW prey aggregation (e.g., high-resolution vertical prey profiles), DFO led sampling missions in the sGSL to make observations of zooplankton in spring (May-June 2022), summer (August 2019), and fall (October 2018), aiming to characterize variation in NARW prey abundance and quality (Table 1, Figure 6). In addition, measurements of individual condition in *Calanus* spp. dominant diapausing stages were made at selected stations in the sGSL. Estimates of individual condition included biomass (individual dry weight) and direct measurements of energy from bomb calorimetry (weight-specific and individual-specific energy), which were used for energy density estimates. Different seasons were targeted to characterize variation in community composition and spatial (i.e., horizontal and vertical) distribution of *Calanus* spp. in different phases of their respective life cycles and different periods of NARW occupation of the sGSL.

Zooplankton sampling was conducted during day and night across a broad area of the western sGSL, including but not limited to the Chaleur and Shediac troughs and head of the western Bradelle Trough (Figure 6). The sampling strategy included surveying a semi-regular grid of stations, repeated sampling at select stations at scales of hours to weeks, and opportunistic sampling associated with NARW field operations (e.g., blow sampling and tagging).

Zooplankton sampling consisted of depth-stratified (MultiNet, ClosingNet, BIONESS) and depth-integrated (JackNet) oblique plankton net deployments to assess zooplankton vertical distribution and community composition at coarse scales (10s of km between stations, > 10 m vertical bins). Median species- and stage-specific depth-integrated abundances of *Calanus* spp. (individuals m⁻²) from JackNet deployments were reported in different sGSL subregions (Figure 6) to describe spatial variation for each sampling mission. In addition, a video plankton recorder (VPR) was used to quantify concentrations of late-stage *Calanus* copepodites, resolved to the taxonomic level of genus, at spatial scales relevant to NARW foraging (3 m vertical bins) along transects or at point locations (Table 1, Figure 6). Further methodological details are provided in the relevant sections below.

The following sections (Supply, Aggregation and Availability) incorporate information from these research projects to provide an overview of how the processes influence NARW prey variability and foraging suitability.

Table 1. Summary of zooplankton sampling from DFO missions in the southern Gulf of St. Lawrence. Mesh size of JackNet and BIONESS plankton nets was 333 µm and the MultiNet and ClosingNet was 200 µm. In each cell, N refers to the number of station occupations. BIONESS, Bedford Institute of Oceanography Net and Environmental Sampling System; VPR, Video Plankton Recorder; MMO, Marine Mammal Observation.

Mission (Date)	Sampling Gear	Calorimetry	NARW Observation
Spring 2022 (24 May-9 June)	JackNet (N = 26) MultiNet (N = 39) ClosingNet (N = 26) VPR (N = 27)	N = 16	MMO Tagging Operations
Summer 2019 (9 August-1 September)	JackNet (N = 57) VPR (N = 34)	N = 19	MMO Tagging Operations
Fall 2018 (14-23 October)	JackNet (N =24) BIONESS (N = 8) VPR (N = 12)	N = 0	MMO

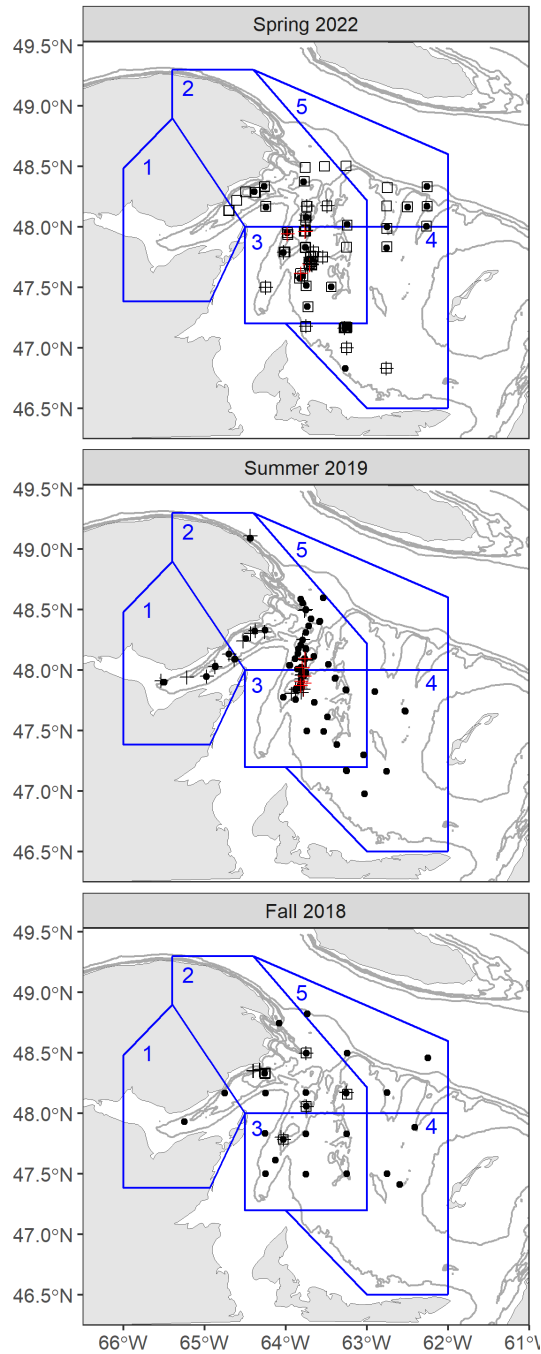


Figure 6. Zooplankton sampling from missions in spring 2022, summer 2019, and fall 2018. Black dots indicate depth-integrated sampling (JackNet). Open squares indicate depth stratified sampling (BIONESS, MultiNet, or ClosingNet; see Table 1). Crosses indicate video plankton recorder (VPR) deployments and red crosses indicate VPR deployments associated with NARW sightings (see “Synthesis” section). Polygons indicate subregions (modified from Le Corre et al. 2023) corresponding to reporting of depth-integrated abundance (1, Chaleur; 2, Gaspé; 3, Central west; 4, Central east; 5, Channel).

SUPPLY

Regional Population Levels

Prey supply reflects the overall population level within and proximate to areas where suitable foraging habitat may form. A major factor influencing supply is regional population level, which can be assessed on the northwest Atlantic shelves using AZMP ocean monitoring data. There has been a broadscale change in the zooplankton community across the Canadian northwest Atlantic shelves starting in about 2012, generally characterized by lower abundances of *C. finmarchicus* and higher abundances of non-copepods, and by higher abundances of total copepods in some areas, reflecting an increase in the abundances of small zooplankton species (DFO 2023). This change was concurrent with widespread above-average temperatures in surface and deep water that started in about 2012 (DFO 2023). Regional population declines in the GOM and on the Scotian Shelf were particularly notable (Sorochan et al. 2019). In the main source regions for the sGSL, the northwest and central GSL, *C. finmarchicus* abundance has been mainly lower in the 2010s and early 2020s than in the 2000s, with extreme low abundances in 2015 (Blais et al. 2023). In these regions, *C. hyperboreus* abundance demonstrates high interannual variability without a clear trend between decades, and low abundances in the early 2020s (Blais et al. 2023). *Calanus hyperboreus* population dynamics in these areas are influenced by the timing of ice melt and the spring phytoplankton bloom, in addition to temperature (Lehoux et al. 2021, Blais et al. 2023). The timing of *C. finmarchicus* population development has shifted earlier in the northwest GSL since observations began in the 1990s (Blais et al. 2023, Lehoux et al. 2021), with potential impacts on the timing and pathways of advection into the sGSL.

Advective Supply

In productive shallow shelf areas like the sGSL, where *Calanus* abundance becomes depleted during the fall and winter months, transport is required to resupply *Calanus* when they emerge from diapause and migrate to the surface layer. The amount and spatial distribution of *Calanus* spp. advected into the sGSL is influenced by upstream concentrations in the source regions, *Calanus* spp. phenology, particularly the timing of their productive period in surface waters, and the local circulation dynamics during their active period. In general, *Calanus* spp. are transported into the sGSL from deep adjacent Laurentian Channel areas, mainly in the northwest and central GSL, frequently via the Gaspé Current (Zakardjian et al. 2003, Maps et al. 2011, Brennan et al. 2019, 2021, Le Corre et al. 2023). Since horizontal current velocities are typically highest in surface water, and diapausing individuals of *Calanus* spp. in the Laurentian Channel are too deep to be transported into the sGSL, the interaction between the timing of *Calanus* spp. active development in the surface layer and circulation dynamics is critical for advective supply to the sGSL.

The effect of interactions between phenology and advection is evident in seasonal changes in *Calanus* spp. relative abundance, stage composition, and horizontal distribution patterns during AZMP and foraging habitat missions in the sGSL. As noted above, the presence of *Calanus* spp. early copepodite stages is an indicator of active development and production in the surface layer. The presence of *C. hyperboreus* early stages in April to June at the Shediac Valley station indicates activity and production only early in the year; *C. glacialis* exhibits a similar pattern (Figure 5). In contrast, the presence of *C. finmarchicus* early stages throughout the sampling season from April to December is consistent with both advection into the sGSL and ongoing production within the region from spring through fall (Figure 5). At the Shediac Valley station, *C. hyperboreus* is on average the most abundant species from April to June, and *C. glacialis* is the second most abundant species in April, reflecting an early-season advective pulse of the arctic

Calanus spp. with an earlier phenology into the Shediac Valley (Figure 5). After June, *C. finmarchicus* is the most abundant species at the Shediac Valley station, followed by *C. hyperboreus*; *C. glacialis* is nearly absent (Figure 5). However, these seasonal patterns can differ in individual years. During the foraging habitat mission in spring 2022 (mid-May to mid-June), the overall abundance of *C. finmarchicus* across the study region was already higher than *C. hyperboreus* and *C. glacialis*, including in the center west area that includes the Shediac Valley station (Figure 7). *Calanus finmarchicus* was also the most abundant species during summer and fall missions (Figure 7). Observations of *Calanus* spp. abundance, composition and stage structure, including a shift in dominance of late-stage copepodites from *C. hyperboreus* in spring to *C. finmarchicus* in summer (albeit in different years), are consistent with the documented phenology of *Calanus* spp. from the Shediac Valley time series station (Figure 5; Blais et al. 2023) and analyses of broadscale survey data in the sGSL from June and August-September (Lehoux et al. 2020). The interpretation that *C. hyperboreus* and *C. glacialis* are supplied through advection to the sGSL only in the spring (circa March to July) while *C. finmarchicus* is supplied through both advection and local production over a longer period, circa March to September, is supported by the contrasting overall abundances and horizontal distributions observed for the two species in the sGSL in fall 2018. During the fall 2018 mission, the horizontal distribution of *C. finmarchicus* abundance was widespread and highly variable, whereas abundances of *C. hyperboreus* and *C. glacialis* were highest on the eastern side of the sampling domain, in the central sGSL (Sorochan et al. 2021b, Figure 7). These observations are consistent with ongoing supply of *C. finmarchicus* and negligible supply of *C. hyperboreus* and *C. glacialis* in summer and fall (Sorochan et al. 2021b).

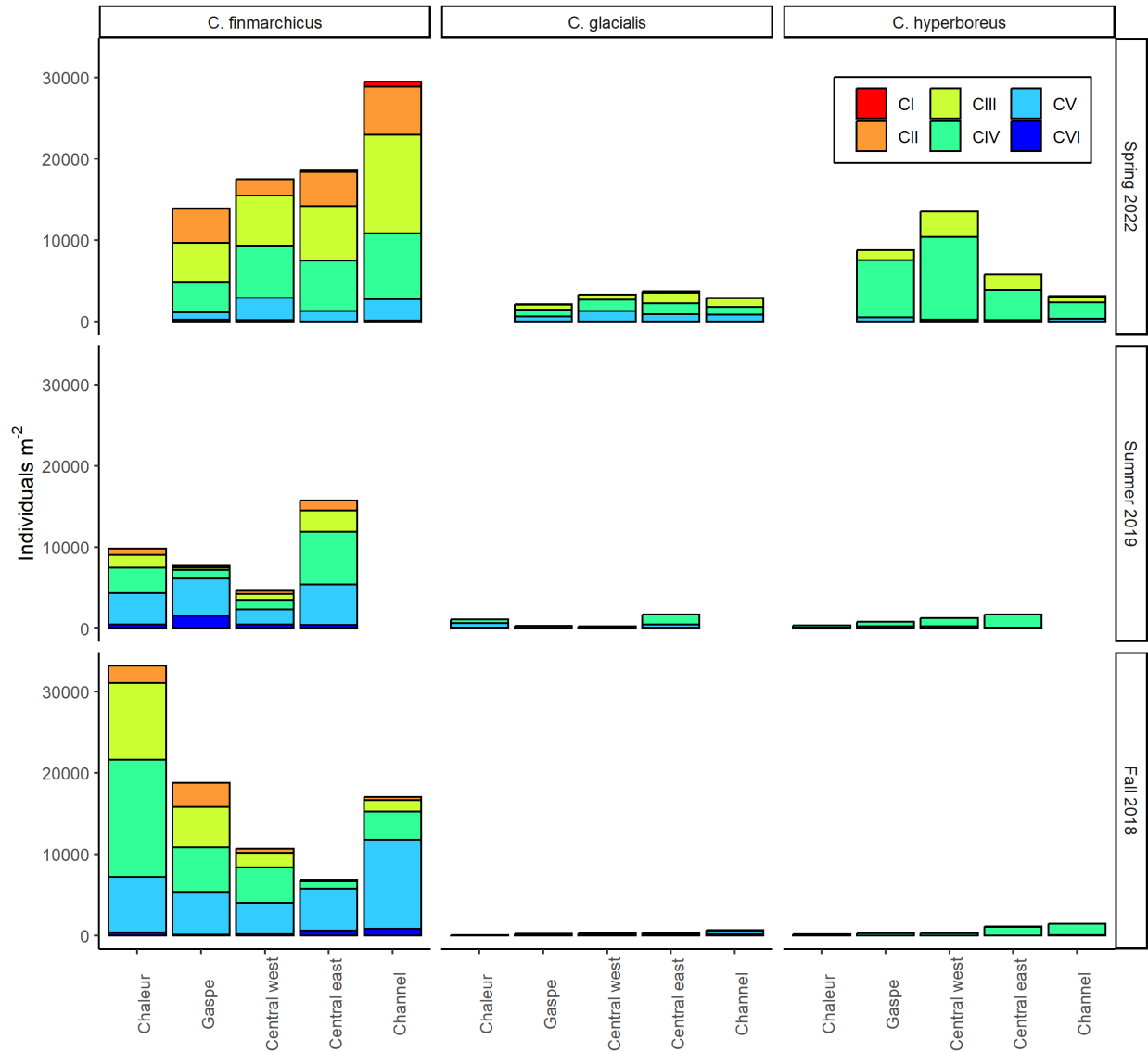


Figure 7. Depth-integrated species- and stage-specific abundance of *Calanus* spp. from JackNet samples. Values indicate the median abundance computed from each subregion in each sampling mission (see Figure 6).

Coupled Hindcast Model Simulations of Prey Supply Dynamics

Previous modelling studies demonstrated that the interaction between the dominant seasonal circulation patterns in the GSL and *C. finmarchicus* vertical behavior influence the spatial distribution of *C. finmarchicus* and its transport from the Laurentian Channel into the sGSL (Zakardjian et al. 2003, Maps et al. 2011). Building on the previous models, the dynamics of *Calanus* supply have been assessed through development and application of 3-D coupled *Calanus* spatial abundance models (Brennan et al. 2019, 2021). These IBMs were initialized from statistical species distribution model (SDM) monthly predictions of copepodite (CI-CVI) abundance, based on environmental predictors and ocean observing data (Albouy-Boyer et al. 2016). In the coupled model, particles representing active and diapausing *C. finmarchicus* and *C. hyperboreus* were seeded over the eastern Canadian shelf, advected for 30 days by

horizontal velocities from a regional hindcast circulation model (CANOPA; Brickman and Drozdowski 2012), and moved vertically towards species-specific preferred depths, informed by statistical models of *Calanus* spp. regional vertical distributions (Krumhansl et al. 2018, Plourde et al. 2019). Simulated *Calanus* spp. experienced stage development and mortality as a function of the along-track temperature; in addition, *C. finmarchicus* abundance was augmented through recruitment to CI, representing contributions from continuing production through the spring and summer. After 30 days of simulation, the late-stage abundance associated with each particle's final position was mapped onto the model grid, to predict the 3-D spatial abundance of late stages of each *Calanus* species available as prey for NARW. Since model simulations were started every two days from spring through fall, the monthly average 3-D spatial abundance was used to predict the seasonal evolution of late-stage *Calanus* spatial abundance. This approach incorporates observations of both estimates of the horizontal distribution of *C. finmarchicus* and *C. hyperboreus* and their vertical positioning during the active growth periods and diapause. Model simulations in contrasting years representing cooler and warmer periods were used to examine the relative effects of regional population levels and the physical environment (including hydrography and circulation) on supply to the sGSL (Brennan et al. 2021).

The coupled model demonstrated that the advective supply of active *Calanus* to the sGSL comes mainly from adjacent areas of the Laurentian Channel, particularly via the Gaspé Current (Brennan et al. 2019). Both upstream population levels and ocean currents influence the influx of *Calanus* to the sGSL. *C. hyperboreus* enters the sGSL mainly in spring, whereas the supply of *C. finmarchicus* to the sGSL increases from the spring to a summer maximum, before declining into fall. The patterns of advective supply of active *Calanus* to Shediac Valley can be disrupted due to environmental variability from river runoff and winds in spring and early summer (Brennan et al. 2021). In the model, particles are sensitive to current dynamics and can move either southward into the Shediac Valley and Magdalen Shallows, or they can move eastward along the shelf edge. The latter was observed in both the model and observations in June 2012, when circulation reversed the normally southward flow from the tip of the Gaspé Peninsula to Shediac Valley (Brennan et al. 2021). This current reversal cuts off the influx of *Calanus* to the southern sGSL, while supplying the northern edge of the sGSL, and highlights how ocean dynamics can affect foraging habitat in the sGSL. Variability in *Calanus* spp. population abundance was also simulated to assess the influence of increases in *C. hyperboreus* and decreases in *C. finmarchicus* population levels observed during recent warm years in the GSL. While *C. hyperboreus* population increases helped to buffer the variable supply into the sGSL in May-July 2012 in the model, the *C. finmarchicus* population declines reduced the active *Calanus* spp. influx to the sGSL in late summer and fall (Brennan et al. 2021). Hindcast modelling demonstrates that the supply of active *Calanus* spp. to the sGSL is sensitive to ocean circulation variability in spring and early summer, whereas in the late summer and fall, supply is more sensitive to upstream *C. finmarchicus* population variation.

The distribution of prey along the northern shelf edge of the sGSL or further south in the sGSL interior impacts NARW distribution and their exposure to risks of vessel strikes and entanglement in early spring, when NARW are migrating into the sGSL (Davies and Brillant 2019, Simard et al. 2019, Crowe et al. 2021). A hindcast model was developed for *C. hyperboreus* to simulate this dynamic, examining the interactions of the spring-bloom-driven timing of new cohort development, vertical distribution, mortality, and transport in circulation fields from the Environment Canada CIOPS-E forecast model (Paquin et al. 2021, 2022, Le Corre et al. 2023). Particles were released as stage CI in deep waters of the GSL over the four years simulated (2016-2019), with spring bloom timing parameterized to control the *C. hyperboreus* development schedule in each sub-region (Lehoux et al. 2021). Particle vertical migrations and positioning in the water column simulated in the model varied with copepodite stage development (CI-CIV), which is temperature dependent, such that the interactions among

ocean currents, spring bloom timing, and temperature produced year-specific spatial distributions of *C. hyperboreus* abundance and biomass in the sGSL. Upstream source regions for particles that diapause in different sub-areas of the sGSL were mainly located in the northwest and central GSL (i.e., south of Anticosti Island), with interannual variation in the relative amount contributed by each region. In the model, differences in the *C. hyperboreus* development schedule strongly contributed to determining diapause entry timing, whereas the effect of spring temperature differences was minor. The model predicted the horizontal and vertical location of maximum biomass accumulated within the sGSL and its seasonal and interannual evolution. Diapause phenology, tightly linked to spring bloom timing in the model, was a key factor in the seasonal evolution of high-density biomass locations within the sGSL. The location of high *C. hyperboreus* densities in the sGSL varied among years in response to varying phenology and transport. The model successfully reproduced *C. hyperboreus* seasonal production timing, the interannual variations in *C. hyperboreus* biomass in June, and the north/south index, a metric for *Calanus* distribution along the shelf edge or in the interior of the sGSL. This index and model were used as a test case for forecasting likely locations of prey and NARW foraging in spring (Le Corre et al. 2023).

AGGREGATION AND AVAILABILITY

Particle concentrating mechanisms in the ocean are inherently dependent on vertical movement (i.e., swimming, sinking and floating) of particles (e.g., Flierl and Woods 2015). Biophysical zooplankton accumulation mechanisms, which can lead to dense layers of zooplankton in the water column, involve an interaction between vertical movement and local-scale flow fields (e.g., Simard et al. 1986, Franks 1992, Epstein and Beardsley 2001). The sea surface and bottom block vertical movement of zooplankton, which can also contribute to their accumulation near these interfaces (Genin 2004). Indeed, near-surface, subsurface, and near-bottom layers of highly concentrated zooplankton, especially late-stage *Calanus* spp. copepodites, have been observed in NARW foraging habitats (e.g., Beardsley et al. 1996, Baumgartner and Mate 2003, Baumgartner et al. 2017, Sorochan et al. 2023). Near the surface, depth maintenance or upward swimming in convergent flow can lead to the accumulation of zooplankton in association with features like fronts, Langmuir circulation cells, and internal wave slicks (Shanks and Wright 1987, Pineda 1999, Stevick et al. 2008, Kingsford et al. 1991). Late-stage *Calanus* spp. have been observed performing diel vertical migrations (DVM; e.g., Baumgartner et al. 2011) and are capable of resisting downward flows up to 2 cm s^{-1} , indicating potential for accumulation in convergence or divergence zones (Franks 1992, Weidberg et al. 2021). This type of near surface prey accumulation mechanism has been proposed in the context of NARW foraging in the Great South Channel and Massachusetts Bay (Epstein and Beardsley 2001, Flierl and Woods 2015).

On the continental shelf, dense layers of late-stage *Calanus* spp. copepods can form near the bottom from seasonal migration associated with diapause onset (e.g., Krumhansl et al. 2018). Depth-seeking particles accumulate in shelf basins if downward migration occurs as individuals are transported over bottom depressions (e.g., Johnson et al. 2006). This may explain observations of high concentrations of *Calanus* spp. copepods in basins with sill depths shallower than the preferred diapausing depth (e.g., Sameoto and Herman 1990, Osgood and Checkley 1997, Johnson 2007). Tidal sloshing of near-bottom zooplankton layers can increase availability of these prey to the NARW on basin margins and potentially further contribute to accumulation (Davies et al. 2013, 2014). Highly concentrated near-bottom zooplankton patches have been documented in zones where near-bottom flows cross isobaths; in this example, depth maintenance in flow across isobaths would lead to near-bottom zooplankton accumulation (e.g., Mackas et al. 1997, Davies et al. 2013). In relatively shallow shelf environments, DVM also likely contributes to near-bottom aggregations of copepods (e.g., Sorochan et al. 2023).

The recurring presence of a large subset of the NARW population in the sGSL from spring through fall since the mid-2010s (Crowe et al. 2021) indicates strong potential for predictable accumulation of prey in this relatively large area. In the sGSL, the shallow bottom depth, mainly < 100 m, appears to play an important role in the accumulation of *Calanus* spp. near the seafloor (Plourde et al. 2019, Sorochan et al. 2023). Furthermore, the interaction between ocean circulation and the shallow seafloor contributes to relatively small-scale variability in flow and formation of local oceanographic features like eddies, fronts, and internal waves (Koutitonsky and Bugden 1991) that could facilitate zooplankton accumulation in convergence zones near the surface. The western side of the sGSL is typically characterized by strong gradients in hydrography and flow associated with intrusion of the Gaspé current (Koutitonsky and Bugden 1991). Sea-surface filaments associated with these features can be detected by analysis of sea surface roughness from Synthetic Aperture Radar. This tool can potentially be used in the sGSL to characterize spatial and temporal variability in surface fine-scale circulation features that could facilitate near-surface zooplankton accumulation (Danielson et al. 2023).

The NARW have occasionally been observed feeding in the sGSL near the surface from aerial surveys in June, July, October, and November (Crowe et al. 2021, Franklin et al. 2022). It is hypothesized that the apparent decline of NARW near-surface feeding observations in August is a consequence of a shift to primarily near-bottom feeding as *Calanus* spp. vertical distribution shifts predominantly to deeper water (Plourde et al. 2019). Currently, there is no published information on NARW feeding behaviour at depth in the sGSL; however, prey aggregations have been observed near the bottom in summer (Sorochan et al. 2023), and observations of NARW with mud on the head in the GSL indicate that individuals at least occasionally dive to the bottom (Hamilton and Kraus 2019).

Fine-scale Field Observations of *Calanus* spp. in the Southern Gulf of St. Lawrence

Field sampling missions in spring, summer, and fall focused on characterizing vertical distributions of *Calanus* spp. in the sGSL. High resolution plankton profiles were made with the VPR, which was deployed to within metres of the surface and bottom during repeated profiles at each station (Table 1). The distance from the surface and bottom was dependent on the sea state and local bathymetry variations, typically ranging from 1-10 m. Due to the challenges of sampling close to the bottom, there are exceedingly few observations within 3 m of the seafloor. The depth and magnitude of *Calanus* spp. aggregations were evaluated from the maximum concentrations obtained from VPR sampling, averaged over profiles performed during a station occupation (max average) and the overall maximum observed in the 3 m bins (max observed; Figure 8). The max average is a conservative measure of maximum abundance and is representative of the entire deployment at 3 m depth intervals. In contrast, the maximum observed is sensitive to fine scale patchiness and is likely a better indicator of the potential maximum concentrations that can occur in the area of the deployment. Neither metric provides a direct measure of the average concentration of prey experienced by a NARW over a given foraging path; however, given that NARW are likely adapted to find high-density prey patches, the maximum observed is a more relevant metric to potential prey fields that may be experienced by NARW. The VPR observations presented here represent a synthesis of published observations from field sampling missions in summer 2019 and fall 2018 (Sorochan et al. 2021b, 2023) and previously unpublished observations from the spring 2022 mission (Table 1). The VPR data from spring 2022 comprise the subset of stations where image classification has been completed.

The VPR deployments and other zooplankton sampling were completed at locations associated with and without NARW visual detection by Marine Mammal Observers (MMO) on the vessel.

The presence of NARW was documented by MMOs during the day (e.g., see Sorochan et al. 2023), and zooplankton sampling was considered “associated with NARW presence” if conducted during the day and within visual range of one or more NARW, or if conducted at night at a location from which a NARW sighting occurred during the previous or following day. True absence of NARW could not be confirmed because it is possible that the presence of NARW was undetected by MMO during the day, and there were no MMO operations during zooplankton sampling at night. In all cases, there was no attempt to sample as close as possible to NARW or at positions where NARW had been observed diving. In spring 2022, VPR sampling associated with NARW presence was conducted during daylight (n = 6). In summer 2019, VPR sampling associated with NARW presence was conducted during the daylight (n = 4) and at night (n = 4). In autumn 2018, no NARW were detected by MMOs.

Plankton net deployments were made at the same stations as VPR deployments to provide complementary information on community composition and vertical distribution. Depth-stratified plankton samples were collected in fall 2018 with a 1 m² BIONESS equipped with 333 µm mesh nets and a strobe (Sorochan et al. 2021b). In spring 2022, depth-stratified samples were collected with either a 0.75 m diameter closing net equipped with 200 µm mesh and towed vertically or with a 0.125 m² MultiNet equipped with 200 µm mesh and towed vertically. No depth-stratified net samples were obtained from summer 2019.

Depth-stratified net data were summarised by plotting the median species- and stage-specific abundance (individual m⁻²) for depth-stratified samples. For stations with bottom depths < 140 m, data were binned into upper (< 50 m) and lower (> 50 m) water column strata, and for stations with bottom depths ≥ 140 m, data were binned into upper (< 50 m), mid (≥ 50 m and < 100 m), and lower (≥ 100 m) water column strata. A qualitative examination of these data indicated differences in species and stage composition of *Calanus* spp. between upper and lower or mid water column strata (Figure 9). In comparison to the lower or mid water column, the upper water column was characterized by higher overall abundances of *C. finmarchicus* composed of mixed copepodite stages and lower abundances of *C. hyperboreus*. Median abundances of stages CIV and CV of *C. hyperboreus* were higher in the lower or mid water column, whereas those of *C. glacialis* (all stages) and stage CV of *C. finmarchicus* were similar between upper and lower or mid water column. In spring 2022, *Calanus* spp. copepodites that occurred in the lower or mid water column were dominated by stage CIV of *C. hyperboreus* indicating potential for early initiation of diapause. This is consistent with an earlier phenology associated with a very early spring bloom throughout much of the GSL in 2022 (Blais et al. 2023). In fall 2018, the lower or mid-water column was dominated by stage CV of *C. finmarchicus*, which is consistent with the presence of a diapausing population of this species at this time of year. However, in the upper water column the mixture of early and late copepodite stages of *C. finmarchicus* and occasional presence of late-stage *C. hyperboreus* indicated ongoing production of *C. finmarchicus* and potential disturbance of diapausing individuals in fall 2018, perhaps associated with strong vertical mixing during storms (Sorochan et al. 2021b).

Across all stations sampled with the VPR, maximum concentrations of *Calanus* spp. covered a broad abundance range; however, at almost all stations associated with NARW sightings, the maximum average and maximum observed metrics were > 1,000 ind m⁻³ (Figure 10). The maximum average and maximum observed concentration metrics differed in magnitude but were generally similar in their patterns of maximum abundance and depth (Figure 10). Agreement in depth between these metrics was interpreted as an indicator that depth of the maximum concentration reflects the primary mode of the vertical distribution. Inconsistency in vertical positioning between metrics can occur when the vertical profile is highly variable or multimodal.

In spring 2022, near-bottom maximum concentrations were likely composed of primarily *C. hyperboreus* CIV, which dominated the lower water column depth stratum (Figure 9). In summer 2019, the highest maximum concentrations were also observed near the bottom in the Shediac Valley area and often associated with NARW visual detection. Our observations in summer 2019 indicated that prey aggregations are patchy in space and over time scales of days to weeks (Sorochan et al. 2023). The associated composition of *Calanus* spp. (from corresponding depth-integrated net samples) was characterized by high densities of *C. finmarchicus*, lower but substantial densities of *C. hyperboreus*, and even lower but variable densities of *C. glacialis* (Sorochan et al. 2023). There is uncertainty regarding the composition of near-bottom layers in summer 2019 due to the absence of depth-stratified net sampling. In fall 2018, the highest maximum concentrations of *Calanus* spp. were lower than those observed in other missions (Figure 10). During this mission, the number of station occupations and spatial extent of VPR sampling was considerably smaller than subsequent missions. At these stations, maximum concentrations occurred throughout the water column; however, the highest maximum concentrations occurred near the surface, with concentrations $> 1,000$ ind m^{-3} observed at several stations. At present, characteristics of near-surface prey aggregations and associated fine-scale circulation environment are not known. Species composition from associated net samples in fall 2018 indicates dominance of *C. finmarchicus* (Figure 7; Sorochan et al. 2021b).

Generally, the vertical distribution of *Calanus* spp. sampled by VPR (profiles not shown) were variable, but higher abundances of *Calanus* spp. occurred near the bottom or surface (Sorochan et al. 2021b, 2023, unpublished data). In spring 2022 and summer 2019, the highest concentrations of late-stage *Calanus* spp. occurred within 20 m above the bottom, at bottom depths ranging from approximately 50-100 m (Figure 10). Concentration peaks were typically observed in VPR depth bins shallower than the maximum depth sampled (Figure 10). Observations within 1-3 m of the bottom were rare, and although the possibility of unobserved hyperbenthic prey layers that could be targeted by NARW cannot be ruled out, this feature was not observed in VPR profiles sampling closest to the bottom. Seasonal diapause migration likely contributed to the presence of high concentration near-bottom layers (e.g., Krumhansl et al. 2018, Plourde et al., 2019), but it is also likely that DVM contributed to variation in the depth, concentration, and compactness of these layers in summer 2019 (Sorochan et al. 2023). Where the VPR was towed across bathymetric gradients (i.e., basin or troughs margins), the highest concentrations were generally maintained around the sill depth of the bathymetric feature (e.g., Sorochan et al. 2021b, 2023). It is hypothesized that the depth of the *Calanus* layer is set at the near-bottom proximate to bathymetric depressions. This may explain maxima of *C. hyperboreus* in the mid-water column stratum at deeper stations (Figure 9). While the Chaleur, Shediac, and Bradelle troughs of the sGSL are relatively shallow and characterized by weak bathymetric gradients, depth-seeking copepods may still accumulate in these features. Coupled modelling of *C. hyperboreus* transport and supply to the sGSL highlighted the importance of vertical position and bathymetry in governing variation in particle retention and density in bathymetric depressions, contributing to consistency in spatial distribution among years (Le Corre et al. 2023). Nevertheless, near-bottom *Calanus* spp. layers with concentrations of approximately $2,000 m^{-3}$, likely dominated by *C. hyperboreus* stage CIV, have been measured at depths as shallow as approximately 50 m in June 2022 (Figure 10).

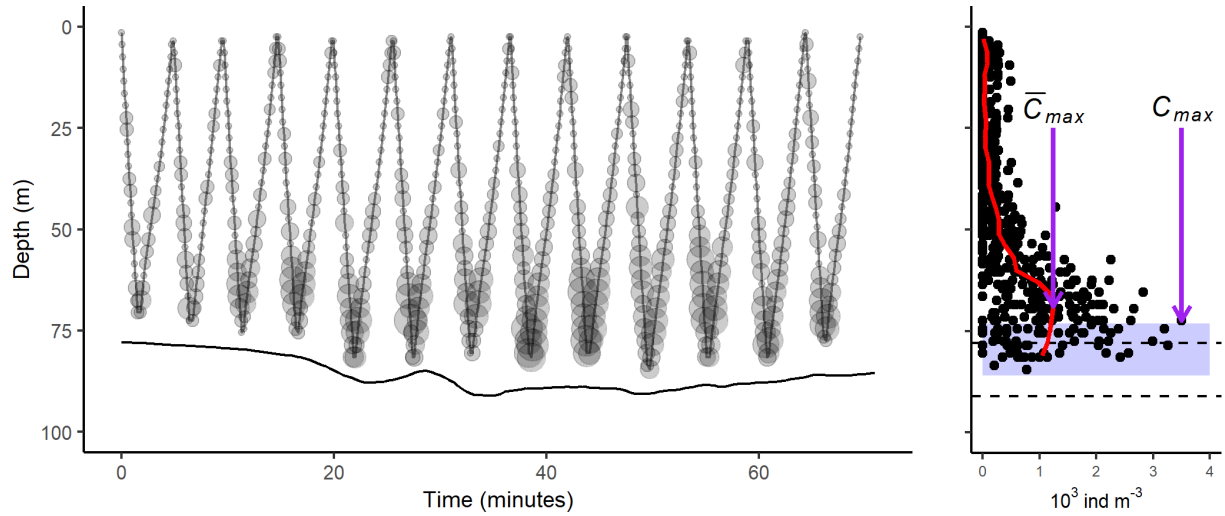


Figure 8. Example of video plankton recorder (VPR) tow deployment with proportional abundance of late-stage *Calanus spp.* copepodites indicated by bubble size and bottom depth indicated by the black line (left panel) and corresponding vertical distribution of abundance with the average abundance in 3 m depth bins indicated by the red line (right panel). Purple arrows indicate the maximum concentration metrics \bar{C}_{max} (maximum average) and C_{max} (maximum observed). In the right panel, the range in bottom depth is indicated by dashed lines and the range in maximum VPR depth is indicated by the blue polygon.

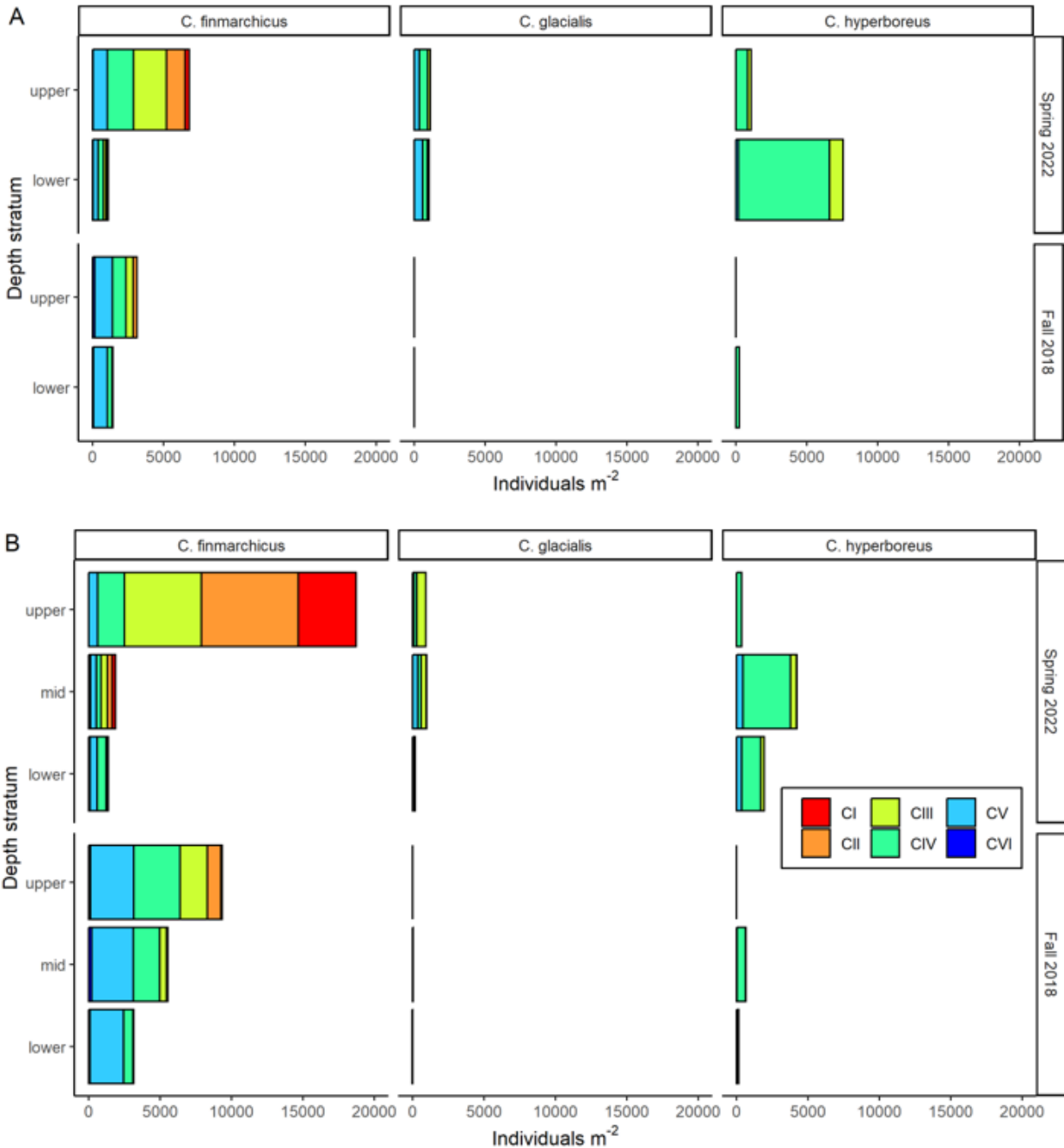


Figure 9. Median depth integrated abundance of *Calanus* spp. in different depth strata in spring 2022 and fall 2018 for bottom depth (A) $z < 140$ m and (B) $z \geq 140$ m. Samples were obtained using MultiNet or ClosingNet (mesh size: $200 \mu\text{m}$) in spring 2022 and BIONESS (mesh size: $333 \mu\text{m}$) in fall 2018. The upper and mid depth strata represent approximately 50 m to surface and 100 m to 50 m layers, respectively. The lower stratum represents the deepest depth layer sampled from the near-bottom to approximately 50 m (in panel A) or 100 m (in panel B).

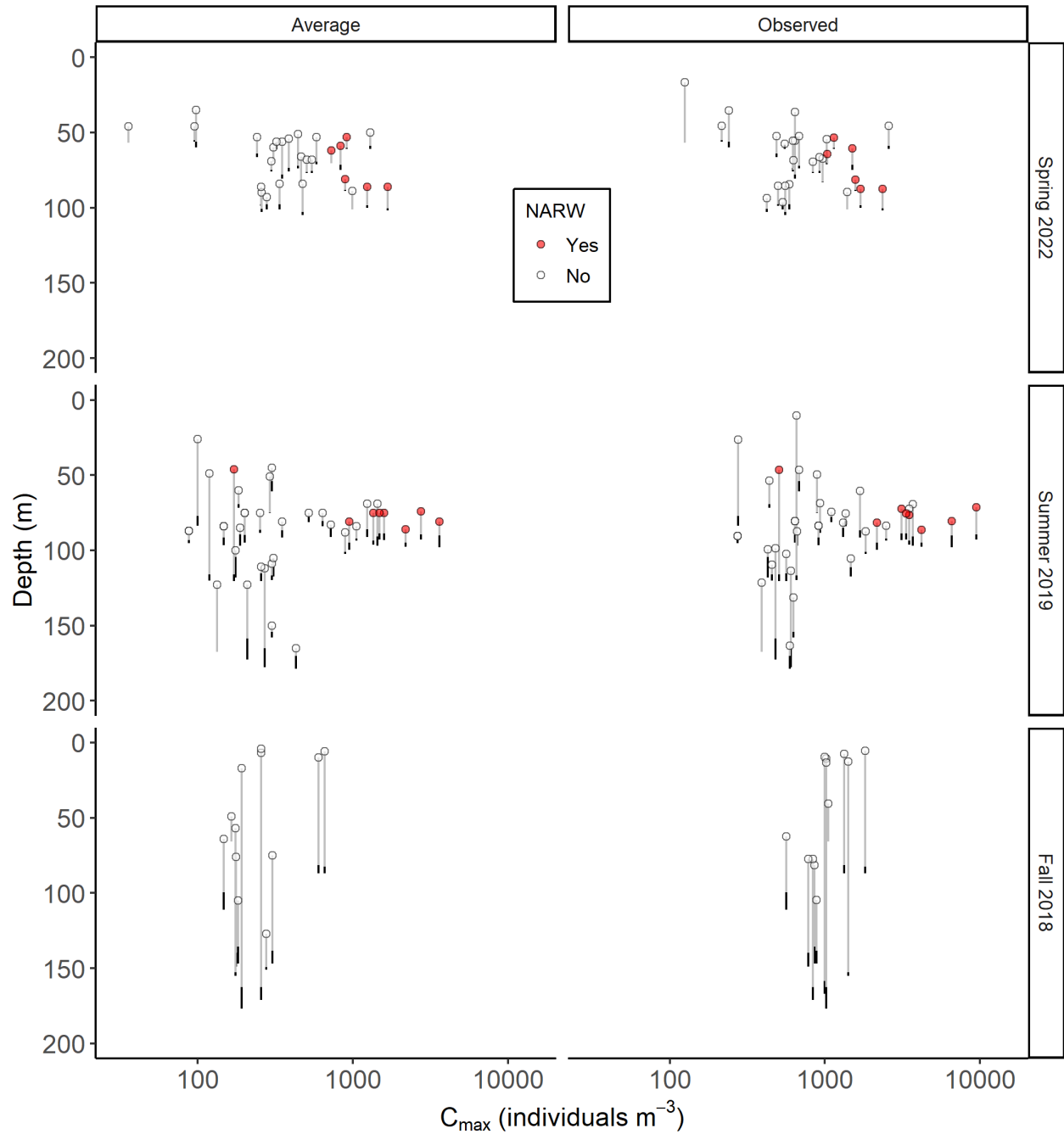


Figure 10. Depth and magnitude of maximum average and maximum observed concentrations of late-stage *Calanus* spp. copepodites from sampling in spring 2022, summer 2019, and fall 2018. The number of samples was lowest in fall 2018 (see Table 1), and no samples were associated with NARW sightings. Vertical segments indicate distance between the depth of maximum concentration (circle) and the maximum VPR sampling depth (grey) and maximum bottom depth (black). Red markers indicate VPR sampling associated with NARW visual presence. Clear markers indicate sampling without confirmed NARW presence.

PREY QUALITY AND ENERGY DENSITY

Energy as the Critical Currency for North Atlantic Right Whale Foraging

Energy is the most relevant prey quality metric linking prey concentration to NARW bioenergetic requirements (e.g., Gavrilchuk et al. 2021). Individual-specific energy content of *Calanus* spp. typically increases with developmental stage until the life stage of maximum lipid storage (i.e., typically diapause stages), due to changes in biomass and body composition from growth, development, and energy storage at each stage (Kattner and Krause 1987, Hygum et al. 2000a). In adult stages, somatic maintenance and reproductive costs decrease their energetic value compared to late copepodite stages (Comita et al. 1966). Stages that enter diapause (e.g., *C. finmarchicus* CV, *C. hyperboreus* CIV, CV, CVI) vary in individual-specific energy over periods of lipid accumulation (energy increase) and diapause (decline) (e.g., Helenius et al. 2023a). During diapause, lipid is used to meet metabolic requirements and to maintain diapausing depth (Pasternak et al. 2001, Pepin and Head 2009).

Individual-specific energy also varies regionally and seasonally in response to environmental conditions experienced during development and growth. The maximum capacity for lipid storage is determined by prosome length (Miller et al. 2000), which is primarily driven by temperature and food effects on development and growth (Campbell et al. 2001). Copepods that develop under warmer conditions are smaller than those that develop under colder conditions, and availability of food during development can also influence size and lipid content (Båmstedt 1988, Hygum et al. 2000b, Wilson et al. 2015 and references within). Such intraspecific variability in size and energy content can affect spatial and temporal variation in quality of NARW prey fields. An analysis of historical *C. finmarchicus* size and lipid content data (1990-2020) in the northwest Atlantic documented larger body size and lipid content in stage CV in the GSL and Newfoundland Shelf compared with those in the warmer regions of the GOM and Scotian Shelf, indicating substantial regional differences in inferred energy content (Helenius et al. 2023b).

Seasonal changes in average individual energy content were estimated for *C. finmarchicus* CV and *C. hyperboreus* CIV and CV in the sGSL from early spring and summer foraging habitat missions using calorimetry (Table 2, including individual energy content from previously published studies for comparison). Life history and timing of diapause transitions differ among species and likely influence the observed contrasting patterns in lipid accumulation and energy content. The seasonal increase in lipid stores in preparation for diapause from early spring to summer was recorded in stage CV copepodites of both *C. finmarchicus* and *C. hyperboreus* and was reflected in increasing energy content. Meanwhile, *C. hyperboreus* stage CIV had overall low energy content in the sGSL in summer, indicating either failure to accumulate lipid during an atypically short and weak spring bloom in 2019, or a large reduction in lipid reserves after diapause initiation that may be due to interruption or inhibition of full entry into diapause at the shallow depths of the sGSL (Helenius et al. in revision¹, Lehoux et al. 2020, Blais et al. 2023).

Energy Density Estimates in the Southern Gulf of St. Lawrence

Prey energy density (energy volume⁻¹) is the concentration of energy in a given prey layer. When measured at scales relevant to NARW foraging and compared to NARW energy density requirements, this metric can be used to evaluate the potential suitability of a NARW foraging habitat. Energy density thresholds (i.e., minimum energy density required to meet energetic

¹ Helenius L.K., Sorochan K.A., Plourde S., Perrin G., Walsh H.J., Orphanides C.D., and Johnson C.L. (in revision) Size and energy content of *Calanus* spp.: linking copepod phenology to variability in their quality as prey.

demand of NARW) were derived for different demographics of female NARW from estimates of daily energy requirements and NARW clearance rate (volume filtered time⁻¹) following Gavrilchuk et al. (2021). Parameters used to derive energy density thresholds are provided in Table 3. Energy density thresholds of 28 kJ m⁻³, 38 kJ m⁻³, and 86 kJ m⁻³ were computed for resting, pregnant, and lactating NARW demographic groups, respectively.

Maximum prey energy densities (ED_{max}; energy m⁻³) in the sGSL were derived from the following information obtained from the field sampling missions (Table 2): (1) species- and stage-specific individual energy content (energy ind.⁻¹) measured from calorimetric analysis of samples in a subset of station occupations; (2) maximum observed late-stage *Calanus* spp. concentration (ind. m⁻³) obtained from VPR sampling associated with NARW presence (Figure 10); and (3) overall species-stage composition of late-stage *Calanus* spp. obtained from corresponding plankton net samples (Table 4). Since the taxonomic identification of *Calanus* copepods from VPR images was only resolved to genus of primarily late stages (CIV-CVI *C. hyperboreus*; CV-CVI *C. finmarchicus* and *C. glacialis*), this approach assumed that the species and stage proportions in the lower water column net stratum in spring 2022 represented those at the depth of the maximum observed concentration. In summer 2019, the composition of near-bottom layers was inferred from depth integrated plankton net samples, because depth-stratified sampling was not conducted.

Individual energy content was estimated for each mission from species-stage proportions of the dominant diapausing stages and mission-specific individual energy contents. Since there were few data on individual energy content of *C. glacialis* and adult stages of *Calanus* spp., the energy content of *C. glacialis* CV was assumed equal to that of *C. finmarchicus*, and the adult stage of *Calanus* spp. was excluded from the analysis. The abundance of adult *Calanus* spp. was negligible in the lower water column stratum in spring 2022, and adult *C. finmarchicus* represented 10% abundance of late-stage *Calanus* spp. in depth-integrated samples from summer 2019. In spring 2022, the overall late-stage *Calanus* spp. concentration in the lower water column stratum at station occupations where NARW were observed was dominated by *C. hyperboreus* CIV (79%) with additional contributions of *C. hyperboreus* CV (2%) and *C. finmarchicus*+*C. glacialis* CV (19%) resulting in a weighted average energy content of 11.8 J ind⁻¹ (Table 4). In summer 2019, *Calanus* spp. abundance was dominated by *C. finmarchicus* CV (53%) and *C. hyperboreus* CIV (37%) with a minor contribution of *C. hyperboreus* CV (10%), resulting in a weighted average energy content of 15.1 J ind⁻¹ (Table 4).

In both spring 2022 and summer 2019, the median and maximum ED_{max} were within the range of energy density measurements from other studies in the lower Bay of Fundy and Roseway Basin in summer, but the depth of ED_{max} was shallower in the sGSL (Table 4; Baumgartner and Mate 2003, Michaud and Taggart 2011, Davies et al. 2014). In spring 2022, the median ED_{max} was less than the requirement for resting female NARW; only maximum ED_{max} was consistent with the requirement. In summer 2019, the median ED_{max} exceeded energy requirements of a resting and pregnant female NARW, and the maximum ED_{max} exceeded that of all demographic groups (Table 4). While there is substantial uncertainty in estimates of energy density and NARW energy requirements (e.g., Gavrilchuk et al. 2021, Hütt et al. 2023) and a limited number of observations, these results indicate that NARW could find prey aggregations consistent with their metabolic demands in the sGSL. Our observations of ED_{max} associated with NARW visual presence likely underestimate actual energy densities experienced by NARW, since *Calanus* spp. concentrations were not sampled along the NARW foraging path.

Table 2. Regional comparison of calorimetrically determined individual mean energy content (EC_{IND} , $J\ ind^{-1}$) in *Calanus* spp. from various studies from northwest Atlantic North Atlantic right whale foraging areas (regions are Scotian Shelf [SS], Bay of Fundy [BoF], Gulf of Maine [GOM] and Gulf of St. Lawrence [GSL]). (NB: depth effects are not being considered here)

Species and Life Stage	Area (Region)	Months and Year(s)	Lipid Accumulation Phase	EC_{IND} ($J\ ind^{-1}$) (SD)	Source
<i>C. finmarchicus</i> CV	Roseway Basin (SS)	September 2007	diapause	4.4 (0.79) 10.9 (2.2)	Davies et al. 2012
<i>C. finmarchicus</i> CV	Grand Manan Basin (BoF)	May-October 2002	onset-diapause	2-8 (depending on size class), mean 2.5-3.5 across classes	Michaud and Taggart 2007
<i>C. finmarchicus</i> CV	Grand Manan Basin (BoF)	July-September 2006-2010	diapause	7.34 (0.67)- 12.67 (0.45)	McKinstry et al. 2013
<i>C. finmarchicus</i> CV	Nantucket Shoals (GOM)	February-March 2020	emergence, activation, growth	3.27 (0.18) (formalin-preserved)	Helenius et al. in revision ¹
<i>C. finmarchicus</i> CV	Southern GSL (GSL)	May-June 2022	growth	7.89 (1.02)	Helenius et al. in revision ¹
<i>C. finmarchicus</i> CV	Southern GSL (GSL)	June 2023	growth	6.61 (2.89)	Helenius et al. in revision ¹
<i>C. finmarchicus</i> CV	Southern GSL (GSL)	August-September 2019	onset	9.4 (1.31)	Helenius et al. in revision ¹
<i>C. hyperboreus</i> CIV	Roseway Basin (SS)	September 2007	diapause	9.4 (1.5) 12.7 (2.5)	Davies et al. 2012
<i>C. hyperboreus</i> CIV	Southern GSL (GSL)	May-June 2022	onset	12.24 (3.1)	Helenius et al. in revision ¹
<i>C. hyperboreus</i> CIV	Southern GSL (GSL)	June 2023	onset	14.01 (2.61)	Helenius et al. in revision ¹
<i>C. hyperboreus</i> CIV	Southern GSL (GSL)	August-September 2019	diapause	9.58 (1.81)	Helenius et al. in revision ¹
<i>C. hyperboreus</i> CV	Southern GSL (GSL)	May-June 2022	onset of 1 st or 2 nd diapause	31.85 (3.48)	Helenius et al. in revision ¹
<i>C. hyperboreus</i> CV	Southern GSL (GSL)	June 2023	onset of 1 st or 2 nd diapause	49.03 (9.38)	Helenius et al. in revision ¹
<i>C. hyperboreus</i> CV	Southern GSL (GSL)	August-September 2019	1 st or 2 nd diapause	65.21 (0.51)	Helenius et al. in revision ¹

Table 3. Parameters for calculation of North Atlantic right whale prey energy density requirements for resting, pregnant, and lactating demographics (values obtained from Gavrilchuk et al. (2021) and references therein). The feeding time per day is assumed independent of dive depth for depths < 150 m.

Parameter	Value or Derivation
Median daily energy requirement (MJ day ⁻¹)	Resting: 1,533 Pregnant: 1,855 Lactating: 4,233
Mouth area (m ²)	1.8
Swimming speed (while feeding) (m s ⁻¹)	1
Travel speed (m s ⁻¹)	1.45
Ascent angle (radians)	$\sin(62 \cdot (\pi/180))$
Descent angle (radians)	$\sin(74 \cdot (\pi/180))$
Assimilation efficiency	0.86
Foraging time per day (h)	16
Dive period (duration of single dive) (s)	surface time + travel time + bottom time
Bottom time (s)	$0.0704 \cdot \text{dive depth} \cdot 60$
Descent time	$(\text{dive depth} / \text{descent angle}) / \text{travel speed}$
Ascent time	$(\text{dive depth} / \text{ascent angle}) / \text{travel speed}$
Travel time (s)	Descent time + ascent time
Surface time – resting (s)	$0.211 \cdot (\text{bottom time} + \text{travel time})$
Surface time – pregnant or lactating (s)	$0.342 \cdot (\text{bottom time} + \text{travel time})$
Number of dives per day	$(1 / \text{dive period}) \cdot \text{foraging time per day}$
Feeding time per day (s)	Number of dives per day * bottom time
Energy density requirement (kJ m ⁻³)	Daily energy requirement / (mouth area * swimming speed * feeding time per day * assimilation efficiency) * 1,000

Table 4. Summary of energy density estimates of late-stage *Calanus* spp. copepodites from field observations collected using video plankton recorder in the southern Gulf of St. Lawrence and optical plankton counter in the Bay of Fundy and western Scotian Shelf. In the southern Gulf of St. Lawrence, concentrations were only examined for data associated with North Atlantic right whale presence, and weighted averages of energy content were computed using the overall relative abundance of the different species-stage combinations obtained from plankton net sampling (see text). Species/stages analysed include *C. finmarchicus* fifth copepodites (CfinCV), *C. glacialis* fifth copepodites (CglaCV), and *C. hyperboreus* fourth, fifth, and sixth copepodites (ChypCIV, ChypCV, ChypCVI). NA indicates metrics that are not available.

Location, Study	Season, Year	Individual Energy (J ind ⁻¹)	Depth of Maximum Concentration (m)	Maximum Concentration (ind m ⁻³)	Maximum Energy Density (kJ m ⁻³)
Southern GSL, This study	Spring 2022	CfinCV and CglaCV (7.9) ChypCIV (12.2) ChypCV (31.9) Weighted avg: 11.8	40-100	Median: 1,540 Maximum: 2,350	Median: 18 Maximum: 28
Southern GSL, This study	Summer 2019	CfinCV and CglaCV (9.4) ChypCIV (9.6) ChypCV (65.2) Weighted avg: 15.1	70-90	Median: 3,420 Maximum: 9,460	Median: 52 Maximum: 143
Lower Bay of Fundy; Michaud and Taggart (2011)	Summer 2002	CfinCV (4.5)	> 140	Median: NA Maximum: 10,100	Median: NA Maximum: 45
Lower Bay of Fundy and Roseway Basin, Baumgartner and Mate (2003)	Summer 2000 and 2001	CfinCV (6.8) Comita et al. 1966 in UK waters	100-170	Median: 6,220 Maximum: 20,610	Median: 42 Maximum: 140
Roseway Basin, Davies et al. (2014)	Summer 2008 and 2009	CfinCV and ChypCVI (size dependent, ranging 3.9-12.2; see Davies et al. 2014)	100-150	Median: NA Maximum: NA	Median: NA Maximum: 23

DISCUSSION

THE SOUTHERN GULF OF ST. LAWRENCE AS AN IMPORTANT FORAGING HABITAT

Recurrent observations of NARW presence and foraging behaviour in the sGSL indicate that the region is an important foraging habitat (Simard et al. 2019, Crowe et al. 2021). Additional evidence was provided by climatological 3-D *Calanus* spp. biomass preyscape analysis identifying a substantial proportion of the sGSL as an area where high densities of prey are likely to form at depths available for NARW feeding (Plourde et al. 2019). The sGSL prey

observations described above and in related publications (Gavrilchuk et al. 2021, Sorochan et al. 2023) provide evidence that prey layers exceeding minimum abundance and energy density requirements for several NARW demographic groups can form in the sGSL and provide suitable foraging habitat for NARW in the region, although not necessarily every year (Gavrilchuk et al. 2021). The presence of *C. finmarchicus* CV in sufficient quantity and quality for NARW foraging is a key attribute identified for historically important NARW foraging habitats in the GOM and western Scotian Shelf. In the GSL, prey fields also include the two larger arctic *Calanus* spp., which should be considered a component of the key attribute of the foraging habitat. In contrast to the GOM where *C. finmarchicus* is the overwhelmingly dominant species, and lipid-rich diapausing stages are most abundant in summer and fall, differences in diapause timing among the three *Calanus* spp. in the GSL could support the availability of lipid-rich late-stage *Calanus* spp. (mainly *C. hyperboreus*) in dense near-bottom layers as early as mid-May.

Based on recent observations and modeling of prey dynamics, the sGSL fulfills the key attribute of “environmental, oceanographic and bathymetric conditions that support and aggregate concentrations of prey” identified in the DFO NARW Action Plan (DFO 2021). Important conditions in the sGSL include (1) a proximate source of relatively high abundance prey in northwest and central GSL sections of the Laurentian Channel; (2) relatively predictable seasonal advective supply through local circulation features including the Gaspé Current; (3) an aggregation mechanism from interaction of vertical migration and shallow bottom depth; and (4) broadscale bottom depths shallower than the NARW maximum foraging depth. Current understanding of sGSL prey dynamics at the simplest level involves an annual cycle of supply, aggregation, and depletion by mortality and flushing. After depletion of *Calanus* in the sGSL during fall and winter, when *Calanus* spp. populations are mainly in diapause in the deep Laurentian Channel, *Calanus* spp. early stages are transported into sGSL from adjacent deep-water areas during their surface active periods, starting in about March, with a greater contribution of the arctic *Calanus* spp. in late winter to spring shifting to mainly *C. finmarchicus* in summer and early fall. Advection is sensitive to Gaspé Current and broader circulation variability, particularly for *C. hyperboreus* during its short transport period. Observations in spring 2022 indicate that near-bottom layers of *C. hyperboreus* can form in the sGSL as early as mid-May. *Calanus finmarchicus* contribute additional biomass to near-bottom layers during late spring through early fall as individuals transported into the sGSL or produced locally reach the CV stage and migrate to deep water. In late fall, *Calanus* spp. abundance declines, likely due to changing circulation that may wash them out of sGSL, reduced supply from surface waters, and mortality due to predation or disturbance at shallow depths that may interfere with sustained diapause. Since the Cold Intermediate Layer, formed through winter wind-driven mixing, reaches the bottom across much of the sGSL (Galbraith et al. 2023), retention of deep *Calanus* spp. in the area through the winter is ultimately improbable.

UNCERTAINTIES ACROSS PROCESSES AND SCALES

While observations and model simulations have provided substantial insight into the environmental, oceanographic and bathymetric conditions that support and aggregate concentrations of prey in the sGSL, information gaps remain. Information gaps on regional *Calanus* spp. distribution and abundance, their vertical migration and life-history status, and interactions with fine-scale and meso-scale circulation features are discussed below. Estimates of abundance and spatial distribution of *Calanus* spp. in areas upstream of the sGSL, which influence *Calanus* spp. flux into the sGSL, are made at a relatively low spatial resolution on a seasonal basis. Sustained observations of *Calanus* spp. phenology and diapause timing are limited to the high frequency time series station in the Lower St. Lawrence Estuary (Rimouski), which is distant from the sGSL, and the Shediac Valley station, which reflects zooplankton conditions within the sGSL. The availability of zooplankton net data typically lags their collection

by at least 69 months. Therefore, model simulations must make assumptions about upstream distribution and abundance, typically based on statistical models of climatological spatial distribution and broadscale annual mean population level (e.g., Brennan et al. 2019, 2021) and relationships between *Calanus* spp. developmental timing and annual environmental signals (e.g., Le Corre et al. 2023). Because annual cycles of zooplankton population development and spatial distribution have similar patterns of recurrence each year in mid-to high-latitude marine ecosystems, estimation based on past observations can provide a reasonable assessment of upstream conditions (Mackas et al. 2012, Blais et al. 2023). However, interannual variability and population changes driven by environmental trends outside of the historical range of variability will introduce uncertainties in model simulations of flux into the sGSL. Since *Calanus* spp. transport into the sGSL is sensitive to interactions between *Calanus* spp. seasonal timing, vertical distribution, and Gaspé Current variability, short time- and space-scale variability in these processes are also a source of uncertainty in supply to the sGSL (Brennan et al. 2019, 2021).

The dominant modes of vertical migration behaviour in *Calanus* spp. are considered to be DVM and seasonal vertical migration, which is associated with diapause. In general throughout marine pelagic environments, *Calanus* spp. DVM can exhibit substantial plasticity, likely related to associated but unobserved factors such as nutritional condition, hunger levels, and predator distributions, introducing uncertainty about vertical distribution during the active phase of development (e.g., Irigoien et al. 2004, Baumgartner et al. 2011, Bandara et al. 2021). In the sGSL, paired day-night observations of relatively compact near-bottom distributions of *Calanus* spp. during the day and more diffuse vertical distribution and elevated near-surface abundance at night in summer are consistent with some portion of the population performing DVM (Sorochan et al. 2023). However, with limited observations, there is uncertainty about how much of the population performs DVM and how this varies spatially and seasonally. During diapause, *Calanus* spp. cease feeding and growth, slow development substantially, and become inactive and torpid, with minimal movement even in response to mechanical disturbance (e.g., Miller et al. 1991, Hirche, 1998). If near-bottom *Calanus* spp. in the sGSL are fully in diapause, their vertical distributions would be expected to remain fairly constant in the absence of vertical water advection and mixing. Therefore, the changes in the vertical structure of the near-bottom prey layer between day and night indicate that a large proportion of deep-dwelling (> 50 m depth) sGSL *Calanus* spp. may not be fully in diapause. In addition, live *Calanus* spp. collected from the deep layer in spring have been observed with full guts and producing fecal pellets (unpublished observations). Even if feeding were initiated after collection (i.e., while copepods were stored for several hours in jars of cold seawater prior to imaging), it indicates capability for immediate initiation of feeding, which would be absent in fully diapausing individuals (Hirche 1998). This further supports the interpretation that individuals in the deep layer may not be fully in diapause, either because they have not yet completed diapause initiation early in the season or because they are unable to enter full diapause in the shallow shelf habitat (e.g., Hirche, 1998, Coguiec et al. 2023). These observations indicate uncertainty about the life history state and vertical migration of *Calanus* spp. in the sGSL from spring to fall, and therefore about the vertical movements that influence the availability of high concentration aggregations over the diel cycle, the persistence of their locations in horizontal space, and the overall retention of *Calanus* spp. in the sGSL.

As described above, interactions between *Calanus* spp. vertical movement and environmental features leading to prey aggregation are rarely observed directly (Sorochan et al. 2021a). It is unknown whether aggregations form at surface circulation features such as salinity-driven fronts that are a common feature in the Shediac Valley in spring and summer, particularly around the Gaspé Current (Doyon and Ingram 2000). It is also unclear whether NARW in the sGSL can

focus feeding efforts on surface aggregations that form predictably in association with persistent circulation features, or rather if they feed opportunistically on transient features.

Interactions between shallow bathymetry in the sGSL and *Calanus* spp. vertical migration provide a mechanism for near-bottom prey aggregation in the region (Sorochan et al. 2021a). While high concentration near-bottom layers are observed at many sites in the sGSL, they are not widespread across the region, and there is uncertainty about the processes driving their dynamics, the vertical structure of near-bottom layers, and their horizontal distribution (Sorochan et al. 2021b, 2023). Horizontal and vertical variability in near-bottom prey concentrations reflects the balance of supply and loss of copepods in near-bottom layers, including local vertical movement of copepods, horizontal movement of deep water, interactions between copepod vertical movement and near-bottom mesoscale circulation features, and mortality in deep water, including predation by pelagic and benthic consumers. Since high temporal- and spatial-resolution observations are limited in the sGSL, these dynamics are difficult to disentangle. The vertical distribution of prey in the depth layer closest to the bottom is a particular source of uncertainty since nets and imaging gear can typically sample safely only to within 35 m above the bottom. High concentrations of epibenthic diapausing copepods have been reported in sparse published (e.g., Hirche et al. 2006) and anecdotal observations (e.g., J. Kirkham, NARW Consortium 2023 Annual Meeting), but it is not clear how prevalent this phenomenon is in the sGSL, or how persistent it is in the face of disturbance by bottom mixing and predation.

In contrast to shelf basins, which are retentive areas for zooplankton at depths below the basin sill depth (e.g., Sameoto and Herman 1990, Davies et al 2013, 2014), the low relief of bottom bathymetry in the sGSL likely provides few features to impede horizontal water and zooplankton movement in the near-bottom layer. Indeed, observations of copepod and acoustic backscatter profiles across low-relief bathymetric depressions in the sGSL in summer often showed the highest densities at depths slightly above the apparent sill depth of the depression, suggesting that the densest layers might be transported from shallower proximate areas over the top of the depressions (summer 2019 field sampling mission, unpublished data). The potential for near-bottom horizontal transport likely contributes to observed patchiness of aggregations in space and their variability on short time scales, with strong changes in the concentration of near-bottom layers observed on time scales as short as two weeks (Sorochan et al. 2023). The processes leading to depletion of deep layers in late summer and fall are also uncertain, but horizontal transport, vertical mixing, and predation all likely contribute. While broad areas with the highest probability of suitable foraging habitat formation in the sGSL can be defined by analysis of the 3-D preyscape and species distribution modeling (Plourde et al. 2019, Plourde et al. 2024), the precise boundaries of important foraging areas in the sGSL at any given time are not well defined due to dynamic bottom processes in this area of low relief bottom bathymetry, likely leading to greater energy expenditure by NARW searching for suitable prey patches.

RISKS TO IMPORTANT FORAGING HABITAT IN THE SOUTHERN GULF OF ST. LAWRENCE

By identifying the processes influencing prey distributions and dynamics in the sGSL, risks to NARW foraging habitat in the region can be assessed. Declines in the abundance of *C. finmarchicus* in the GOM and on the Scotian Shelf, at the southern end of its contemporary range, and in the abundances of *C. hyperboreus* and *C. glacialis* on the Scotian Shelf were associated with warmer conditions in the 2010s and large-scale changes in northwest Atlantic Ocean circulation (Meyer-Gutbrod et al. 2021, Sorochan et al. 2019). Ocean warming in the GSL continued in the early 2020s, with warmer overall temperatures than in the late 2010s, including record high surface temperatures in the sGSL, northern GSL, and Estuary, record low

Cold Intermediate Layer volumes, and record high deep water (200 – 300 m) temperatures in the Cabot Strait observed during this period (DFO 2023, Galbraith et al. 2023). The spatial extent of anomalously warm deep temperature maxima in the GSL expanded since 2015, with temperatures > 7 °C extending into the northwest GSL, St. Lawrence Estuary, and northeast GSL in the early 2020s, reflecting changes in the deep offshore waters that supply the Laurentian Channel at the continental shelf break (Galbraith et al. 2023). These changes suggest that future warming outside of the historically observed range could pose a risk to *Calanus* spp. populations in the GSL, and indeed record low abundances of *C. hyperboreus* were observed in the northwest GSL in 2022 (Blais et al 2023). *Calanus hyperboreus* and *C. glacialis* are at the southern ends of their contemporary reproductive range in the GSL, where they would be expected to be most vulnerable to warming conditions (Lehoux et al. 2024).

During diapause, *Calanus* spp. reduce their metabolic rates to slow development and preserve energy stores for resumption of development and reproduction prior to the spring bloom (Miller et al. 1991, Hirche 1996). Warmer temperatures in deep water increase metabolic rates during diapause, leading to greater lipid depletion and the potential for higher mortality during diapause, lower egg production following diapause, and mismatches in emergence timing relative to the spring bloom (Plourde et al. 2003, Saumweber and Durbin 2006, Maps et al. 2012, Pierson et al. 2015). Changes in the seasonal timing of surface environmental variability can also influence *Calanus* spp. production dynamics. Along with surface warming, seasonal sea ice volume has also been declining in the GSL since 1990, with relatively high interannual variability in the 2010s and early 2020s. The timing of the spring bloom in the GSL is related to water column stratification following the breakup of the seasonal ice cover (de Lafontaine et al. 1991, Lavoie et al. 2021). Ice retreat and earlier spring bloom timing are associated with earlier *C. hyperboreus* developmental timing, while *C. finmarchicus* developmental timing and abundance are more related to the timing of spring warming (Lehoux et al. 2021). This suggests that future changes in these habitat properties might disrupt the inherent synchrony between key events of their life cycle and impact their overall production cycles.

Environmental changes, particularly warming, can affect prey quality for NARW. The size and lipid content of *Calanus* spp. are influenced by temperature and food conditions experienced during growth and development (Campbell et al. 2001, Helenius et al. 2023b). In copepods, growth and development in higher temperature environments leads to smaller body size (Campbell et al. 2001), and smaller *Calanus* spp. have a lower maximum capacity for lipid storage in their oil sacs (Miller et al. 2000, Renaud et al. 2018, Helenius et al. 2023b). Realized lipid storage (i.e., the proportion of the maximum capacity that is filled) is negatively impacted by poor food availability during preparation for diapause, through effects on energy allocated to storage (Båmstedt 1988, Hygum et al. 2000b, Miller et al. 2000, Wilson et al. 2015). Interannual changes in prey quality in the Bay of Fundy and regional variation in prey quality among warmer and cooler regions demonstrate the potential impact of warmer and more stratified conditions on prey quality (McKinstry et al. 2013, Helenius et al. 2023b).

While environmental changes in the sGSL pose risks to *Calanus* spp. population abundance, seasonal timing, and energy content, several factors support potential resilience in sGSL foraging habitat. First, the three *Calanus* spp. species in the sGSL have different expressions of diapause in their life cycle, providing potential for different responses to environmental change that may buffer declines in abundance and quality of the *Calanus* spp. complex as a whole. Projections of *Calanus* spp. abundance to the end of the 21st century, based on species distribution models and temperature-dependent body size, support this buffering capacity to some extent, predicting a decline in the abundances of *C. hyperboreus* and *C. glacialis* in the GSL, and an increase in *C. finmarchicus* abundance, with an overall decline in *Calanus* spp. biomass driven by the change in *C. hyperboreus* abundance (Lehoux et al. 2024). Species-

specific diapause patterns have potential to mitigate the impact of environmental change in different ways. *C. finmarchicus* is an income breeder that can produce more than one generation per year, which supports both a longer period of advective supply into the sGSL and local production in the sGSL. This characteristic spreads diapause entry timing over a longer period, which can mitigate the population impact of shorter diapause duration in warm deep water if individuals entering diapause later can survive to emerge just prior to the spring bloom (Saumweber and Durbin 2006, Maps et al. 2012). In contrast, the large size and high lipid storage capacity of *C. hyperboreus* supports survival through a long diapause duration, and its multi-year life cycle and life cycle plasticity can buffer the impact of interannual environmental variability (Falk-Peterson et al. 2009). However, its disappearance from the GOM following the cold 1960s period when a population was sustained there, and its projected declines in the GSL indicate the limits of its ability to adapt to warming (Conover 1988, Lehoux et al. 2024). Second, warming impacts may be mitigated in subregions with specific favorable population interactions with regional circulation, as observed in the Maine Coastal Current and downstream areas in the western GOM (i.e., Runge et al. 2014, Ji et al. 2017). The cool, nutrient rich, productive Maine Coastal Current supports *C. finmarchicus* growth and reproduction during the summer and supplies late-stage *C. finmarchicus* to deep waters in the western Gulf of Maine where diapausing stages are retained. This sub-regional process, termed the Coastal Amplification of Supply and Transport (CAST) hypothesis (Ji et al. 2017), reduces the impacts of warming and stratification observed in the broader Gulf of Maine. The St Lawrence Estuary – Gaspé Current region also has circulation features that may support production of certain zooplankton species despite broader regional warming. In this region, strong upwelling and vertical mixing cools and supplies nutrients to the surface layer, stimulating phytoplankton production, while the estuarine circulation pattern can transport deep dwelling plankton such as *Calanus* spp. and krill into this productive area and export them in surface waters to supply the northwest GSL and Gaspé Current (Plourde et al. 2003, Zakardjian et al. 2003, Benkort et al. 2020). This subregional interaction of *Calanus* spp. population growth and circulation may increase resilience of the upstream supply to the sGSL to increasing temperature and stratification in the GSL.

As described above, the abundance and distribution of *C. hyperboreus*, the dominant NARW prey in the sGSL in spring, are sensitive to variability in advective supply due to their short period of active development in surface waters. This was highlighted in the model results described above, simulating alternate transport pathways into the sGSL or along the southern edge of the Laurentian Channel. The short period of potential transport for *C. hyperboreus* poses a risk to spring sGSL foraging habitat, since supply can be reduced by a mismatch between the active period and variable advection into the interior of the sGSL, and results in strong interannual variability in *C. hyperboreus* abundance in the sGSL (Sorochan et al. 2019, Blais et al. 2023). Since *C. hyperboreus* phenology is related to spring bloom timing, which exhibits strong interannual variability (Le Corre et al. 2023, Blais et al. 2023), and the Gaspé Current path is influenced by drivers that change on short time scales (Brennan et al. 2021), interannual variability will likely continue to be a strong component of future changes in *C. hyperboreus* supply to the sGSL. A similar dynamic is likely for *C. glacialis*. The advective supply of *C. finmarchicus* to the sGSL is less sensitive to variability in circulation due to their longer active period in surface waters upstream of the sGSL, smoothing out variability in the Gaspé Current path over time. Overall, this suggests that there is greater risk to sGSL foraging habitat from changes in advective supply in spring than in the summer, especially given predicted future declines in *C. hyperboreus* and *C. glacialis* populations in the GSL (Lehoux et al. 2024). The potential for more substantial changes in GSL circulation beyond historical observations, for example due to changes in upstream water column density structure, has not yet been assessed.

CONCLUSIONS

Observations of high concentration prey layers, including layers with estimated energy densities in the range required for adult NARW in the sGSL, provide evidence that the sGSL is an important foraging habitat for NARW. The presence of the *Calanus* spp. complex (i.e., *C. finmarchicus*, *C. glacialis*, *C. hyperboreus*) and particularly their diapausing stages should be considered a key attribute of NARW foraging habitat in the sGSL. In this region, the environmental, oceanographic and bathymetric conditions that supply and aggregate high concentrations of prey recur annually. Development of suitable foraging habitat requires adequate *Calanus* spp. upstream population levels and transport of *Calanus* spp. into the sGSL via the Gaspé Current and other cross-shelf currents during their active periods in near-surface waters. High concentration layers of late stage *Calanus* spp. (i.e., > 1,000 individuals m⁻³) have mainly been observed near the bottom of the sGSL in spring and summer, where the interaction of seasonal or diel vertical migration and bottom depth contributes to aggregation. Since the sGSL is relatively shallow, mainly < 100 m, near-bottom aggregations are available for NARW feeding. *Calanus* spp. layers can also form in near-surface waters, with concentrations > 1,000 m⁻³ observed at several stations in fall 2018, but high concentration near-surface prey layers have not yet been observed near NARW in the sGSL.

Compared to foraging habitats in the GOM and on the western Scotian Shelf the species composition in the GSL, including large arctic *Calanus* spp., and regional differences in late stage *Calanus* spp. size and energy content appear to augment the quality of foraging habitat in the sGSL. The early active periods of the arctic *Calanus* spp., particularly *C. hyperboreus*, support development of near-bottom prey layers with high energy density as early as mid- to late-May. Supply to the sGSL in spring appears sensitive to the interaction of *C. hyperboreus* activity period and Gaspé Current dynamics, but once spatial patterns of near-bottom *C. hyperboreus* are set up in the sGSL on their descent, they may provide a relatively spatially predictable source of prey for NARW in late spring – early summer (Le Corre et al. 2023). As the dominance of *C. finmarchicus* in deep (> 50 m) layers increases in summer-fall, higher variability in near-surface drivers of *C. finmarchicus* supply and local production, along with spatially variable near-bottom circulation and *Calanus* spp. mortality, may contribute to a decline in the predictability of the spatial distribution of prey aggregations. This seasonal shift in the processes influencing prey distribution may contribute to changes in the pattern of NARW observations, from more tightly clustered in the Shediac Valley in May to June/July, to more dispersed through the sGSL and other GSL areas after July (St-Pierre et al. 2024, Crowe et al. 2021). Overall, the environmental and circulation changes that drove shifts in foraging habitat in the 2010s are ongoing, with potential for further impacts on foraging habitat in the future. Increasing temperature in surface waters and the deep Laurentian Channel and changes in seasonal sea ice dynamics and spring bloom timing may negatively impact *Calanus* spp. populations. However, differences in the life cycles and seasonal timing of the three GSL *Calanus* spp., and plasticity in their diapause responses, could provide greater resilience to change for the *Calanus* spp. complex in the GSL than for the *C. finmarchicus* dominated community in the GOM.

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