Reconciling Behavioural, Bioenergetic, and Oceanographic Views of Bowhead Whale Predation on Overwintering Copepods at an Arctic Hotspot (Disko Bay, Greenland)

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Bowhead whales (*Balaena mysticetus*) visit Disko Bay, West Greenland in winter and early spring to feed on *Calanus* spp., at a time of year when the copepods are still mostly in diapause and concentrated in near-bottom patches. Combining past observations of copepod abundance and distribution with detailed observations of bowhead whale foraging behaviour from telemetry suggests that if the whales target the highest-density patches, they likely consume 26–75% of the *Calanus* standing stock annually. A parallel bioenergetic calculation further suggests that the whales' patch selection must be close to optimally efficient at finding hotspots of high density copepods near the sea floor in order for foraging in Disko Bay to be a net energetic gain. Annual *Calanus* consumption by bowhead whales is similar to median estimates of consumption by each of three zooplankton taxa (jellies, chaetognaths, and predatory copepods), and much greater than the median estimate of consumption by fish larvae, as derived from seasonal abundance and specific ingestion rates from the literature. The copepods' self-concentration during diapause, far from providing a refuge from predation, is the behaviour that makes this strong trophic link possible. Because the grazing impact of the whales comes 6–10 months later than the annual peak in primary production, and because Disko Bay sits at the end of rapid advective pathways (here delineated by a simple numerical particle-tracking experiment), it is likely that these *Calanus* populations act in part as a long-distance energetic bridge between the whales and primary production hundreds or thousands of km away.

Keywords: Bowhead whale (*Balaena mysticetus*), *Calanus*, Arctic, optimal foraging, advection, zooplankton

1. INTRODUCTION

Calanus spp. and other calanoid copepods are a crucial link in mid- and high-latitude marine food webs, often dominating the biomass of primary consumers that transfer primary production to predators like fish, seabirds, and marine mammals (Falk-Petersen et al., 2007; Aarflot et al., 2017; Kimmel et al., 2017; Møller and Nielsen, 2020). These copepods might be thought of as the smallest members of the "wasp waist" (Hunt and McKinnell, 2006), the commonly observed trophic bottleneck at which the individual and population biology of a handful of species comes to have ecosystem-level consequences. Large-scale syntheses have suggested that the Arctic as a whole is a net sink for *Calanus* (Wassmann et al., 2015) and have begun to quantify the energy and carbon flux associated with the advective flux of *Calanus* spp. through the Arctic gateways (Basedow et al., 2018; Wassmann et al., 2019); but it is difficult to focus this general or bulk-biomass understanding down to the specifics of predation in particular hotspots. *Calanus* spp. have many predators, both they and their predators have patchy distributions and complex patterns of behaviour and selectivity, and it is possible that there is no system where the data exist to properly, empirically close the *Calanus* carbon budget.

Often this problem is dealt with using inverse food web models or other mass-balance approaches (Vézina and Platt, 1988; Aydin et al., 2002; Heath, 2012), which by definition harmonise incomplete and mismatched information into a smooth, best-guess picture. It is difficult, however, to make room in these approaches for the biology of particular predator species, or for that matter the biology of the prey. In this Brief Report we describe an alternate approach, intended to clarify the questions raised by past observations of a distinctive, particularly short Arctic food chain, from phytoplankton to copepods to bowhead whales, the largest Arctic marine mammal (Laidre et al., 2007; Simon et al., 2009; Moore, 2016).

After almost a century of absence, bowhead whales started to reappear in Disko Bay around 2000, and increased through the mid to late 2000s (Reeves and Heide Jørgensen, 1996; Heide-Jørgensen et al., 2007; Rekdal et al., 2014). These whales are part of the Eastern Canada-West Greenland stock that migrates in concert with annual sea-ice formation and break-up in the Canadian Arctic and along the west coast of Greenland (Eschricht and Reinhardt, 1861; Ferguson et al., 2010). Telemetry from 39 whales tagged in Disko Bay shows that these whales have high plasticity in their use of foraging areas in Baffin Bay and surrounding waters (Nielsen et al., 2015), but Disko Bay stands out in these behavioural data as a particular focus of foraging activity. In Disko Bay, they are typically found southwest of Disko Island (Eschricht and Reinhardt, 1861), an area thought to be a mating ground, based upon acoustic studies of singing whales (Stafford et al., 2008; Tervo et al., 2009), and the fact that few subadult whales or calves are observed there (Heide-Jørgensen et al., 2007, 2010).

The aggregation of bowhead whales in Disko Bay takes place earlier in the annual cycle than the appearance of capelin and other mobile predators that come to Disko Bay to feed on active *Calanus* in the surface layer. Studies of the whales' feeding behaviour have shown that mean dive depths are 50–100 m but also reach depths of >400 m. Most dives in winter and early spring target the bottom of the bay, with dive durations up to 40 min or even longer (Laidre et al., 2007). These patterns, along with analysis of stomach contents (Norden Andersen et al., 2014), support the idea that the whales are foraging on copepods that are still in diapause and aggregated at the bottom (Simon et al., 2009). Acoustic surveys (Laidre et al., 2007; Heide-Jørgensen et al., 2013) have shown that this copepod biomass is concentrated in a very dense near-bottom layer, and that whale dives matched the depth of this layer. The Disko Bay copepod community is dominated, in biomass terms, by three congeners, *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* (Swalethorp et al., 2011). Late spring sampling for *Calanus* in 13 years between 1992 and 2018 (Møller and Nielsen, 2020) has shown that the biomass of *C. finmarchicus* is correlated with the fraction of Atlantic water in deep Disko Bay, and accordingly is trending upward. The spring biomass of *C. glacialis* and *C. hyperboreus*, meanwhile, is correlated with ice cover, a relationship which might reflect either local growth conditions or variability in the intrusion of cold Baffin Bay water.

In this study, we synthesise the existing patchwork of observations (copepod and planktivore abundance patterns; bowhead whale foraging behaviour; bioenergetic parameters) and a simple numerical model experiment to address a pair of questions: first, what role does bowhead whale foraging on dormant *Calanus* have in the ecology of these copepod populations, compared with the role of their classical predators (macrozooplankton and fish larvae)? Second, what role does it play in the annual routine of the whales? These are as much questions of spatiotemporal scale as of energy or carbon budgets.

2. METHODS

2.1. Bowhead Whale Foraging Calculations

The magnitude of annual bowhead whale predation on copepods in Disko Bay was estimated by two semi-independent calculations, the first based on information in the literature about whale diving and foraging behaviour from telemetry, the second based on bioenergetics, following Laidre et al. (2007). Quantities used in these calculations are summarised in **Table 1**.

The annual clearance capacity of the bowhead whale population (in m³ of prey per year) can be written as

$$C = N_{graz} \, f_{graz} \, \Delta t_{graz} \, a_{mouth} \, u_{swim} \qquad (1)$$

The number of whales foraging in Disko Bay at any one time, N_{graz}, was taken from a snapshot aerial-survey estimate by Rekdal et al. (2014): 740 whales, 95% CI = 360–1,460. The foraging season was estimated as Feb–May (a duration Δt_{graz} = 120 d), although whales may arrive up to 2 weeks earlier or depart up to 2 weeks later in any given year (Laidre and Heide-Jørgensen, 2012). The fraction of time that an individual whale spends actively feeding during that period was estimated, based on visual observation of whales in the field, to be between 5 and 10 h per day (f_{graz} = 0.3 ± 0.1). Whale kinematics during foraging dives were described in detail by Simon et al. (2009)

Symbol	Definition	Units	Value	Uncertainty	Source
Habitat parameters					
A_{disko}	Bay area	km^2	6,000		Laidre et al., 2010; Laidre and Heide-Jørgensen, 2012
h_{cop}	Thickness of deep copepod layer	m	5	(2, 18)	Heide-Jørgensen et al., 2013, Figure 6
B_{cop}	Area-specific copepod biomass	gC m^{-2}	3.6	(0.14, 11)	
Foraging parameters					
N_{graz}	Number of whales foraging at one time		740	(360, 1,460)	Rekdal et al., 2014
a_{mouth}	Mouth area	m^2	4		Werth, 2004
u_{swim}	Bowhead swimming speed	m s^{-1}	0.7	± 0.1	Simon et al., 2009
Δt_{graz}	Duration of annual foraging period	d	120	± 15	Laidre et al., 2007
f_{graz}	Fraction of day actively foraging		0.3	(0.2, 0.4)	
Bioenergetic parameters					
E_{whale}	Indiv. metabolic requirement	kcal d^{-1}	1.1×10^6		Laidre et al., 2007, assuming 80% adult female + 10% adult male + 10% juveniles
e_{cop}	Energy density of copepods	kcal gC^{-1}	16		Weslawski et al., 1994, assuming 0.4 gC (g dry wt)$^{-1}$

using data from digital tags with three-axis accelerometers. Based on these observations, we assume that at the bottom of a U-shaped foraging dive, whale swimming speed u_{swim} is 0.7 m s^{-1}, corresponding to a filtration rate of 2.8 m^3 s^{-1} whale^{-1} for a mouth area of 4 m^2 (Werth, 2004).

The grazing rate G (in gC of prey per year) corresponding to the clearance rate C can be written

$$G = C \frac{B_{cop}^{graz}}{h_{cop}} \tag{2}$$

where h_{cop} is the thickness of the deep layer of overwintering copepods, and B_{cop}^{graz} is the areal prey density (gC m^{-2}) in the patches where bowhead whales feed. B_{cop}^{graz} is presumably greater than or equal to B_{cop}, the bay-wide average. The fraction of bay-total standing stock ($A_{disko}B_{cop}$) consumed by the whale population in each foraging season is then

$$F = \frac{C}{A_{disko} h_{cop}} \frac{B_{cop}^{graz}}{B_{cop}} \tag{3}$$

where A_{disko} is the area of the bay. Subscripts on F below denote particular estimates under contrasting sets of assumptions, whereas F by itself denotes the true value.

We estimated h_{cop} by digitising Figure 6 in Heide-Jørgensen et al. (2013), which gives detailed echosounder data from a survey on 6 May 2009 (evenly spaced image measurements, $n = 43$, ± 4dB from peak backscatter, digitisation error < 1%). The area-specific copepod biomass B_{cop} was estimated from data on *Calanus* spp. biomass in the upper 250 m of an approximately 300 m water column from April and May 1997–2012 at 69° 14' N, 53° 23' W ($n = 63$; Møller and Nielsen, 2020). Samples in 2016–2018 spanning only the upper 100 m (Møller and Nielsen, 2020) were excluded, although we expect that most of the *Calanus* biomass is in the upper water column during these months (Madsen et al., 2001; Swalethorp et al., 2011). Møller and Nielsen (2020) found

no long-term trend in *Calanus* biomass in Disko Bay (although the *C. finmarchicus* fraction has increased), and so the lack of recent years in the B_{cop} calculation is unlikely to be a major source of bias. Prosome length was measured for 10 individuals in each species/stage group, and the biomass was calculated using length:C-weight regressions from the literature (Hirche and Mumm, 1992; Madsen et al., 2001).These observations suggest an absolute density of animals within the near-bottom layer, in an order-of-magnitude sense, $\sim 10^4$ ind m^{-3} (calculated coarsely as B_{cop} / h_{cop} / 300 μgC ind^{-1}), consistent with a number of past studies that have also observed extremely dense near-bottom concentrations of copepods, up to 65,000 ind m^{-3} (Hirche et al., 2016).

The ratio B_{cop}^{graz}/B_{cop} is a measure of the whales' patch selectivity in an areal sense, which we bracket with a pair of estimates that provide lower and upper bounds on F. A simple lower bound could be determined by setting $B_{cop}^{graz} = B_{cop}$, a scenario in which the whales choose foraging areas at random (while still optimising their position in the vertical):

$$F_{random} = \frac{C}{A_{disko} h_{cop}} \tag{4}$$

This lower bound can be refined by dividing by a factor $(1 - F)$ to account for the fact that the net samples from which we estimated B_{cop} were taken at the end of the whale foraging period:

$$F_{min}^{graz} = \frac{F_{random}}{1 - F_{random}} \tag{5}$$

A complementary upper bound F_{max}^{graz} can be determined as the point at which B_{cop}^{graz} equals the average over percentiles $(1 - F) \cdot 100$–100% of copepod areal densities in our net-sample data, i.e., a scenario in which the whales choose the highest-density patches available (assuming that areal variance in copepod density is comparable to the temporal variance across our 63 samples

at one station over multiple years). F_{max}^{graz} is awkward to write algebraically but straightforward to calculate numerically.

Finally, F can also be estimated via bioenergetic considerations. An alternate lower bound F_{min}^{ener} is the break-even point at which the total energy content of ingested prey, $G\,e_{cop}$, balances the metabolic costs of the foraging population during the foraging period:

$$G\,e_{cop} = E_{whale}\,N_{graz}\,\Delta t_{graz} \tag{6}$$

(see **Table 1**). This criterion is equivalent to

$$F_{min}^{ener} = \frac{E_{whale}\,N_{graz}\,\Delta t_{graz}}{A_{disko}\,B_{cop}\,e_{cop}} \tag{7}$$

Median estimates and confidence limits on these calculations were determined by a Monte Carlo procedure ($n = 100{,}000$) in which the six key parameters were represented as distributions (**Table 1**). Bootstrap statistics were used for h_{cop} and B_{cop} (i.e., resampling with replacement of individual observations, $n = 43$ and $n = 63$, respectively); a lognormal distribution was assumed for N_{graz}; and normal distributions were used for $u_{swim}\,\Delta t_{graz}$, and f_{graz}. This approach to uncertainty is a compromise between simply writing out the arithmetic in the equations above on the back of an envelope, and giving up entirely on quantifying this trophic link because of data limitations.

2.2. Foraging by Other Predators

For comparison, potential consumption of copepods by four other taxa was estimated using abundance estimates from monthly sampling during 1996–97 and weekly to bi-weekly sampling April–June 2008 (Swalethorp et al., 2011). Sampling in 1996–97 was carried out with a WP-2 net (200 μm mesh size) or with a submersible pump (3,000 l min^{-1}) equipped with a conical net (50 μm mesh size). Additional hauls were conducted with a Hensen net (50 μm mesh size) in order to sample nauplii. All sampling devices were equipped with a flowmeter (Madsen et al., 2001). Sampling in 2008 was with a 50 μm Hydrobios Multinet. Associated length measurements were converted to individual biomass using literature relationships (fish larvae, Froese, 2006; the jelly *Aglantha digitale*, Matthews and Hestad, 1977; the chaetognath *Sagitta elegans*, Conway and Robins, 1991; the predatory copepod *Paraeuchaeta* spp., Tönnesson et al., 2006). Amphipods and krill, other potential predators, are not included in this analysis because the sampling net used does not reliably collect the large individuals that prey on *Calanus* spp.

Individual biomass was used to estimate total daily ingestion capacity per predator taxon using allometric relationships at $0°C$ from Kiørboe and Hirst (2014). For simplicity, these were not corrected for temperature. Abundance measurements and the corresponding ingestion estimates were categorised into three seasons—"winter" (November to mid-April, 165 d), "bloom" (mid-April to end of May, 45 d), and "summer/autumn" (June to October, 155 d)—in order to scale up, coarsely, to an estimate of annual copepod consumption per predator type (**Table 2**). Estimates of annual consumption were determined by a Monte Carlo procedure, using bootstrapping for abundance and assuming normal distributions for the mean and intercept

of log individual ingestion rates (**Table 1** in Kiørboe and Hirst, 2014). These are necessarily high per-taxon estimates, since they assume prey-saturated ingestion 24 h per day.

2.3. Large-Scale Transport and Connectivity

Parallel to these energetic calculations, we used a simple numerical particle-tracking experiment to estimate the potential area of ocean from which the copepods ingested by bowhead whales in Disko Bay might be derived. Virtual particles were tracked in a 10-year hindcast (2008–2017) of the pan-Arctic SINMOD model run at 20 km horizontal resolution (Slagstad et al., 2015; Armstrong et al., 2019). Particles were tracked from 1 Apr of each year until 1 Apr of the next, using 0–150 m average currents to mimic shelf-depth transport during the copepods' likely active period (1 Apr–30 Sep), followed by slope-depth currents (150–500 m) during the likely diapause period (1 Oct–1 Apr). In reality, copepod behaviour interacts with velocity shear in ways we have not attempted to model here (although a sensitivity experiment suggests that this interaction has only a secondary effect on the scale of transport in this robust boundary-current system). Likewise the physical dynamics of the entrance sill itself are beyond the reach of available circulation models.

3. RESULTS

The lower bound on bowhead whale ingestion F_{min}^{graz} was estimated to fall between 0.08 and 0.39 (95% c.l.s), with a median value of 0.17, and the corresponding upper bound F_{max}^{graz} was found to fall between 0.26 and 0.75, with a median estimate of 0.44 (**Figure 2**). The ratio of these median estimates is 2.6, implying that despite the huge observed variance in copepod biomass, lateral patch selectivity can at most increase the whales' prey intake by less than a factor of three (In contrast, vertical selectivity, foraging within the deep overwintering layer, is crucial: if the whales' prey were spread over a layer 50 m thick instead of approximately 5 m, F and G would drop by factor of 10). F_{max}^{graz} corresponds to a median estimate of G, annual consumption of *Calanus* by bowhead whales in Disko Bay, of 1.6 gC m^{-2} yr^{-1} (c.l.s 0.90, 2.8).

The alternate lower bound derived from bioenergetic considerations, F_{min}^{ener}, is 0.28 (c.l.s 0.15, 0.54: **Figure 2**). This estimate is only slightly lower than F_{max}^{graz}, suggesting that patch selectivity by the whales is likely quite high, and in fact necessary if Disko Bay spring foraging is to provide a net benefit to them energetically. Of the three variants of the F estimation, F_{max}^{graz} is thus the most plausible biologically. A more involved estimation of F, based on the joint probability that a given value is greater than F_{min}^{graz} and F_{min}^{ener} and less than F_{max}^{graz}, gives very similar confidence limits.

To summarise, one can construct a consistent picture of predator and prey abundance patterns, foraging kinematics, and whale bioenergetics if the aggregation of whales in Disko Bay consumes 26–75% of the standing stock of copepods each winter/spring. This level of annual grazing is equivalent to 0.90–2.8 g C m^{-2} yr^{-1}.

TABLE 2 | Measurements of abundance and individual size, and estimates of individual biomass and ingestion capacity for four taxa of predators on copepods.

Taxon	Season[a]	Abundance	S.d.	n	Mean length mm	Indiv. biomass[b] mgC	Mass-specific ingestion rate[c] d⁻¹	Ingestion by pop. per day mgC m⁻² d⁻¹	Ingestion by pop. per year gC m⁻² yr⁻¹
Fish larvae	Winter	0.7		3	3.3	0.12	0.18	0.0081	**0.19**
	Bloom	27		1	3.3	0.12	0.18	0.57	(0.02, 1.9)
	Summer	17	9	7	10.4	4.2	0.029	1.72	
Jellies	Winter	18	15	6	3.1	0.062	0.25	0.16	**0.78**
(*A. digitale*)	Bloom	82	25	12	12.5	4.3	0.029	9.7	(0.09, 6.7)
	Summer	21	6	4	10.1	2.3	0.040	1.7	
Chaetognaths	Winter	130	50	9	13.0	0.070	0.093	0.80	**0.87**
(*S. elegans*)	Bloom	560	140	13	17.1	0.17	0.057	5.3	(0.61, 1.2)
	Summer	560	130	11	14.3	0.093	0.080	4.0	
Predatory	Winter	33	12	6	1.7	0.021	0.67	0.45	**2.3**
copepods	Bloom	440	70	12	1.8	0.025	0.65	7.1	(1.2, 3.9)
(*Paraeuchaeta*)	Summer	500	160	4	2.1	0.042	0.58	12	
Bowhead whales									**1.6[d]**
									(0.90, 2.8)

An estimate of area-specific grazing on copepods by bowhead whales is given for comparison. Total ingestion by population per year is reported as 50th (5th, 95th) percentiles of Monte Carlo estimates. Bold values are the 50th.
[a]*Winter = yeardays < 105 and > 250; bloom = yeardays 105–150; summer = yeardays 150–250.*
[b]*Sources for length-weight relationships: Fish larvae, Froese (2006); A. digitale, Matthews and Hestad (1977); S. elegans, Conway and Robins (1991); Paraeuchaeta spp., Tönnesson et al. (2006).*
[c]*Mass-dependent specific ingestion rates by taxon from Kiørboe and Hirst (2014). A. digitale is assumed to follow the same allometry as fish larvae.*
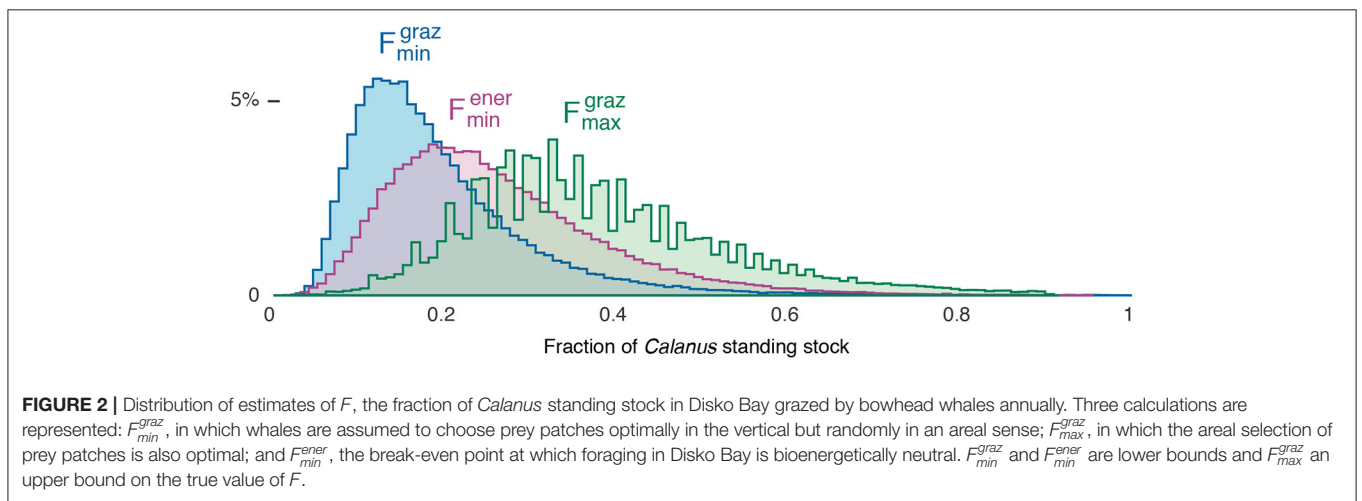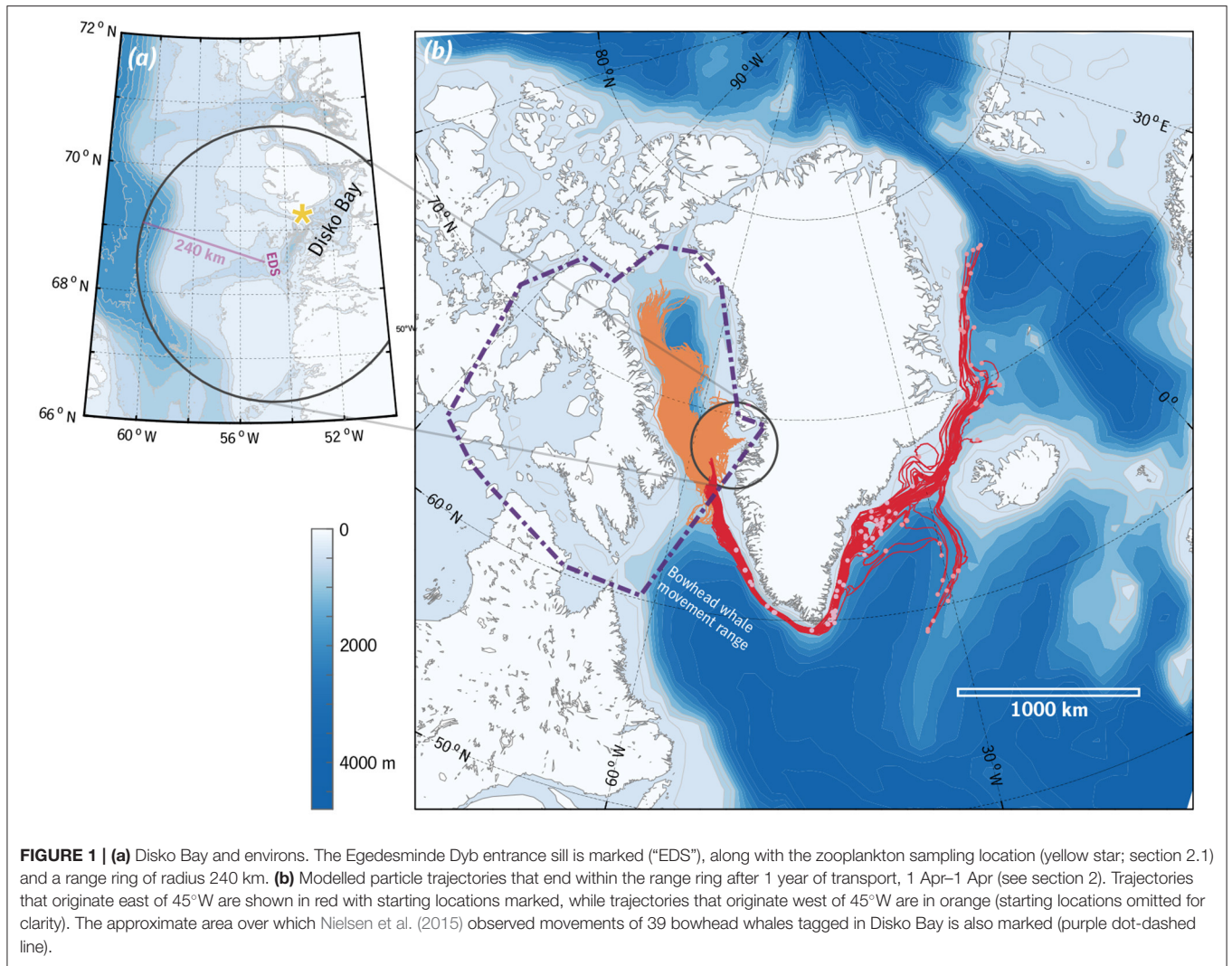[d]*Estimates of G corresponding to F_{max}^{graz}.*

Estimates of grazing by other taxa (**Table 2**) are extremely variable, in part because of the sparsity of abundance observations relative to their natural patchiness, but even moreso because of uncertainty in lab-based estimates of specific ingestion rates (Kiørboe and Hirst, 2014). Our estimate of annualised bowhead whale grazing is comparable to the median estimates of consumption by jellies, chaetognaths, and predatory copepods, and an order of magnitude greater than the median estimate of consumption by fish larvae, although we cannot rank these consumption levels with any confidence. This comparison rather serves as a consistency check. As shown above, bowhead whale grazing appears to be a first-order process relative to copepod standing stock, and here we confirm that there is no reason to believe it is not first-order in comparison with other predators. Note again that the simple assumptions behind the zooplankton- and fish larvae estimates (no correction for prey selectivity, or vertical or temporal predator-prey overlap) almost certainly bias these estimates high.

Particle tracking (**Figure 1**) suggests the distances over which an advected *Calanus* community found in the vicinity of the Egedesminde Dyb entrance sill might have travelled in 12 months. The envelope of these trajectories encompasses northeastern Baffin Bay and the Greenland shelf and slope as far eastward as Fram Strait, as well as a portion of the Irminger Current in deeper waters southeast of Greenland: up to 3,700 km of transport. Note that in reality, smaller-scale circulation patterns and interactions between vertical migration and current shear might well reduce, or even increase, this net transport.

4. DISCUSSION

4.1. Implications for the Bowhead Whale Population

Comparison of two independent estimates of bowhead whale grazing (F_{max}^{graz} vs. F_{min}^{ener}, **Figure 2**) indicates that bowhead whales must be extremely efficient at finding hotspots of high density copepods near the sea floor in order for foraging in Disko Bay to be a net energetic gain. They must target the right depths and at the same time be in the right areal patches in order to be effective. It is unknown how bowhead whales locate the hot spots of high-density prey. There may be some local memory involved, bathymetric features that signal good areas for foraging, or potentially, as has been suggested for other species, visual cues (Cronin et al., 2017; Fasick et al., 2017). Bowhead whales likely rely on their extreme blubber layer, the largest of any marine mammal, as a buffer against the extreme patchiness and episodic accessibility of their prey, allowing them to go for long periods without foraging. At the same time, the provisional calculations above indicate that there is not an unlimited amount of copepods in Disko Bay for a growing bowhead aggregation, which may thus be prey-limited. The whales already consume a first-order fraction of what is available, using near-optimal patch selection in both the horizontal and the vertical. Accordingly, it is likely that any future substantial increases in the size of this population of whales or the density of animals foraging in West Greenland in spring would require the whales to expand to other foraging grounds.

FIGURE 1 | (a) Disko Bay and environs. The Egedesminde Dyb entrance sill is marked ("EDS"), along with the zooplankton sampling location (yellow star; section 2.1) and a range ring of radius 240 km. **(b)** Modelled particle trajectories that end within the range ring after 1 year of transport, 1 Apr–1 Apr (see section 2). Trajectories that originate east of 45°W are shown in red with starting locations marked, while trajectories that originate west of 45°W are in orange (starting locations omitted for clarity). The approximate area over which Nielsen et al. (2015) observed movements of 39 bowhead whales tagged in Disko Bay is also marked (purple dot-dashed line).

FIGURE 2 | Distribution of estimates of F, the fraction of *Calanus* standing stock in Disko Bay grazed by bowhead whales annually. Three calculations are represented: F_{min}^{graz}, in which whales are assumed to choose prey patches optimally in the vertical but randomly in an areal sense; F_{max}^{graz}, in which the areal selection of prey patches is also optimal; and F_{min}^{ener}, the break-even point at which foraging in Disko Bay is bioenergetically neutral. F_{min}^{graz} and F_{min}^{ener} are lower bounds and F_{max}^{graz} an upper bound on the true value of F.

4.2. Implications for *Calanus* Populations

If the "classical" view of marine food chains focuses on predatory zooplankton and fish larvae as consumers of *Calanus*, then the trophic link to bowhead whales fails to conform to the classical picture in at least two ways. Bowhead whales are big, violating the rules-of-thumb of predator-prey size ratios, and they graze on *Calanus* in Disko Bay not during but earlier in the year than the period of significant primary and secondary production. This raises the possibility that their ingestion of *Calanus* in Disko Bay is significantly decoupled from the production of *Calanus* in space and not merely in time.

C. finmarchicus in this region have a typical generation length of 1 year, *C. hyperboreus* in Disko Bay appear to have a 2-year cycle, and *C. glacialis* might follow either pattern (Madsen et al., 2001; Daase et al., 2013; Banas et al., 2016). If a cohort of *C. finmarchicus* grew in summer of 1 year and then were consumed by bowhead whales late the following winter, then the temporal separation between the phytoplankton–copepod and copepod–whale trophic links is 7–11 months. For a *Calanus* cohort with a multi-year life cycle, the temporal lag between growth on phytoplankton to consumption by bowhead whales might be a full year longer. The particle-tracking experiment shown in **Figure 1** for illustrative purposes spans 12 months, a middle value among these life-cycle-dependent temporal lags.

Whatever fraction of the late-winter *Calanus* population has arrived via the annual winter overturning of the deep layer (Gladish et al., 2015) is likely to have travelled hundreds or thousands of km (**Figure 1**) during that lag. We do not know what fraction of the population this is, but given that subarctic *C. finmarchicus* have increased in concert with the Atlantification of Disko Bay's physical water properties over the past decades (Møller and Nielsen, 2020), there is no reason to think that it is small. There is no continuous path into the Disko Bay deep basins except across ∼200 km of shallower habitat, and so whether one imagines the *C. finmarchicus* and *C. hyperboreus* found in the basins at the end of winter to have travelled throughout the winter at shelf depth, to have appeared recently from deep Baffin Bay, or to represent local production that avoided the winter flushing, one is faced with a transport puzzle, a behavioural puzzle, or both. Clarifying this picture will require well-coordinated biophysical observations and modelling; it is not simply a matter of improving circulation models.

Laidre et al. (2010) found extremely low correlation between local satellite-derived chlorophyll estimates and the location and timing of bowhead whale foraging in Disko Bay, and in light of the results above, this is not surprising: not merely because detecting correlations in a patchy, undersampled ocean is difficult, but because it seems likely that Disko Bay itself is only one of several regional seas in which one needs to look for the phytoplankton that feed Disko Bay's copepods and whales. If so, then Disko Bay joins a provocatively long list of case studies in which high-latitude bowhead and right whales have been found to forage on mesozooplankton prey advected from elsewhere (Rogachev et al., 2008; Ashjian et al., 2010; Walkusz et al., 2012; Boertmann et al., 2015; Brennan et al., 2018).

4.3. Is Diapause Maladaptive in Disko Bay?

Instead of analyzing this and similar situations in terms of advection of biomass and energy (the source–sink framework), it might be useful to analyze them in terms of advection of traits and strategies. A few trait-based model studies have considered balances between trait advection and local selection in phytoplankton (Clayton et al., 2013), but these frameworks have not been extended to long-lived mesozooplankton. In particular, it is not clear whether diapause, or remaining in diapause into Feb–Apr, can be said to provide any benefit to *Calanus* spp. in Disko Bay.

Diapause in copepods is usually explained in terms of three advantages that it confers: (i) reduction of energetic losses through partial metabolic shutdown, (ii) reduction of energetic losses through cold water temperature, and (iii) reduction of predation losses. Explanation (ii) does not apply in Disko Bay, because the influence of ice and the west Greenland current means that bottom water is not generally colder than surface water (Hansen et al., 2012; Gladish et al., 2015). Explanation (i) is more difficult to evaluate, but Swalethorp et al. (2011) found that all three species of Calanus in Disko Bay have ample storage lipids remaining at the end of winter (wax esters 35–70% of total body carbon in late March 2008). This suggests that these populations are well above the threshold of winter starvation, such that the timing of exit from diapause in spring has at most an indirect effect on their population viability. Finally, our results show that explanation (iii) fails to hold in Disko Bay: predation by whales during diapause is intense, and it is specifically the concentration of the copepods in a near-bottom layer that makes it possible.

It is likely, however, that the adaptive value of diapause is very different in Baffin Bay and along the larger-scale advective pathways to which Disko Bay connects. Bottom depth is one crucial factor: in the East Greenland Sea, for example, *C. hyperboreus* overwinters at 2300–2500 m (Hirche et al., 2006), far below the diving range of bowhead whales. *C. glacialis* is generally regarded as a shelf species, but *C. finmarchicus* and *C. hyperboreus* in Disko Bay can perhaps be thought of as trapped in a relatively shallow environment where the deep (> 500 m) winter habitat they are typically associated with is unavailable (Kvile et al., 2019).

5. SUMMARY

To review, the most self-consistent picture we can construct, from many lines of fragmentary evidence, is that bowhead whales consume between 26–75% of the spring standing stock of *Calanus* in Disko Bay, despite this consumption taking place during copepod diapause, which is often assumed to be a predation refuge. This is also a time of year at which many of the *Calanus* being consumed are likely to have been recently advected into Disko Bay with the deep overturning circulation. These dynamics create the possibility of a strange symmetry in which a significant fraction of the whales' copepod prey arrive in Disko Bay at the same time that the whales arrive to eat them, having traversed similar distances over their annual routine (**Figure 1b**).

The information demands for fully tracing such long-distance energy flows are high, spanning multiple scales of physical

oceanography as well as many trophic levels, from foraging behaviour and diet preferences to abundance patterns, transport speeds, and changes in lower-trophic production in advectively upstream regions. However, it may prove that relatively small, tenuous amounts of information on all these scales are enough to establish which species, processes, and ocean regions are leading elements of the story linking climate change to a particular predator population. Our calculations above illustrate the idea that triangulating among several independent, competing estimates of a trophic link (**Figure 2**) can yield a coherent picture even when it is impossible to properly close mass balances. In this case, the results highlight a need to expand our perspective on *Calanus* predation along the predator size spectrum and across the map.

DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: Our analysis consists of re-analysis and integration of observational and numerical data previously described in the peer-reviewed literature. Requests to access these datasets should be directed to Neil Banas, neil.banas@strath.ac.uk.

AUTHOR CONTRIBUTIONS

NB, TN, and EM conceived the study, and together with KL and MS compiled data and performed the foraging calculations. NB and IE performed the circulation model analysis. All authors contributed to the interpretation of results and the writing of the manuscript.

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