Benthic habitat is an integral part of freshwater Mysis ecology

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Abstract

1. Diel vertical migration (DVM) is common in aquatic organisms. The trade-off between reduced predation risk in deeper, darker waters during the day and increased foraging opportunities closer to the surface at night is a leading hypothesis for DVM behaviour.

2. Diel vertical migration behaviour has dominated research and assessment frameworks for Mysis, an omnivorous mid-trophic level macroinvertebrate that exhibits strong DVM between benthic and pelagic habitats and plays key roles in many deep lake ecosystems. However, some historical literature and more recent evidence indicate that mysids also remain on the bottom at night, counter to expectations of DVM.

3. We surveyed the freshwater Mysis literature using Web of Science (WoS; 1945–2019) to quantify the frequency of studies on demographics, diets, and feeding experiments that considered, assessed, or included Mysis that did not migrate vertically but remained in benthic habitats. We supplemented our WoS survey with literature searches for relevant papers published prior to 1945, journal articles and theses not listed in WoS, and additional references known to the authors but missing from WoS (e.g. only 47% of the papers used to evaluate in situ diets were identified by WoS).

4. Results from the survey suggest that relatively little attention has been paid to the benthic components of Mysis ecology. Moreover, the literature suggests that reliance on Mysis sampling protocols using pelagic gear at night provides an incomplete picture of Mysis populations and their role in ecosystem structure and function.

5. We summarise current knowledge of Mysis DVM and provide an expanded framework that more fully considers the role of benthic habitat. Acknowledging benthic habitat as an integral part of Mysis ecology will enable research to better understand the role of Mysis in food web processes.

KEYWORDS
detritus, diel vertical migration, mysids, omnivore, predation risk
INTRODUCTION

In many deep freshwater systems, macrocrustaceans of the genus *Mysis* play important roles in the food web (Devlin et al., 2016; Lasenby, Northcote, & Furst, 1986; Sierszen et al., 2014). *Mysis* spp. are omnivorous (Grossnickle, 1982) and can feed on detritus, phytoplankton, benthic invertebrates, zooplankton, and even fish embryos (Seale & Binkowski, 1988). *Mysis* can alter ecosystem structure and function through intense predation on zooplankton, which results in competition with planktivorous fishes (Ellis et al., 2011; Goldman, Morgan, Threlkeld, & Angeli, 1979; Martinez & Bergersen, 1991). In addition to their competitive roles in food webs, *Mysis* also serves as an important prey for both benthic and pelagic prey fishes and juvenile life-stages of many piscivorous fish species (Elrod & O’Gorman, 1991; Gambling, Hrabik, Stockwell, & Yule, 2011; Gambling, Hrabik, Yule, & Stockwell, 2011).

*Mysis* exhibit diel vertical migration (DVM), whereby individuals ascend to the pelagic zone as light levels decline at sunset, and then descend to the bottom as sunrise approaches (Beeton & Bowers, 1982). Temperature and light gradients define pelagic conditions that limit the vertical extent of *Mysis* migration (Boscarno, Rudstam, Minson, & Freund, 1989; Boscarno, Rudstam, Tallbass, Janssens, & Loew, 2010; Gal, Rudstam, & Johannsson, 2004; Rudstam, Danielsson, Hansson, & Johannsson, 1989; Teraguchi, Hasler, & Beeton, 1975). *Mysis* assessments and specimen collections are often conducted at night, when *Mysis* can be sampled with relative ease using pelagic nets and hydroacoustics (Jude et al., 2018; McCoy, 2015; Watkins et al., 2015). For example, standard sampling protocols for *Mysis* in the Laurentian Great Lakes call for pelagic sampling to commence 1 hr post-sunset when the population is assumed to have migrated (EPA, 2015). Such sampling strategies are based on the assumption that all or most of the population regularly migrates to the pelagic zone at night and that resultant samples quantitatively represent the population.

Recent studies, however, indicate that *Mysis* exhibit partial DVM, whereby a portion of the population does not ascend but remains on bottom at night (Euclide, Hansson, & Stockwell, 2017; Ogonowski, Duberg, Hansson, & Gorokhova, 2013; O’Malley, Dillon, Paddock, Hansson, & Stockwell, 2018; O’Malley, Hansson, & Stockwell, 2018). Although partial DVM in *Mysis* has been observed in a number of systems including the Laurentian Great Lakes (Bowers, 1988; Johannsson, Rudstam, Gal, & Mills, 2003) and the Baltic Sea (Rudstam et al., 1989), the magnitude of the population that remains benthic at night is not well understood and this portion of the population is typically excluded from population assessments and evaluations of the importance of *Mysis* in the ecosystem. We surveyed the literature to evaluate the extent to which benthic *Mysis* have been included in research. We restricted our analyses to freshwater *Mysis* (Porter, Meland, & Price, 2008) except for the marine *Mysis mixta*, as this species has been extensively studied in the Baltic Sea where it coexists with freshwater congenerics *Mysis relicta* and *Mysis salemaai* and has similar ecological roles (Salemaa, Tyyssjärviņu, & Aron, 1986; Salemaa, Vuorinen, & Välipakka, 1990). Our survey results suggest that benthic habitat is more important to *Mysis* ecology than previously assumed, and is necessary to consider this to better understand *Mysis*’s production and its roles in food webs. We conclude with a set of questions and hypotheses to help frame research directions to fill in knowledge gaps in *Mysis* ecology.

LITERATURE SURVEY ON *MYYSIS* ECOLOGY

We conducted literature surveys for three aspects of freshwater *Mysis* ecology—demographics, in situ diets, and experiments that examined *Mysis* feeding behaviour. Each survey was initiated using Web of Science (WoS) with varying sets of search terms, spanning 1945–2019. For demographics, we surveyed WoS using the terms “*Mysis*” AND “abundance OR density” OR “biomass” OR “growth OR size OR length OR distribution” under the field “Topic.” We used the terms “*Mysis*” AND “diet OR gut OR stomach” under the field “Topic” to survey WoS for in situ diets. For experiments on *Mysis* feeding behaviour, we used two sets of terms under the field “Topic”. The first included “*Mysis*” AND “feeding OR predation” AND “experiment” under the field “Topic”, and the second included “*Mysis*” AND “contaminant* OR toxi*” under the field “Topic”.

We examined the resultant titles and abstracts for relevance to each topic, and extracted the relevant information from each study. However, several relevant papers were not identified by the WoS search. For example, at the conclusion of the literature survey, only 47% of the papers used to evaluate in situ diets were identified by WoS. Therefore, during the survey, we examined the cited references in all relevant papers that were published prior to 1945 (the earliest year for WoS search), journal articles and theses that were not listed in WoS, and additional references known to the authors. We did not include papers that developed new sampling devices (Lasenby & Sherman, 1991) or relied solely on acoustics without net samples (Levy, 1991; Miller, 2003). Papers that relied on previously published values (Morgan, 1985; Morgan, Threlkeld, & Goldman, 1978; Sell, 1982; Sullivan & Rudstam, 2016) were not included. Theses and dissertations were included unless data were published in peer-reviewed literature. In those cases (e.g. Morgan, 1985), information from the published papers was used. Studies that reported metrics but no methods were excluded (Adare & Lasenby, 1994; Lasenby & Langford, 1972). More details are provided in Tables S1–S3, and the results are summarised below. Also note that *Mysis* taxonomy was revised in the mid-2000s, with new names given to four sibling species formerly known as *M. relicta* (*M. salemaai*, *Mysis segerstaehl*, *Mysis diluviana*, and *M. relicta*; Audžiūnaitė & Väinölä, 2005). With the exception of the high Arctic, the only mysid species in North America is *M. diluviana*. Even so, wherever we report a particular species, we refer to the name used in the cited publication.

The results of the literature survey clearly show that freshwater *Mysis* research has largely ignored benthic-caught individuals and their benthic environment (Figures 1 and 2). *Mysis* demographics (*n* = 142 total studies) included benthic-caught individuals in a
minority of studies, ranging from 15% of the studies that estimated 
biomass (n = 40) to 40% of studies that assessed life-stages (n = 76; 
Figure 1; Table S1). Conversely, such estimates were based solely 
on pelagic-caught individuals in 60–85% of demographic studies. 
However, in a handful of studies which sampled pelagic and benthic 
habitats at night, variable but potentially very high proportions of 
vertebrates (Johannsson et al., 2001, 2003; Lasenby & Shi, 2004; 
Lehtiniemi, Kiljunen, & Jones, 2009; Lehtiniemi, Viitasalo, & 
Kuosa, 2002; Parker, 1980). Pelagic-caught individuals were solely 
examined in 56% of the identified in situ diet studies (Table S2).

Our survey of in situ diet studies revealed that benthic-caught 
Mysis were examined in only 44% of identified studies (n = 32 total 
studies; Table S2), despite their well-known benthic distributions 
and omnivorous diets, which can include detritus and benthic invertebrates (Johannsson et al., 2001, 2003; Lasenby & Shi, 2004; 
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Detritus was reported in Mysis stomachs in 19 of the 32 studies, 
including nine of 10 studies that included both benthic- and pelagic-caught Mysis, and somewhat surprisingly, in eight of 18 studies that only examined pelagic-caught Mysis. If mysids feed continuously 
when on bottom, then pelagic-caught Mysis sampled early in 
the night, soon after ascent, may still contain benthic resources in 
their guts. The remaining 10 pelagic-only studies did not include detritus as a possible prey category (Table S2). In a recent study, 
benthic-caught Mysis during the night and day had similar amounts of 
detritus in their stomachs, suggesting that Mysis feed continuously 
when on the bottom (O’Malley & Stockwell, 2019) and benthic re-
sources are likely to contribute significantly to Mysis growth and 
production (Lehtiniemi et al., 2002; Sierszen, Kelly, Corry, Scharold, & Yurista, 2011; Whall & Lasenby, 2009).

We also found that Mysis feeding ecology experiments (n = 58 
total studies) used benthic- or combined benthic- and pelagic-caught 
individuals in only 21% of the studies, whereas 43% of the studies 
used only pelagic-caught individuals and 36% did not report the hab-
abitat from which Mysis were captured for the experiments (Table S3). 
Pelagic zooplankton was by far the most used prey item in feeding 
experiments (>90% of experimental studies), followed by brine 
shrimp Artemia, which is not a natural prey of Mysis (22% of studies; 
Figure 2, Table S3). We found few studies where detritus, benthic in-
vertebrates, or algae were used in experiments (n ≤ 7 each, Figure 2, 
Table S3) despite their presence in field diets (see Role of benthic food 
resources below).

The lack of historical focus on the benthic environment may bias 
our basic understanding of Mysis ecology and the role of Mysis in eco-
systems. As evidenced by findings from studies that have examined 
benthic and pelagic Mysis at night (Table 1), only a fraction of a pop-
ulation may inhabit the pelagic environment at night (Naesje, 1995). 
The ecology of Mysis is more complex than that of an animal simply 
hiding on the bottom during the day waiting for the cover of dark-
ness to migrate up the water column at night to feed on plankton.

Researchers have probably focused on the pelagic phase of 
Mysis for several reasons. First, Mysis DVM has been assumed to 
be a population-level phenomenon and consequently, night pelagic 
samples should provide representative estimates of abundance and 
other population demographics. Second, pelagic habitat is easier to 
sample than benthic habitat. Sampling devices towed along the bot-
tom can fill with substrate (e.g. mud, silt, detritus, dreissenid muss-

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TABLE 1 Compilation of studies documenting partial diel vertical migration in Mysis spp. (Mysis diluviana, Mysis relicta, Mysis mixta, Mysis salameii) at night. Studies that did not report quantitative values of Mysis spp. on bottom at night were only included if they reported presence/absence

| Species      | Water body | Depth (m) | % on bottom at night | Method       | Source                                |
|--------------|------------|-----------|----------------------|--------------|---------------------------------------|
| M. relicta   | Superior   | 250       | 50                   | Submarine; Net | Bowers (1988)                         |
| M. relicta   | Snasvatnet | 48        | 23–70                | Sled; Net    | Moen and Langeland (1989)             |
| M. relicta   | Jonsvatn   | 10–80     | 7–84\(^{a}\)        | Sled; Net    | Naesje et al. (2003)                  |
| M. mixta     | Baltic     | 28–40     | 30                   | Sled; Net    | Rudstam et al., (1989)                |
| M. relicta   | Ontario    | 35–100    | < 5                  | Sled; Net    | Shea and Makarewicz (1989)            |
| M. relicta   | Breiter, Schmaler Luzin | 14–40 | Pr  | Scuba; Net | Waterstraat, Krappe, Riel, and Rumpf (2005) |
| M. relicta   | Ontario    | 35–75     | Pr                   | Predator diet | Brandt (1986)                        |
| M. mixta, M. relicta, M. salemaii | Ontario | 125      | Pr                   | Sled; Net    | Johannsson et al. (2001), Johannsson et al. (2003) |
| M. relicta, M. salemaii | Baltic | 20–40     | 15                   | Camera       | A. Staaf & S. Hansson (unpublished data, Stockholm Univ.) |
| M. diluviana | Baltic     | 30–35     | Pr                   | Sled         | Ogonowski et al. (2013)               |
| M. diluviana | Champlain  | 70–120    | Pr                   | Sled         | Euclide et al. (2017)                 |
| M. diluviana | Champlain  | 60–100    | 3–46                 | Sled; Net    | O’Malley, Hansson, et al. (2018)      |
| M. diluviana | Champlain  | 60        | Pr                   | Sled; Camera | O’Malley, Dillon, et al. (2018)      |

\(^{a}\) Based on biomass.

Kinsten & Olsén, 1981; Lasenby et al., 1986, which may have increased effort to understand their pelagic implications for fisheries management at the expense of examining their benthic role. Similar consequences of Mysis introductions on benthic environments are not as apparent in the literature and probably more difficult to study and detect, although several studies have noted their importance as prey to benthic fish communities in systems affected by Mysis introductions (e.g. Ellis et al., 2011).

3 | THE NEED FOR AN EXPANDED FRAMEWORK ON MYSIS BENTHIC RESOURCES AND HABITAT

The focus on pelagic Mysis restricts our understanding of its general ecology, and poses several potentially large knowledge gaps with implications for population assessments, food web ecology, and fisheries management (Kitchell et al., 2000; Pothoven & Madenjian, 2008; Pothoven, Nalepa, Schneeberger, & Brandt, 2001).

3.1 | Mysis demographics and benthic habitat sampling

Mysis occupy benthic habitat night and day (Table 1). Evidence suggests that the individuals caught on the bottom both night and day are represented by disproportionately more adults, including gravid females, compared to pelagic individuals caught during the night (Figure 3; Euclide et al., 2017; McWilliam, 1970; O’Malley, Hansson, et al., 2018; Reynolds & DeGraeve, 1972). Consequently, assessments based on night pelagic samples may underestimate population density and biomass—the latter to a greater extent because of the exponential increase in mass with length. Population size–structure and life-stages from night pelagic samples may also bias our inferences of population demographics.

Research using cameras (Bergersen & Maiolie, 1981) and video (O’Malley, Dillon, et al., 2018) indicate that benthic Mysis densities may be 2–10\(x\) greater than estimates based on traditional benthic sled collections, suggesting that estimates of the proportion of Mysis that are benthic at night based on benthic sleds (Table 1) are probably conservative. Further, wide variability in mysid density estimates has been observed in some benthic collections; however, where reported, the precision of benthic density estimates appears similar in magnitude to that of pelagic density estimates. For example, Moen and Langeland (1989) report coefficients of variation (CV) of 24 and 27% for day and night bottom samples collected with a beam trawl. Naesje, Saksgard, Jensen, and Sandlund (2003) found parallel (side-by-side) vertical water column hauls had an average CV of 27%, and among three stations vertical water column hauls had an average CV of 45%. Parallel bottom samples with a beam trawl had an average CV of 42%. O’Malley, Dillon, et al. (2018), O’Malley, Dillon, et al. (2018) found average CV of 23 (day) and 68% (night) for pelagic sampling, and 41 (day) and 32% (night) for benthic sampling. Understanding sampling gear bias and precision is critical for measuring potential demographic differences among habitats. Adoption and refinement of digital recording systems, in concert with benthic sleds, are promising methods to
more fully assess mysids in benthic habitats. Deployment of such technologies can take a variety of forms, including stationary observatories (e.g. Grossman, Gallager, & Mitarai, 2014; O’Malley, Dillon, et al., 2018) and mobile platforms such as remotely operated vehicles, autonomous underwater vehicles, drop-frames, benthic sleds, and fish trawls (e.g. Bethoney & Stokesbury, 2018; Brandt et al., 2013; Gutt & Siegel, 1994; Karatayev, Mehler, Burlakova, Hinchey, & Warren, 2018; Kilpatrick, Ewing, Lamb, Welsford, & Constable, 2011; Rosenkranz, Gallager, Shepard, & Blakeslee, 2008). Future methodological evaluations and sampling recommendations for benthic resources in those habitats including detritus and possibly benthic macro- and meio-fauna (Karlson & Viitasalo-Frosen, 2009). Growth and mortality estimates based solely on pelagic samples may underestimate rates, respectively because larger (and gravid) individuals of a population may disproportionately occupy benthic habitat at night (Figure 3). Furthermore, the lower temperature in bottom waters may increase energy conversion efficiency and lipid content and hence energy density of mysids (Chess & Stanford, 1999).

Overall, the literature suggests that assessments of Mysis at night using pelagic gear, and their application to ecological processes (e.g. production, zooplanktonivory), provide an incomplete picture of Mysis populations and their role in ecosystem structure and function.

3.2 | Role of benthic food resources

Benthic food resources probably play a significant role in Mysis energy dynamics. Mysis consume and grow on a variety of benthic foods including detritus, zooplankton eggs, amphipods, and benthic zooplankton (Albertsson, 2004; Johannsson et al., 2001; Karlson & Viitasalo-Frosen, 2009; Parker, 1980; Sierszen et al., 2011; Viitasalo & Viitasalo, 2004). For example, no differences in growth rates or survival were observed for M. mixta fed Artemia nauplii versus dried and ground plant material (Enteromorpha spp.), with growth rates similar to those observed in situ (Gorokhova & Hansson, 1999). Neomysis americana also grew well on a diet of cordgrass (Spartina alterniflora) detritus (Zagursky & Feller, 1985). Similar results were reported for mysids fed fresh and decaying plant material and detritus (Irvine, Moss, Bales, & Snook, 1993; Lasenby & Van Duyn, 1992; Lesutiene, Gorokhova, Gasiunaite, & Razinkovas, 2008; Speirs, Lawrie, Raffaelli, Gurney, & Emes, 2002). Ingestion rates of detritus were approximately double those of phytoplankton in laboratory feeding experiments, on a caloric basis, and suggested that detritus played a significant role in growth of Lake Tahoe Mysis (Morgan, 1979). Large Mysis captured in the pelagia of Lake Superior at night in September relied on benthic sources for 27–58% of their diet (Sierszen et al., 2011), Mysis from Okanagan Lake assimilated 4–59% of their carbon from benthic sources (Whall & Lasenby, 2009), and pelagic zooplankton could not solely support Mysis growth in Lake Ontario (Johannsson, Rudstrom, & Lasenby, 1994), providing further evidence that benthic food resources contribute to assimilated energy. Detritus has been found in the stomachs of almost all species of mysids from freshwater to marine habitats (Mauchline, 1980; Takahashi, 2004). Such results are not surprising, as mysids are efficient at digesting detritus and contain gut enzymes needed to breakdown plant material (Foulds & Mann, 1978; Friesen, Mann, & Novitsky, 1986; Wainwright & Mann, 1982). Consequently, more consideration and better estimates of daytime foraging are needed to fully realise the contribution of benthic resources to mysid growth and survival, and by extension, the influence of mysids on ecosystems.

Production estimates need to take into account the demographic distribution of mysids in both pelagic and benthic habitats, and the resources in those habitats including detritus and possibly benthic macro- and meio-fauna (Karlson & Viitasalo-Frosen, 2009). Growth and mortality estimates based solely on pelagic samples may under- and overestimate rates, respectively, because larger (and gravid) individuals of a population may disproportionately occupy benthic habitat at night (Figure 3). Furthermore, the lower temperature in bottom waters may increase energy conversion efficiency and lipid content and hence energy density of mysids (Chess & Stanford, 1999).

3.3 | Benthic behaviour

In addition to mysids’ ability to consume benthic resources, Mysis probably use benthic habitat to further reduce their vulnerability to visual predators. For example, bloater (Coregonus hoyi) capture success rate for Mysis off bottom was nearly double that when Mysis were on bottom (Crowder & Binkowski, 1983). The sediment surface is used by Mysis to propel away from predators with greater acceleration and maximum speed than possible in pelagic habitat and to maintain their position on top of sediment in strong currents, and they can also burrow into the sediment (Bowers, 1988; Bowers, Cooper, & Hall, 1990; O’Malley, Dillon, et al., 2018;
Robertson, Powers, & Anderson, 1968; Sellers, 1995). Deepwater sculpin (Myoxocephalus thompsonii) and other sculpin species (Cottus bairdi, Cottus rici, Cottus cognatus), the primary demersal fishes that prey upon mysids in the Laurentian Great Lakes (Gamble, Harbik, Stockwell, et al., 2011; Gamble, Harbik, Yule, et al., 2011; Hondorf, Pothoven, & Brandt, 2011; Weidel et al., 2017), consume prey on or in the sediment (Kraft & Kitchell, 1986; Selgeby, 1988) using vibration to detect prey (Hoekstra & Janssen, 1985; Janssen, 1990). Such a foraging strategy, however, may be relatively ineffective on Mysis (Bowers, 1988) given sculpins’ capture success rates of only c. 10% for Mysis compared to 45 and 78% for less agile amphipod and chironomid prey, respectively (Hondorp, 2006). In systems where dreissenid mussels have colonised and expanded into Mysis benthic habitat, the additional complex shell habitat and organic matter could influence Mysis interaction with predators and sediments (Stewart, Miner, & Lowe, 1998), but this remains to be tested.

Mysis behaviour on and in sediment may also influence benthic habitat biogeochemistry. For example, perturbation of sediments by Mysis burrowing into or disturbing the sediment surface can increase oxygen transport across the diffusive boundary layer and reduce the growth of sulfur-producing bacteria typical of anoxic conditions (Lindström & Sandberg-Kilpi, 2008), and thus potentially contribute to and impact benthic–pelagic fluxes in organic matter, metabolites, and nutrients (Carlsson, Hulth, Ringdahl, & Rosenberg, 2005; Kristensen, 2000; Lohrer, Thrush, & Gibbs, 2004). In systems where benthic invertebrates may be reduced (e.g. Diporeia in the Laurentian Great Lakes; Nalepa, Fanslow, Pothoven, Foley, & Lang, 2007), bio-perturbation by Mysis could play an increasingly important role in biogeochemical processes at the sediment–water interface. Similarly, in systems where nonnative dreissenid mussels have colonised and expanded into Mysis benthic habitat, the importance of Mysis-sediment dynamics will probably be greater than in systems without deep, filter-feeding mussels.

3.4 | Food web and ecosystem effects

Mysis use of benthic food resources probably has compounding effects. The total energy consumption by Mysis populations may be underestimated if based on pelagic feeding rates. When energy consumption is inferred from growth rates and bioenergetics models, part of that energy intake will be from benthic resources and, if not accounted for, will bias high the inferred effects on zooplankton. Thus, the pathways by which energy flows through mysid populations are probably different from the estimates and inferences drawn from pelagic-focused literature (Johannsson et al., 1994; Lehtiniemi et al., 2002, 2009; Viherluoto, Kuosa, Flinkman, & Viitasalo, 2000). For example, estimates of Mysis consumption have generally assumed a diet of 100% zooplankton (Bunnell, Davis, Warner, Chrisinske, & Roseman, 2011; Chippa & Bennett, 2000; Gal et al., 2006; Hryck et al., 2015; Murtough, 1984; Rudstam et al., 1989; Rudstam, Hansson, Johansson, & Larsson, 1992; but see Stewart & Sprules, 2011). The impact that Mysis can have on zooplankton community composition and size structure and the subsequent negative consequences for pelagic planktivorous fishes is unequivocal, as clearly seen in systems where Mysis have been introduced (Devlin et al., 2016; Lasenby et al., 1986; Nesler & Bergersen, 1991). However, estimates of Mysis zooplanktivory based on pelagic sampling, bioenergetics, and assumed consumption of 100% zooplankton will be biased high because these estimates under-represent how much benthic energy flows through Mysis, and consequently the amount of benthic energy that flows through other components of the food web that directly or indirectly interact with Mysis (Johannsson et al., 1994, 2001; Viherluoto et al., 2000).

Benthic Mysis and benthic resources used by Mysis may explain why mass-balance food web models often estimate greater fish predation on Mysis than observed Mysis production or biomass can support. Mysis biomass and production had to be increased 2–3-fold over observed values to meet the estimated consumption demands of planktivorous fishes in a Lake Ontario model (Stewart & Sprules, 2011). Lake Michigan mass-balance food web models also estimated fish predation of Mysis to be greater than Mysis biomass observations (Rogers, Bunnell, Madenjian, & Warner, 2014). Similarly, in the Baltic Sea, zooplankton production was insufficient to support the quantity of Mysis consumed by fishes (Harvey, Cox, Essington, Hansson, & Kitchell, 2003) when pelagic invertebrates were assumed to consume 100% zooplankton (Sandberg, Elmgren, & Wulff, 2000). To account for the imbalance, and based on results from stable isotope analyses (Hansson et al., 1997), a 50/50 diet balance of zooplankton and plant material for Mysis was needed in the food web model (Harvey et al., 2003). The evidence from the literature suggests such holes in mass balance food web models could be filled by accounting for Mysis in benthic habitats and their use of benthic resources.

One consequence of the pelagic focus of Mysis research in freshwater systems is the implicit inference that pelagic production is the dominant energy pathway for Mysis. Our literature survey, however, suggests that Mysis may spend more time on the bottom than assumed. In winter, when pelagic production is low and Mysis fecundity is high, the motivation to migrate into the water column at night is also presumably low and a greater proportion of the population probably spends more time on bottom than during the other seasons (e.g. Johannsson et al., 2001; Salemaa et al., 1986; but see Lehtiniemi et al., 2009; Figure 4). Conversely, in summer when pelagic production is high, the motivation to migrate is also presumably high but short nights limit access to pelagic resources. Additionally, the abundance and quality of benthic resources is influenced by season and water column depth (Auer, Cannon, & Auer (2009); Eadie, Chambers, Gardner, & Bell, 1984; Ostrom, Long, Bell, & Beals, 1998; Scharold, Lozano, & Corry, 2004), suggesting dynamic cost:benefit trade-offs to migration over space and time, which probably influences the amount of benthic feeding by mysids (Johannsson et al., 2001; Sierszen et al., 2011, 2014). However, when integrated over a year, the proportion of time and the proportion of mysids that occupy benthic habitat is probably greater than pelagic habitat. Because Mysis continuously feed when on bottom, regardless of time of day
O’Malley & Stockwell, 2019), detritus and other benthic resources are likely to compose a large portion of *Mysis* diets and thus energy processing and assimilation.

An underlying theme in *Mysis* research, either implicitly implied or explicitly stated by the focus on the pelagia, is that benthic resources act as a resource subsidy to support *Mysis* populations through periods of low pelagic production (Chipps & Bennett, 2000; Patwa, Christensen, Lasenby, Webster, & MacKay, 2007). An alternative theme is that pelagic production serves as a seasonal resource subsidy or provides a limiting nutrient for a foundational benthic energy pathway. The potential for benthic resources to be the dominant energy source for mysids, and the role *Mysis* may play in moving, distributing, and cycling benthic-derived energy and nutrients at the sediment–water boundary and between benthic and pelagic habitats in lakes could be far greater than we thought, and remains a hypothesis to be tested.

### 4 | Research Questions and Hypotheses

Below, we identify a series of important questions and hypotheses that we believe will advance our understanding of the role of benthic habitat to *Mysis* ecology. We organised the questions under three themes: (1) what drives decisions to migrate or not; (2) the importance of benthic habitat for *Mysis* assessment; and (3) how benthic resources may impact *Mysis* dynamics in a broader ecosystem context.

#### 4.1 | (1) What body-states and environmental conditions determine whether mysids migrate?

Conditions in benthic and pelagic habitats vary seasonally (Figure 4), as do mysids (e.g. life-stages, body-state). To understand mysid migration, we need to consider external and internal conditions (Nathan et al., 2008) and evaluate whether variation in migration behaviour at the population level is a result of evolutionarily developed life histories/behaviours or individual decision making. In this context, we pose a series of sub-questions on processes and mechanisms that may drive emergent population-level migration behaviours.

(1a) Is partial DVM a result of fixed or plastic behaviours at the individual or group level? Whether a *Mysis* population can be divided into sub-groups that each behave consistently within groups but differentially among groups, or *Mysis* behaviour is an outcome of individual choice in response to external conditions or internal states, remains unclear. Several early studies proposed such alternative behaviours (Morgan, 1980; Rybock, 1978), and more recent studies using stable isotopes and genetics have found suggestive but mixed results (Euclide et al., 2017; Ogonowski et al., 2013). Another possibility is the presence of personality traits that influence, or at least reflect, differences in movement, including migration (Chapman et al., 2011; Mettke-Hofmann, Ebert, Schmidt, Steiger, & Stieb, 2005; Nilsson, Nilsson, Alerstam, & Backman, 2010; Sih & Watters, 2005). In situ tests of fixed or plastic DVM behaviour remain difficult in the absence of the technology to track individual *Mysis* behaviour throughout time, although laboratory experiments and agent-based models are viable options (e.g. DeAngelis & Diaz, 2019; Langer et al., 2019).

(1b) What is the relative importance of pelagic and benthic prey resources for *Mysis* growth? How is growth influenced by prey availability and nutritional quality between benthic and pelagic habitats and across seasons? Do individuals need to migrate to survive, grow, and reproduce? Our synthesis suggests that a more diverse perspective is needed to better quantify the absolute and relative roles of benthic and pelagic prey resources for *Mysis* growth. However, observations that individuals captured in pelagic habitat during the day tend to be smaller, that smaller individuals move higher up in the water column at night, and larger individuals tend to dominate night benthic habitat (e.g.
Beeton, 1960; Boscarino, Rudstam, Tirabassi, et al., 2010; O’Malley, Dillon, et al., 2018; Ogonowski et al., 2013; Salemaa et al., 1986) suggest that ontogeny and body-state need to be incorporated into such studies.

(1c) Are predation risks higher in benthic or pelagic habitats? Are DVM patterns dependent on Mysis density and the presumably closer proximity to predators when on the bottom (2-D habitat) than in the water column (3-D habitat)? To our knowledge, studies on Mysis predation risk to fish have been primarily focused on pelagic settings (e.g. Boscarino, Rudstam, Tirabassi, et al., 2010; Jensen, Hrabik, Martell, Walters, & Kitchell, 2006; Levy, 1991; Mason & Patrick, 1993). More information is needed to explore risk/benefit aspects of staying on bottom (c.f. Crowder & Binkowski, 1983; Harrington, Hrabik, & Mensinger, 2015; Janssen, 1990) compared to the pelagia. Cannibalism (Fraser, Cahill, Lasenby, Mackay, & Milford, 2005; Quirt & Lasenby, 2002) also needs to be considered as part of the equation to migrate or not, especially as Mysis density can rapidly increase and concentrate in benthic habitats (O’Malley, Dillon, et al., 2018) compared to dispersal in a 3-D pelagic environment. Modelling encounter rates between Mysis and their predators in 3-D (Gerritsen & Strickler, 1977) and 2-D (Hutchinson & Waser, 2007) foraging arenas may prove useful to this end.

4.2 | (2) How much does the presence of benthic Mysis affect estimates of abundance and production?

Fundamental questions remain about the extent to which pelagic-only sampling biases our inferences about Mysis population dynamics.

(2a) What proportion of Mysis populations remain benthic at night? What proportion remain pelagic during the day? The proportion of Mysis that remains on the bottom at night probably varies among sites, lakes, and seasons, as does the proportion that remains suspended in the pelagic zone during the day (O’Malley, Hansson, et al., 2018). Exploration of Mysis behaviour in extreme environments may provide useful insights as to what conditions may influence DVM behaviour. For example, our conceptual model predicts limited DVM behaviour in winter when pelagic resources are at annual lows (Figure 4). By extension, do Mysis populations exhibit restricted DVM behaviour in clear, high-latitude oligotrophic systems, where benthic production in the littoral zone is the dominant source of system primary production (Ask et al., 2009; Sierszen, McDonald, & Jensen, 2003; Vadeboncoeur et al., 2003)? Conversely, do Mysis populations exhibit increased suspension in pelagic habitat during the day in dark-water, productive systems (Ball, Mihuc, Myers, & Stockwell, 2015; Griffiths, 2007; Penk, 2011)?

(2b) What are the demographic differences between benthic- and pelagic-caught mysids, and how do such differences influence population production estimates? Assessing demographic differences between benthic and pelagic habitats across bathymetric depths, time of day, and seasons will provide more accurate population assessments, as well as contribute to questions and hypotheses about the mechanisms driving partial DVM (see questions 1a–c above) and to fill in missing biomass and production in food web models (see Food web and ecosystem effects above).

4.3 | (3) How does mysids’ use of benthic resources affect their ecological resistance to system change and their ecosystem function?

Zooplanktivity by Mysis can be intense and alter zooplankton community structure and function (Lasenby et al., 1986; Nesler & Bergersen, 1991). However, decreases in pelagic zooplankton may not necessarily induce a negative feedback in Mysis abundance or growth because they can exploit benthic resources (Chippa & Bennett, 2000) and thus exhibit a high degree of adaptive capacity with changing conditions (McMeans et al., 2016). For example, in addition to withstanding intense competition for pelagic zooplankton (Bunnell et al., 2011), Mysis may also be able to resist declines in system productivity as a result of oligotrophication (Barbiero, Lesht, & Warren, 2012) and shifts in energy flow from green (pelagic) to brown (benthic) pathways induced by invasive species (Vanderploeg, Liebig, Nalepa, Fahnenstiel, & Pothoven, 2010). The ability of mysids to use both pelagic and benthic resources probably serves as a buffer against declines in either resource, such that they can maintain their role as an energy conduit across habitats and trophic levels during periods of system change (Johannsson et al., 2001).

5 | CONCLUSION

The disproportionate focus on the pelagic phase of Mysis DVM in the published literature and the likely, but perhaps under-appreciated, role that benthic habitat plays in Mysis ecology suggests a complementary lens through which we should approach Mysis research. Partial DVM in freshwater mysids appears to be the norm rather than the exception. Thus, instead of the seemingly implicit assumption that the pelagic habitat is the most important habitat for Mysis and the benthic environment is simply a hiding place during daylight hours, we propose an alternative and perhaps provocative perspective that benthic habitat is equally, if not more, important than pelagic habitat to understanding Mysis ecology. Such a shift in perspective requires testing that focuses research more equally on the two habitats. A more-balanced perspective will result in a better understanding of the drivers of Mysis DVM behaviour and yield new insights into the ecosystem effects of animals, such as mysids, that rely on both benthic and pelagic habitats.

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DATA AVAILABILITY STATEMENT
As this is a review paper there are no data.

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SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section.

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