

HABITAT COUPLING BY MID-LATITUDE, SUBTIDAL, MARINE MYSIDS: IMPORT-SUBSIDISED OMNIVORES

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Abstract Mysids often dominate mobile benthic epifaunas of mid-latitude continental shelves. Macquart-Moulin & Ribera Maycas (1995) reported that the six most abundant species on western and southern European shelves are all strong diel migrators. Published daytime epibenthic sledge (sled) data from the surf zone to the shelf edge matched with published behavioural data on the most abundant species were used to test, confirm and extend that relationship to other coastal regions and to identify an association of abundant migrators with species that are important in fish diets. They also reveal another pattern: a correspondence between abundant surf-zone species and species that dominate estuarine faunas seasonally. Population concentrations at estuary mouths, sills of fjords and in the surf zone suggest a lifestyle dependent upon horizontal fluxes. Marine mysids that migrate between habitats are chronically undersampled in the field, however, and are underrepresented in food-web models. Unfortunately, no single methodology samples both pelagic and benthic individuals well and nearly all shelf measurements so far reported must be considered underestimates of local abundance. Mysids are major dietary components for many benthic and pelagic fishes, mammals, cephalopods and decapods, often for key life stages, and often because mysid migrations result in encounters with predators. Mysids can be extraordinarily omnivorous, with demonstrated capabilities to digest cellulose and diets spanning macrophyte detritus, more labile detritus, large microalgae, and smaller animals and heterotrophic protists. They can be sufficiently abundant and active to play roles in sediment transport. Contributing factors to their underappreciation have been the lack of fidelity of mysids to single habitats, coupled with higher fidelity of investigators to the study of single habitats. Sampling with classical methods has been problematic because of effective evasion by mysids, compounded by extreme patchiness associated with mysid schooling. Their frequent absence from coastal and even estuarine food-web models has not been more conspicuous because the combination of their migration and omnivory spreads their feeding impacts and because they are subsidised by horizontally imported plankton and seston and are themselves horizontally exported in the form of predator gut contents and biomass. They clearly link pelagic and benthic food webs in two important and ecosystem-stabilising ways, however, by feeding in both habitats and by succumbing in both habitats to both cruising and sit-and-wait predators. Consideration of resource and predation gradients and limited data implicate horizontal, diel migrations as well, extending these linkages, especially in the onshore-offshore direction. Somewhat paradoxically, the same features that have made them difficult to study by classical means, in particular schooling, diet breadth, ontogenetic change in diet and migration between habitats, suit migrating mysids well to new, individual- or agent-based modelling approaches. Moreover, benthic observatories deploying acoustic technologies with spatial and temporal resolution sufficient to resolve individual migratory behaviours promise powerful tests of such models.

Introduction

For nearly two centuries, observations of zooplankton vertical migrations have aroused curiosity and elicited alternative and compound explanations (Pearre 2003). Selective forces evoking and altering these migrations include vertical gradients in resources, in predation risks and in environmental drivers of physiological rates (i.e., temperature and salinity). Such gradients in risks and benefits can be even steeper within the bottom boundary layer, including its upper layers of sediment (Boudreau & Jørgensen 2001), and laterally across fronts, than they are in the overlying water column. The focus of this review is on migrations between benthic and pelagic habitats by a subset of the animal community that may also move horizontally, both across and along isobaths, connecting more than two habitats. For that reason, in this review the more general term ‘habitat coupling’ is used rather than benthic–pelagic coupling (Schindler & Scheuerell 2002).

Widespread use of echo sounders after the rapid advance of underwater acoustics in World War II brought attention to the ubiquity of vertical migrations and specifically to the oceanic deep scattering layer. Echo-sounder frequencies near 12 kHz that were useful for locating the bottom proved sensitive to air bladders of fishes and siphonophores. Based partly on such observations, Vinogradov (1962) developed a conceptual scheme subsequently dubbed ‘Vinogradov’s ladder’: although diel migrations from deeper than 600 m are rare, many deeper-dwelling species migrate part of the way to the surface, so that predatory interactions provide a chain or ladder for vertical redistribution of energy and materials that daily extends to depths in excess of 1000 m in the open ocean. The proliferation of acoustic Doppler current profilers (ADCPs, operating typically at 300–600 kHz; Brierly et al. 1998) and of bioacoustic instruments designed to detect zooplankton at acoustic frequencies typically ranging from 250 kHz to a few megahertz (e.g., Gal et al. 1999) is revealing the ubiquity and intensity in shallow waters of an inherently more complicated phenomenon that has been dubbed the shallow scattering layer (Kringel et al. 2003). In waters too shallow to hold a deep scattering layer, animals from many taxa have evolved foraging patterns and morphologies compatible with living in or on the bottom, usually during the day, and rising into the water column, usually at night. Although there is no need for a vertical ladder where the water is a single rung deep, early data already show the outlines of a horizontal or oblique, onshore–offshore ladder in the coastal zone.

Though still quite limited in number, deliberate, multifrequency acoustic studies of shallow-water migrators suggest that water-column abundances (depth-integrated biomasses) of these migrants may frequently exceed those of the holoplankton. This suggestion led to a systematic examination of corroborative evidence for the ecological importance of these migrants. For pragmatic reasons, in this review analysis is limited to a single large taxon, the Mysidacea (commonly known as opossum shrimp), that appears in shallow, mid-latitude seas and often dominates such migrations. Similarly, the focus is limited to subtidal, coastal habitats of mid-latitudes and to species that occur outside estuaries during at least some seasons of the year. Work in other marine, estuarine and freshwater environments is cited selectively when comparable information was not at hand for mid-latitude marine systems. Literature on freshwater species or (oligohaline and mesohaline) estuarine endemics has not been reviewed for the simple reason that the importance of vertically migrating mysids in these systems is widely appreciated (e.g., Rudstam et al. 1989, Kotta & Kotta 2001a, Viitasalo et al. 2001). To avoid inflation of inferred importance by selective extraction of conspicuous examples of migration and to give some insight into migrations of individual species, a two-step process was used. The first step was to identify a few regional studies of mysids notable for the spatial or temporal extent (or both) of their epibenthic sledge sampling. Thus, this review is also focused away from hard bottoms, caves and vegetation, all habitats well exploited by mysids but ones requiring different census methods. The second step was to review characteristics of migrations in the mysid species that dominated samples in these studies. In both steps emphasis

has been on studies published after the major review by Mauchline (1980), citing prior literature primarily when a particular citation was omitted by Mauchline (1980) or when focusing on information that was not summarised by Mauchline (1980).

Additional information was then reviewed, substantiating the importance of mysids to coastal and estuarine ecosystems. Confluence of multiple lines of evidence for the importance of migrating mysids to both benthic and pelagic systems proved compelling. They often dominate diets of both pelagic and benthic fishes in coastal waters and estuaries, highlighting the multiple risks inherent in the migratory lifestyle. Mysids also appear to be important to the population abundances of some of their prey species, but for the most part mysids are remarkable dietary generalists when all life stages and habitat phases are included, and so are underappreciated stabilisers of the communities that they inhabit and transit (McCann & Hastings 1997). Recently, their migrations have been implicated as an important factor in sediment dynamics (Roast et al. 2004). Major habitat changes due to climate, introduced species or human intervention have often produced major changes in mysid populations that resonate through the food web. Despite underlying differences between mysid-containing food webs in fresh and marine waters, analogy with lake systems takes advantage of their closed boundaries to assess effects of mysid introduction, which are detected both up and down the food web. Another indicator of potential importance is the latitudinal range and habitat diversity over which high abundances of even single species are found; *Neomysis americana* (S.I. Smith, 1873) is abundant from Nova Scotia to Florida and from shelf habitats 100 m deep to salt marshes; in the last century it was introduced to the Atlantic coast of South America, where it has become an important food-web component. The importance of *N. americana* as food for both benthic and pelagic fishes over a broad geographic range was recognised in its original species description (Smith 1873).

The question naturally arises as to why, despite engaging, comprehensive treatments of their capabilities and roles (e.g., Mauchline 1980) and intense and sustained interest among the specialists cited in this review, mysids do not figure more prominently in fisheries and oceanographic models and texts. The most direct comparison is with the largely holoplanktonic euphausiids, a group of similar body size and also large dietary breadth (but less expansion into detritivory) as a group. The summary by Mauchline (1980) of both groups followed a parallel structure for each. Tellingly, his chapter on “Mysids in the marine economy” is half as long as its counterpart for euphausiids, and only a small portion is devoted to shallow-water species that migrate. Biological oceanographic textbooks in general give an even more lopsided treatment.

Reasons for this shortage of information are manifold. Shallow-water migrations are fundamentally more complicated than better-studied migrations in the open ocean or in coastal holoplankton because component populations in benthic and pelagic habitats cannot be studied by the same means and often are not sampled by a single investigator. Their natural reference frame shifts back and forth between an Eulerian fixed reference frame and a Lagrangian, water-mass-following reference frame with the change between benthic and pelagic habitats, respectively, seriously complicating description and analysis. Even when they stay within the pelagic or benthic habitat, mysids are notoriously poorly captured because of their effective evasive behaviours. More subtly, their lack of freely released eggs or larvae leaves no evidence of large mysid populations in low-flow or small-aperture capture devices, such as continuous plankton recorders, that efficiently recover those non- or weakly swimming life stages in euphausiids, decapods and fishes. Extreme patchiness of mysid populations, reinforced by schooling behaviours, make precise abundance estimates even more difficult to achieve than they are for non-schooling animals. The migratory lifestyle gives mysids access to horizontally imported pelagic food sources and leads through encounter to their local export as gut contents and assimilated biomass of fishes and decapods, effectively camouflaging their importance to local food webs and energy budgets; a large *net* import or export would be far more conspicuous.

Migrations between the sea bed and the water column also generate semantic difficulties. Mees & Jones (1997) took a habitat point of view and defined the hyperbenthos as those animals living in the water layer immediately above the bottom. In this sense, migratory mysids spend part of their time as hyperbenthos. The term fails, however, to capture the range of habitats occupied by migratory mysids because in clear, shallow waters without bottom cover in the form of crevices or vegetation, mysids often bury themselves during daylight, disappearing from the hyperbenthos. Mysid migrations also exhibit considerable plasticity, varying in timing, intensity and vertical extent seasonally, night to night and with tides (e.g., Abello et al. 2005, Taylor et al. 2005). To pursue these migrations further from a habitat perspective thus would require more elaborate terminology than even the refinements proposed recently by Dauvin & Vallet (2006). Instead, in the present review an alternative approach is adopted that may lead more readily to quantitative models and predictions by taking the perspective of an individual migrating through habitats. It is noted that, because mysids swim actively when pelagic and may do so at times during their benthic phases, this perspective is not truly Lagrangian (in the normal physical oceanographic sense of tracking a parcel of water), although it follows that same spirit of following the entity of interest. Seeking the simplest terminology that has this behavioural focus, the term ‘emergence’ is used herein to describe the overall vertical migration behaviour between habitats and more specifically the upward component of the migration (leaving the distinction to context). This usage follows precedent for those who have focused on the migratory behaviour rather than on community structure in the hyperbenthic habitat (Saigusa 2001). When the shift is from pelagic to benthic, the term ‘re-entry’ is used in the current review, reflecting the author’s benthic background.

Two recent developments promise accelerated understanding of the role of migratory mysids. One development is the continued evolution of bioacoustic instrumentation and its deployment methods, particularly in the context of high-power, high-bandwidth ocean observatories. The second advance is the rapid development of flexible, individual-based models (IBMs). Many of the same features that have made mysids difficult to study make them excellent subjects for applications and tests of IBMs (i.e., their schooling behaviours, their occupation of multiple habitats, their use of multiple food resources and their shifts in behaviour during development) (Grimm & Railsback 2005, Grimm et al. 2005). The combination of new technologies and models promises accelerated advances in understanding of the extents, causes and consequences of mysid migrations through tests of predictions about habitat usage.

Migratory capabilities, schooling and their consequences

Credibility of evidence for migrations rests in some measure on the sensitivities of sensory mechanisms to guide them and on swimming capabilities. Mysids as a group are well endowed in both of these categories (Mauchline 1980). The earliest (Carboniferous to Jurassic) mysids appear to have been holopelagic, and the transition to emergence to have been marked by the evolution of statocysts with mineralised statoliths (Ariani et al. 1993), likely associated with the fitness enhancement of directional guidance in emergence and re-entry. Marine species generally (including *Neomysis americana*) secrete fluorite (CaF_2), whereas low-salinity estuarine and freshwater species generally secrete vaterite (a CaCO_3 polymorph of calcite and aragonite), although particular species provide exceptions to each generalisation that reflect their lineages (Ariani et al. 1993). Mysids have major impact on the marine fluorine cycle (Wittman & Ariani 1996), and their statoliths may be abundant enough in some fossil marine strata to warrant extraction (Voicu 1981). Likewise, calcite (transformed vaterite) from statocysts represents a substantial fraction of some Miocene Paratethys deposits in the Ponto-Caspian region, where use of calcium carbonate minerals appears to have first evolved in mysids (Ariani et al. 1993). Emergent mysids thus appear to have been very abundant in coastal ecosystems for a very long time, and they are still abundant enough to leave

detectable statoliths in modern shelf sediments (Enbysk & Linger 1966). In addition to a pair of statocysts for vertical orientation, a less well-identified mechanism for sensing depth is present (Rice 1961, 1964) that is sensitive to pressure changes equivalent to less than 1 m of water and that probably enables observed tidal rhythms in activity cycles (Mauchline 1980, Saigusa 2001, Gibson 2003, Taylor et al. 2005).

In terms of horizontal navigation, mysids have long been known to utilise polarised light (Bainbridge & Waterman 1957, 1958), and movements of their stalked eyes are co-ordinated with information from the statocysts (Neil 1975a,b,c). Contrary to opinion in many recent references, polarisation (specifically e-vector orientation) is a useful indicator of solar azimuth throughout continental shelf depths and through most of the day, with the highest information content near dusk and dawn because of high inclination of the e-vector with respect to the horizontal (Waterman 2005). Seasonal onshore–offshore migrations have been inferred from asynchronous seasonal changes in abundance across habitats (e.g., Bamber & Henderson 1994), and polarised light probably provides the directional cue, although it often is not clear to what extent the asynchrony in local abundance is due to migration versus seasonally changing, local differences in population growth and mortality (Mees et al. 1993). For reasons that also are not yet clear, a majority of onshore–offshore migrators show winter maxima offshore, extending in high abundance into shallower water and estuaries during some or much of the period from spring to fall (Mauchline 1980). Diel homing to the same location over smaller scales has been documented experimentally in reef mysids (Twining et al. 2000). Utilisation of estuarine circulations to help maintain horizontal position on intermediate scales has also been observed (i.e., either an interaction of horizontal and vertical bias or directed navigation) (e.g., Orsi 1986, Moffat & Jones 1993, Schlacher & Wooldridge 1994, Kimmerer et al. 1998a,b), although variation in such behaviours with local conditions from year to year can be considerable (Kimmerer 2002), as can differences among mysid species at the same estuarine location (Sutherland & Closs 2001). Retention-assisting, horizontal migrations also have been observed during slack tides (Köpcke & Kausch 1996).

Many mysid species are documented to be strong swimmers. Sustained swimming at 10 body lengths s^{-1} is not unusual, with bursts in some species exceeding 20 body lengths s^{-1} (Mauchline 1980). At these sustained speeds, diel vertical, diagonal or horizontal excursions on the order of 1 km would be feasible, depending on local flow velocities, so diel vertical migrations to the shelf edge are well within mysid capabilities. Habitats with flow speeds in excess of sustainable swimming speeds appear to be avoided, however, and mysids shelter behind flow obstructions and in the most slowly moving water layer directly over the bottom (Roast et al. 1998, Lawrie et al. 1999).

Perhaps the most important point to emphasise in this introduction is the reason to focus on both abundance and migration. A point forgotten all too easily is that ecological importance to individuals of another species is usually a function of interspecific encounter rates (Hurlbert 1971), themselves a product of areal or volumetric abundance times relative velocity (e.g., Jumars 1993). The combination of good sensory guiding mechanisms and strong swimming capabilities would tend toward ballistic encounter during organised migrations, an advantage in feeding but a disadvantage when being preyed upon (Visser & Kiørboe 2006).

Encounters in mysids are often modulated by schooling behaviours. Mysids use visual and tactile senses to form and maintain both highly polarised schools and less polarised aggregations or swarms (Ritz 1994). Very large aggregations of varying local density and orientation are termed shoals (Clutter 1969). Typical mysid schools range from 1–10 m in linear dimensions and 1–15 m^3 in volume (Ritz 1994). Near the bottom, school shapes often become planar, typically with more than one layer of mysids and sometimes differing in vertical structure by sex and life stage. Moving schools tend to be elongate, whereas stationary swarms (albeit containing milling individuals) are more circular (when near the sea bed) or spherical (Clutter 1969, Wittman 1977, Ohtsuka et al. 1995). Schooling is typical of animals out from the cover of vegetation and swimming off the

bottom (i.e., in the pelagic phase), even when only a few centimetres from the bottom, but schools may maintain oriented, evenly spaced formation while on the bottom. Mysids on or near the bottom typically orient into the current (Mauchline 1980). Densities in swarms are often near 10^5 of individuals (ind.) m^{-3} , with mean interindividual separation distances near 2 cm; for a single layer, that spacing yields about 2500 ind. m^{-2} (Mauchline 1980). The first emergence event of the night shows clear schooling and a constant ascent velocity dependent on depth and local light conditions, but later emergence does not appear to be as organised; schooling may not be maintained through the night (Kringel et al. 2003, Abello et al. 2005, Taylor et al. 2005). One function of schooling is to reduce average risk per individual (Ritz 1994) to individual predators, although schooling predators or large individual predators (e.g., whales) may be quite effective in the presence of mysid schooling. It is clear from gut contents of benthic and pelagic fishes that migrating mysids still incur fatal risk and that fitness loss must be counterbalanced by even greater gain from migrations if the migrations persist.

Hence, the observations made by Macquart-Moulin & Ribera Maycas (1995) in an exhaustive sampling programme of the pelagic phase of mysids throughout the water column in the north-western Mediterranean take on particular significance: they observed that the most abundant mysids found on the continental shelves of Europe are diel migrators between the sea bed and the pelagic environment. Based on the integration of a large number of studies with varying types of sampling gear over a long period, Macquart-Moulin & Ribera Maycas (1995) concluded that six species showed high benthic abundance on the shelf: *Gastrosaccus sanctus* (Van Beneden, 1861), *G. spinifer* (Goës, 1863), *Anchialina agilis* (G.O. Sars, 1877), *Haplostylus lobatus* (Nouvel, 1951), *H. lobatus* var. *armata* (Nouvel, 1951), and *H. normani* (G.O. Sars, 1877). They provided compelling new data from the region near Marseille of migration to the surface in all six of these taxa. Deprez et al. (2005) regard *Gastrosaccus sanctus* as a synonym of *G. spinifer* and *Haplostylus normani* as a synonym of *H. lobatus*. Macquart-Moulin & Ribera Maycas (1995) also found strong evidence of offshore migration or transport of *Anchialina agilis* and *Haplostylus lobatus*, both captured over bottoms 700–1000 m deep, where individuals are not known to occur on the bottom. They captured pelagic *Anchialina agilis* in bathyal waters during the day and collected a high percentage of dead animals, suggesting that occurrence in waters deeper than 500 m is an extension beyond suitable habitat.

Methods of data collection

To identify recent published records of mysid abundance, three sources have been used in this review: the Food and Agriculture Organisation of the United Nations' Aquatic Sciences and Fisheries Abstracts (ASFA), Thomson Scientific's Web of Science and Google Scholar. The first two sources are limited primarily to citations later than those in the review of Mauchline (1980), but the third source is expanding rapidly into older literature. Into the search fields of the first two databases, 'mysi*' was entered and a country name that has a continental shelf, or in the case of the United States or Canada, a state or province name, respectively. For Google Scholar 'mysid' was used and the place name. For ASFA and the Web of Science, the 'and' is a Boolean operator. For Google Scholar, it was omitted (as Google in general ignores small, common words unless they are within explicit quotation marks). From the references returned, selected were those that documented mysid abundance either over an extensive period (a year or more) or a broad geographic area or both during daytime on the basis of epibenthic sledge samples. Many of these sledge studies used multiple, vertically arrayed nets (e.g., Zouhri et al. 1998) to get information on near-bottom vertical distributions, biased to an unknown degree by species-specific escape responses. Such samples are referred to as 'vertically resolved, epibenthic-sledge samples'. From the data provided, mysids have been ranked in terms of their abundances, selecting the one to five abundant and

HABITAT COUPLING BY MID-LATITUDE, SUBTIDAL, MARINE MYSIDS

frequent species, using a smaller number when a natural break point in abundance occurred (a difference of an order of magnitude or more in absolute abundance), and using the largest number when a long study over a large area showed consistent dominance of one species in at least one location and season. In each case, the choices of taxa are explained. Species names in quotation marks were then used as search terms in the same three databases to determine the migratory behaviour of the most abundant species. In addition, species names were searched in the NeMys database (Deprez et al. 2004, 2005) using the inclusive list of species names (valid and invalid) for references on behaviour and as a further check for inclusivity of publications with extensive sampling of field abundance and publications on migratory behaviour. The NeMys database was also used as one source of taxonomic authority, indicated on first use of the species name in the body of this review, and for some information (especially for European species) about geographic and depth ranges. For brevity, depth ranges of the species are summarised only in tabular form (Table 1). For consistency, only benthic capture records were used. Where taxonomic ambiguities or disputes over synonymy might affect conclusions, all databases were searched under both names.

Table 1 Mysid species identified as abundant in epibenthic sledge samples, along with their known depth ranges, diel migratory behaviours and the study that established their high abundance

Species	Depth limits (m) (respective citations)	Diel migratory behaviour (citations)	Source of information on abundance
<i>Mesopodopsis slabberi</i>	1–42 (Buhl-Jensen & Fosså 1991, Beyst et al. 2001)	Very strong swimmer, extends vertical distribution at night (Apel 1992, Wang & Dauvin 1994)	Beyst et al. 2001
<i>Schistomysis spiritus</i>	1–116 (Buhl-Jensen & Fosså 1991, Beyst et al. 2001)	Moderately strong swimmer, extends vertical distribution at night (Apel 1992, Wang & Dauvin 1994)	Beyst et al. 2001
<i>Schistomysis kervillei</i>	1–25 (Cornet et al. 1983, Beyst et al. 2001)	Weaker swimmer, extends vertical distribution at night (Apel 1992, Wang & Dauvin 1994)	Beyst et al. 2001
<i>Anchialina agilis</i>	2–493 (Bacescu 1941, Cartes & Sorbe 1995)	Strongest swimmer and migrator to limits of its benthic depth distribution; most of the population leaves the bottom every night (Macquart-Moulin & Ribera Maycas 1995)	Dauvin et al. 2000
<i>Gastrosaccus spinifer</i>	1–260 (Lagardère & Nouvel 1980, San Vicente & Munilla 2000)	Strong swimmers and migrators (Macquart-Moulin & Ribera Maycas 1995)	Dauvin et al. 2000
<i>Haplostylus lobatus</i>	17–420 (Lagardère & Nouvel 1980, Dauvin et al. 2000)	Strong swimmers and migrators (Macquart-Moulin & Ribera Maycas 1995)	Dauvin et al. 2000
<i>Haplostylus normani</i>	10–150 (Lagardère & Nouvel 1980, Dauvin et al. 2000)	Strong swimmers and migrators (Macquart-Moulin & Ribera Maycas 1995)	Dauvin et al. 2000
<i>Erythropelegans elegans</i>	1–125 (Bacescu & Schiecke 1974, Cunha et al. 1997)	May be a diel migrator (Vallet et al. 1995)	Zouhiri et al. 1998
<i>Schistomysis ornata</i>	6–407 (Brattegard & Meland 1997)	Collected in nighttime surface samples in some seasons; may be a diel migrator (Sorbe 1991)	Zouhiri et al. 1998
<i>Leptomysis gracilis</i>	5–512 (Elizalde et al. 1991, San Vicente & Munilla 2000)	Strong migrator (Mauchline 1980, Kaarvedt 1989)	Cornet et al. 1983, Cunha et al. 1997

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Table 1 (continued) Mysid species identified as abundant in epibenthic sledge samples, along with their known depth ranges, diel migratory behaviours and the study that established their high abundance

Species	Depth limits (m) (respective citations)	Diel migratory behaviour (citations)	Source of information on abundance
<i>Mysideis parva</i>	120–519 (Bacescu & Schiecke 1974, Elizalde et al. 1991)	Non-migrator (Elizalde et al. 1991). No description found.	Cornet et al. 1983, Cunha et al. 1997
<i>Neomysis americana</i>	1–232 (Wigley & Burns 1971)	Strong diel, tidally modulated migrator, but perhaps not to the full extent of its depth range (Herman 1963, Brown et al. 2005, Taylor et al. 2005)	Wigley & Burns 1971
<i>Americamysis bigelowi</i>	4–179 (Wigley & Burns 1971, Allen 1984)	Strong diel migrator (Williams 1972)	Wigley & Burns 1971
<i>Erythroops erythrophthalma</i>	16–450 (Petryashev 2002a)	Migrates at least in some environments (Brunel 1979)	Wigley & Burns 1971
<i>Metamysidopsis elongata</i>	1–14 (Clutter 1967)	Slight upward shift of population mode at night (Clutter 1969)	Clutter 1967
<i>Neomysis kadiakensis</i>	1–210 (Petryashev 2005)	Strong diel migrator (Kringel et al. 2003)	Clutter 1967
<i>Xenacanthomysis pseudomacropsis</i>	1–104 (Petryashev 2005)	Caught in mid-water trawls (Wing & Barr 1977)	Kim & Oliver 1989
<i>Neomysis rayii</i>	1–79 (Petryashev 2005)	Caught in mid-water trawls (Wing & Barr 1977)	Kim & Oliver 1989
<i>Acanthomysis stelleri</i>	1–104 (Petryashev 2005)	Poorly known	Kim & Oliver 1989
<i>Archaeomysis kokuboi</i>	0–2 (Petryashev 2005)	Strong diel migrators (Takahashi & Kawaguchi 1997)	Takahashi & Kawaguchi 1997
<i>Archaeomysis japonica</i>	1–50 (Hanamura 1997)	Strong diel migrators (Takahashi & Kawaguchi 1997)	Takahashi & Kawaguchi 1997
<i>Iiella ohshimai</i>	1–5 (Takahashi & Kawaguchi 1995)	Strong diel migrators (Takahashi & Kawaguchi 1997)	Takahashi & Kawaguchi 1997
<i>Nipponomysis ornata</i>	1–5 (Yamamoto & Tominaga 2005)	Undescribed?	Hanamura & Matsuoka 2003, Yamamoto & Tominaga 2005

Given demonstrated mysid capabilities for social aggregation and movement, reported maximal local abundances per unit of volume of water are not very informative regarding typical regional abundances, and documentation of consistently high abundance over a long time or broad region is a better indicator of consistent importance. This review therefore focused on a subset of those references that provide abundance estimates from epibenthic sledge samples taken during the benthic phase (i.e., when individuals are most susceptible to capture by a sledge). Drawbacks are that these studies varied widely in the geometries of the net mouth openings used and that many of these papers reported only numbers per unit of volume filtered (as determined by flow meter). No attempt was made to express abundances per unit of volume or per unit of area when the original author did not do so. For ease of comparison, however, all areal or volumetric abundance estimates given per total area or volume of tow were converted to numbers per square or cubic metre.

Regionally abundant mysids and their migration habits

European shelves

One of the most challenging environments to sample with respect to abundance and emergence behaviours is the shallow subtidal and in particular the surf zone. In 15 monthly samples with a bottom sledge hauled by hand from four sites in the Belgian surf zone, Beyst et al. (2001) found average animal densities to exceed 15 ind. m⁻² and to vary in ash-free dry weight (AFDW) from 3 to >30 mg m⁻². Three quarters of individuals overall were mysids, primarily of three dominant species (*Mesopodopsis slabberi* (Van Beneden, 1861), *Schistomysis spiritus* (Norman, 1860) and *S. kervillei* (G.O. Sars, 1885)), and mysids dominated AFDW in some seasons. As is typical of such estimates, sampling efficiency is unknown for this sledge with these species and is assumed to be 100% for purposes of the calculation, so true densities must be higher. The three-species group also dominates the Voor delta, where *Gastrosaccus spinifer* is also abundant (Mees et al. 1993).

Patterns of diel migration in *Mesopodopsis slabberi* are not as well known as might be expected. The species was described from *in situ* observations (Wittman 1977) as active and colourless during the day, showing no visible substrata preferences and changing leadership within schools spontaneously. Wittman (1977) also noted that schools did not appear to return to the same location and that predator-evading swarms veered horizontally without changing depth unless the predator attacked from above, a behaviour that should aid in capture by an epibenthic sledge. Daytime schools swam up to 50 cm above the substratum. Although Wittman (1977) did not specifically name *M. slabberi* in that context, he implied that nocturnal expansion among the mysids he studied was the norm. Wang & Dauvin (1994) found *M. slabberi* in epibenthic sledge samples both night and day and concluded from its upward skewed distribution among vertically resolved samples that it is an active swimmer, consistent with the observations of Wittman (1977). Wang & Dauvin (1994) caught more individuals in nighttime sledge samples but remarked that it might have been because of increased capture efficiency (less evasion in the dark). Zouhiri et al. (1998) in another series of epibenthic sledge samples found crepuscular peaks in capture of *M. slabberi*, consistent with the idea of distribution broadening above the bottom at night (and perhaps net evasion in the light).

An inference consistent with most observations and directly supported by paired benthic and pelagic samples in the Jade estuary is that *M. slabberi* is concentrated near the bottom during the day but spreads into the water column at night (Apel 1992). This spreading includes a horizontal component, into the intertidal zone of at least one estuary during the night (Colman & Segrove 1955). It is worth noting that whether a seaward expansion also occurs in surface waters is unknown. In a long-term study of the polyhaline zone of the very turbid Gironde estuary, however, *M. slabberi* was captured abundantly in surface waters during daylight (Castel 1993, David et al. 2005). In addition, in the region of South African surf-zone diatom blooms *M. wooldridgei* Wittman, 1992 (closely enough related that it was previously identified as *M. slabberi*) also migrated onshore at night to take advantage of sinking surf-zone diatoms carried offshore in rip currents (Webb & Wooldridge 1990) at the same time that another mysid species, *Gastrosaccus psammodytes* Tattersall, 1958, migrated offshore from its inner surf-zone, daytime habitat to take advantage of that same resource (Webb et al. 1988). *Mesopodopsis slabberi* appears to migrate offshore in winter but to include vertical migrations in its repertoire there at 20 m water depth (van der Baan & Holthuis 1971). Even in winter, however, this species is observed inside but near the mouths of some estuaries (Mees & Hamerlynck 1992), so the entire population does not migrate offshore seasonally, and both migration and site-dependent mortality need to be examined as components of the distributional shift. Seasonally, *M. slabberi* also enters tidal creeks of salt marshes at high tides in sufficient abundance to be important as a prey species there (Hampel et al. 2003a), but it

is unclear to what extent active behaviour versus passive advection is responsible (Hampel et al. 2003b). Recent molecular genetic work shows some genetic differentiation among populations in the northeast Atlantic and Mediterranean and Black Seas (Remerie et al. 2006) and also shows what may be an important mysid trait allowing rapid adaptation (i.e., high intrapopulation genetic diversity).

Schistomysis spiritus and *S. kervillei* show similar migration patterns to *Mesopodopsis slabberi*, including nocturnal vertical spreading (van der Baan & Holthuis 1971, Apel 1992, Wang & Dauvin 1994). Of these two congeners, nighttime expansion into very shallow water has been reported for *Schistomysis spiritus* (Colman & Segrove 1955). Wang & Dauvin (1994) documented near-bottom, daytime vertical distributions and near-bottom, nighttime spreading patterns in vertically resolved sledge samples that allowed them to rank swimming activity as *Mesopodopsis slabberi* > *Schistomysis spiritus* > *S. kervillei*, with *Gastrosaccus spinifer* in the same category as *Schistomysis kervillei* and none of these mysids in their lowest activity category.

Mesopodopsis slabberi is the most widely distributed of the three species geographically, ranging from Iceland in the Atlantic to North Africa, widely through the Baltic and Mediterranean and into the Black Sea (Deprez et al. 2005). Both *Schistomysis* congeners have somewhat more restricted geographic distributions than *Mesopodopsis slabberi*, with *Schistomysis spiritus* ranging from the Baltic to northern France and *S. kervillei* ranging from the North Sea to the southern Atlantic coast of France (with a report from northwest Africa), but its habitat distribution is comparable, ranging from shallow estuarine to shelf depths (Deprez et al. 2005). Within the North Sea, *S. spiritus*, *S. kervillei* and *Mesopodopsis slabberi* peaked in abundance near shore (Dewicke et al. 2003). Late-summer abundances (all mysids combined) averaged near 30 m⁻³ and 30 mg AFDW m⁻³ in sledge samples from the nearshore zone. All three species, however, reached even higher densities in the polyhaline and mesohaline zones of estuaries (e.g., Castel 1993, Wang & Dauvin 1994, Delgado et al. 1997, Azeiteiro et al. 1999, Lock & Mees 1999, Dauvin et al. 2000, Mouny et al. 2000, Wittman 2001, Drake et al. 2002, Dewicke et al. 2003). In terms of winter distributions, all three species are known to occur inside estuaries (near the mouth of the Schelde; cf. Mees & Hamerlynck 1992), in shallow coastal waters of warm regions (e.g., Lock & Mees 1999) and also offshore (van der Baan & Holthuis 1971).

In deeper waters of the English Channel and the European shelf, other mysid species become dominant. Dauvin et al. (2000) presented a summary of 432 epibenthic sledge samples taken at 15 stations in the English Channel, including 3 stations within the Seine estuary, and covering the years 1988–1996. Those three stations have been excluded from the analysis in this review, except to note that they support the habitat pattern observed elsewhere for *M. slabberi* (i.e., shallow-water marine plus polyhaline-mesohaline estuarine water). The indisputable dominant in terms of abundance and frequency of occurrence outside the Seine estuary is *Anchialina agilis*, with mean abundances >1 ind. m⁻³ at both of the deepest stations, a coarse sand off Roscoff and a medium sand off Plymouth, both at 75 m depth. The species occurred at all the stations outside the Seine. Four other species occurred at over one half of the non-estuarine stations and reached mean abundances of at least 1 ind. m⁻³ at a minimum of one station: *Gastrosaccus spinifer*, *Haplostylus lobatus*, *H. normani* and *Schistomysis ornata* (G.O. Sars, 1864). Other studies in the same region by the same group of investigators appear consonant with these broad conclusions (e.g., Vallet et al. 1995, Vallet & Dauvin 1998, 2001), although Zouhiri et al. (1998) clearly showed *Erythrops elegans* (G.O. Sars, 1863) to be co-dominant with *Anchialina agilis* and *Schistomysis ornata* in autumn samples from the 75-m station near Plymouth, so *Erythrops elegans* has been added to the list of species for investigation of migratory habits in this review. Samples off Arcachon, France (Cornet et al. 1983), and off Aveiro, Portugal (Cunha et al. 1997), support the ubiquity and abundance of *Anchialina agilis* at shelf depths ≤125 m and the inclusion of *Erythrops elegans* as a frequent and abundantly caught mysid. They also support adding *Leptomysis gracilis* (G.O. Sars, 1864) as a

frequent co-dominant and occasional dominant at 52–125 m depth. Both of these sampling efforts also found relatively high abundances of *Mysideis parva* Zimmer, 1915 at 85–120 m depth, so this species has been added to the list of abundant species (Table 1).

Anchialina agilis, *Gastrosaccus spinifer*, *Haplostylus lobatus* and *H. normani* are included in the list of six species provided by Macquart-Moulin & Ribera Maycas (1995), along with incontrovertible evidence of their emergence at night. As its specific name implies, *Anchialina agilis* is an exceptionally strong swimmer. As for most shelf mysids, direct observations are rare. Wittman (1977) described *A. agilis* during the day in diving depths to be inactive and colourless and to cling to leaves of *Zostera* without showing any reaction to natural predators or to touch by a diver. This description is incompatible with inferences from vertically resolved epibenthic sledge samples, where *Anchialina agilis* is usually nearly uniformly distributed among vertically arrayed nets near the bottom (e.g., Zouhiri & Dauvin 1996). Either the behaviour of this species varies spatially or they show an eventual escape response to the sledge that is strong enough to randomise their vertical distribution at the sledge mouth. Given their ubiquity, observations with a remote underwater vehicle or other camera system should be feasible to resolve their daytime behaviours beyond comfortable depths for divers. Both *A. agilis* and *Haplostylus normani* showed decreases of abundance in bottom trawls (Zouhiri & Dauvin 1996) and increases in surface plankton tows (Macquart-Moulin & Ribera Maycas 1995) at night, when *Anchialina agilis* showed remarkable concentration in the very surface 10 cm of the water column (Champalbert & Macquart-Moulin 1970). Few other species are so reduced in abundance in nighttime epibenthic sledge samples (Zouhiri & Dauvin 1996), prompting the conclusion that most of the *A. agilis* and *Haplostylus normani* populations undergo diel migration (Macquart-Moulin & Ribera Maycas 1995, Vallet et al. 1995). *Anchialina agilis* has been caught at the surface in water columns 1000 m deep, likely due to cross-isobath advection of surface waters during emergence (Macquart-Moulin & Patriiti 1993, Macquart-Moulin & Ribera Maycas 1995), yet it is difficult from extant data to exclude the possibility of an active horizontal component to the migration as a contributor (Macquart-Moulin & Ribera Maycas 1995). Suggestive of accidental expatriation is the capture in bathyal waters during the day of dead specimens (Macquart-Moulin & Ribera Maycas 1995). Macquart-Moulin & Ribera Maycas (1995) also concluded that the whole population of *Gastrosaccus spinifer* became pelagic at night.

Of the migrators discussed by Macquart-Moulin & Ribera Maycas (1995) and included under the abundance criteria in this review, *Anchialinja agilis* is distributed from the North Sea to the northern Mediterranean and is captured in estuaries only as stray specimens. *Haplostylus lobatus* and *H. normani*, with synonymy that has been disputed (Deprez et al. 2005), together cover a range from the Porcupine Bight to the northern Mediterranean and also are rare in estuaries. *Gastrosaccus spinifer* ranges from Norway, in all the seas surrounding the British Isles and into the northern Mediterranean and along the adjacent North African coast, with disjunct reports from Ivory Coast and the South Shetland Islands in the Southern Ocean (Deprez et al. 2005). It is found further into estuaries than the others but generally in reduced numbers compared with the nearby shelf (e.g., Buhl-Jensen & Fosså 1991).

Macquart-Moulin & Ribera Maycas (1995) did not list *Erythroops elegans*, *Schistomysis ornata*, *Leptomysis gracilis* or *Mysideis parva* among the most abundant shelf mysids and thus did not assess their migratory capabilities. Little published information is available on migration in *Erythroops elegans*. Zouhiri et al. (1998) on the basis of vertically resolved epibenthic sledge samples listed it as a weak swimmer, along with *Gastrosaccus spinifer* and *Schistomysis ornata*, because it tended to be caught in the lower nets. Vallet et al. (1995), quoted in Zouhiri & Dauvin (1996), suggested that *Erythroops elegans* migrates on a diel cycle (up at night) from the bottom boundary layer to the surface.

Mauchline (1980) found negative evidence in the Clyde Sea and Loch Etive for diel migration of *S. ornata* and in the Clyde for *Erythroops elegans*. He did not comment on migration of *Mysideis*

parva. In an extensive series of vertical plankton tows from the continental shelf of western France over the span of 2 yr, Beaudouin (1979) reported *Schistomysis ornata* only from February tows near the Gironde. Sorbe (1991) reported this species to be abundant from 91 to 179 m depth off Arcachon in southwest France. Based on qualitative plankton tows over the 91-m station, he reported vertical migration in this species and suggested based on size-frequency data that the species migrates seasonally across isobaths. Zouhiri et al. (1998) found *S. ornata* and *Erythropeleus elegans* in high abundance in the western English Channel, but their data showing nighttime disappearance of mysids as a group from sledge samples (with crepuscular peaks in abundance) came from a station in the eastern channel. They captured both *Schistomysis ornata* and *Erythropeleus elegans* primarily in the lower two sampling nets of their epibenthic sledge, prompting the classification of these two species in the group of weakest swimmers. Dauvin et al. (2000) captured *Schistomysis ornata* only in nighttime sledge tows. Vallet & Dauvin (2001), however, captured roughly equal biomasses of this species in day and night tows with peak autumn abundances reaching 21 ind. m⁻². Vallet et al. (1995), quoted in Zouhiri & Dauvin (1996), suggested that *S. ornata* remained planktonic all day. Kaartvedt (1989) in the abstract of his study on mysid migration in Masfjorden, Norway, listed *S. ornata* as a vertical migrator, but in that paper reported capture in 57 mostly nighttime Isaacs-Kidd mid-water trawls of only 10 individuals (7 in the shallowest region sampled, above a bottom 35–40 m deep and 3 singletons elsewhere) but made reference to unpublished data from Kaartvedt et al. (1988) to support the conclusion of frequent migration. Earlier observations, summarised by Tattersall (1938), suggested that a small subset of breeding individuals enters the water column at night. Also supporting a case for reduced migration in this species compared with the others already explored is its reported occurrence in the guts of relatively few fish species in the three databases queried (i.e., Gibson & Ezzi 1980, Mauchline 1980, Astthorsson, 1985), but Mauchline (1980) included several more predators, including herring (*Clupea harengus*), so the issue of the degree of diel migration is not well settled in terms of the fraction of the population participating, the seasonality of the phenomenon, its short-term frequency or the height above bottom at which potentially enhanced swimming activity occurs. *Schistomysis ornata* also appears to be able seasonally to congregate at a coastal front, presumably via horizontal migration, to take advantage of the concentrated food resources there (Dewicke et al. 2002).

Mauchline (1980) cited abundant evidence of diel vertical migration in *Leptomysis gracilis*, a highly mobile swarmer. Subsequent observations underscore the diel migratory activities of *L. gracilis* (into the water column at night; e.g., Kaartvedt 1985, 1989). Zouhiri & Dauvin (1996), however, captured more individuals in epibenthic sledges at night than during the day, suggesting that part of the population stays on or returns to the bottom and that it may be more easily captured at night. They also observed this species to be concentrated in the lower nets of vertically resolved tows, nominally indicating lower activity but perhaps indicating a species-specific escape response.

Very little information is available on the migratory behaviour of *Mysideis parva*. Elizalde et al. (1991) reported that the species was concentrated in the lower nets of their sledge samples, indicating weak swimming ability, though nocturnal activity cycles have not been ruled out. In terms of predator gut contents, it has been reported only from thornback rays (*Raja clavata*) (see Mauchline 1980), lending some support to the conclusion that little migration occurs.

Erythropeleus elegans is somewhat narrowly distributed latitudinally in the North Atlantic (not reported from northern Norway, Iceland or Morocco) but it is found broadly in the northern Mediterranean. Although it is found in some fjords, it has not been reported from shallower estuaries or from salinities much below that of sea water. *Schistomysis ornata* occurs in the North Atlantic off Iceland, from Norway to France along the European west coast and in coastal seas surrounding the British Isles. To the east it extends into the Baltic. It is also reported from Morocco, but not from the Mediterranean. Like *Leptomysis gracilis*, it occurs frequently in fjords. *Leptomysis gracilis* is distributed from Norway south around the British Isles, through the Baltic and broadly in the

northern Mediterranean. It occurs frequently in fjords and in some shallower estuaries. *Mysideis parva* has been reported on only a few occasions and only at strictly marine sites stretching from southern Ireland to the Ionian Sea.

Erythroops elegans, *Schistomysis ornata* and *Leptomysis gracilis* co-occur in western Norwegian fjords, where their depth ranges are generally narrower and shallower than the inclusive ones quoted in Table 1 (Fosså & Brattegard 1990). *Erythroops elegans* was collected by Fosså & Brattegard (1990) at 32–100 m depth and had a median depth of occurrence of 40 m. In the fjords, *Schistomysis ornata* and *Leptomysis gracilis* had depth ranges of 32–350 m and 32–166 m and median depths of occurrence of 66 and 89 m, respectively. The four shallowest stations in this wide-area survey were at 32, 40, 74 and 100 m depth. Even more interesting is the horizontal distribution in detailed studies of a single fjord of western Sweden (Buhl-Jensen & Fosså 1991). *Erythroops elegans*, *Leptomysis gracilis*, *Mesopodopsis slabberi*, *Schistomysis ornata* and *S. spiritus* all reached high abundances on one or both of the sill stations. *Erythroops elegans* and *Mesopodopsis slabberi* occurred only on the sill. *Leptomysis gracilis* had highest abundance on the sill but also occurred throughout the fjord. *Schistomysis ornata* peaked on the shelf just beyond the sill (with second- and third-ranked abundances on the sill) but was distributed across all stations except the shallowest, most upstream station (depth 33 m). *Erythroops erythrophthalma* (Goës, 1864) showed a similar pattern, with high abundance just outside the sill, at the inner sill station, and the highest abundance shown by any mysid (11 ind. m⁻²) just inshore of the sill at 72 m depth.

Northwest Atlantic shelves

Regrettably, systematic, intensive epibenthic sledge sampling has not been practised so frequently on other shelves. On the west side of the Atlantic, the collection of the U.S. National Marine Fisheries Service (NMFS) from the U.S. Atlantic coast remains indisputably the most comprehensive (Wigley & Burns 1971). It includes samples with an epibenthic sledge ('bottom skimmer') and 11 other kinds of samplers. Although this study and a follow-up analysis (Wigley & Theroux 1981) included abundant core samples from areas further south, sledge samples were limited to the region between Nova Scotia and Long Island. The NMFS survey left no room for doubt about the single most dominant species (Wigley & Burns 1971): "*N[eomysis]. americana* is the most common mysid inhabiting the northeastern coastal waters of the United States and undoubtedly the most abundant mysid in the western North Atlantic Ocean. ...The NMFS [National Marine Fisheries Service] collection originally contained over 2 million specimens...". The next most abundant mysids in the NMFS collection were *Erythroops erythrophthalma*, with 4573 specimens, and *Americamysis bigelowi* (Tattersall, 1926), with 2031 specimens (Wigley & Burns 1971). No other species yielded >382 specimens. No areal or volumetric abundance estimates were attempted by Wigley & Burns (1971), who were quite sensitive to issues of sampling bias (e.g., Wigley 1967).

Mauchline (1980) cited abundant evidence that *Neomysis americana* is a frequent migrator in shallow water but noted (p. 74) that Whiteley (1948) "found no evidence of a regular diel migration in *Neomysis americana* on Georges Bank where the depth at which they were living, as deep as 75 m, was greater than in the coastal regions where this species is known to migrate fairly regularly". Brown et al. (2005) from an extensive collection of zooplankton samples documented seasonal emergence, peaking in April and May, over the period from 1995 to 1989. In most years, peak abundances captured in these plankton samples were 0.1–1 ind. m⁻³. The present author and coworkers have been collecting emergence-trap and acoustic data on this species in the Damariscotta River estuary, in the U.S. mid-coast region of Maine for over 5 yr and at depth ranges of 10–20 m; it undergoes diel, tidally modulated emergence from approximately late June until early November, although emergence may be weak or absent on any particular day (Abello et al. 2005, Taylor et al. 2005, P.A. Jumars, unpublished observations). *Neomysis americana* appears to be a strongly diel

migrator in some seasons in most habitats from which it has been reported (e.g., Calliari et al. 2001). *Neomysis americana* also shows spectacular ability to aggregate (up to 2500 ind. m⁻²) in bottom-water salinity fronts of estuaries (Schiariti et al. 2006).

Mauchline (1980) did not comment on migration in *Americamysis bigelowi*. The 10-year study of Williams (1972) left no doubt, however, that *A. bigelowi* migrates above the bottom in large numbers. Further support comes from its presence in the guts of Atlantic silversides (*Menidia menidia*) in 20 m of water off New York (Warkentine & Rachlin 1989).

Mauchline (1980) cited Brunel (1979) for documentation of vertical migration of *Erythroops erythrophthalma* in the Gulf of St. Lawrence. More recently, Carter & Dadswell (1983) reported planktonic capture of *E. erythrophthalma* in the very turbid Saint John River estuary, New Brunswick, year-round, including all life stages, but they took no benthic samples. Beaudouin (1979) reported it from only three of her vertical plankton hauls off Gascogne during one winter. It is among the species reported by Astthorsson (1985) from cod (*Gadus morhua*) guts, but the small number of observations leaves the regularity and depth limits of its diel migratory status uncertain.

When this review was written, Deprez et al. (2005) had not entered many geographic data on mid-latitude mysids outside Europe and Africa so, herein, original reports are cited instead. The natural range of *Neomysis americana* is from the Gulf of St. Lawrence to northeastern Florida (Williams et al. 1974). Such a broad geographic range that includes high abundances at both its extremes of latitude strongly suggests a very successful opportunist or generalist, a conclusion supported by its invasion of coastal waters and estuaries of South America, where it was first reported from Uruguay (González 1974), but has spread south at least as far as San Blas, Argentina (Orensanz et al. 2002). Some fishes have come to depend on this resource (e.g., Sardiña & Lopez Cazorla 2005a,b), and some sympatric copepod populations have declined (Hoffmeyer 2004, although she does not attribute the effect to *N. americana*; M.S. Hoffmeyer, personal communication). *Americamysis bigelowi* is known from Georges Bank southward to Florida (Wigley & Burns 1971). The species frequently co-occurs with, but in substantially lower abundance than, *Neomysis americana* (e.g., Allen 1984). These two species are capable of substantial carnivory (Fulton 1982). *Americamysis bigelowi* (as *Mysidopsis bigelowi*) was thought to range into the Gulf of Mexico to the Texas coast, but is replaced by a pair of closely related species in the Gulf of Mexico (Price et al. 1994): *Americamysis alleni* Price, Heard & Stuck, 1994 and *A. stucki* Price, Heard & Stuck, 1994. The former species is found in poly- and mesohaline estuaries and the surf zone to 15 m, whereas the latter species has a deeper distribution out to the shelf edge (Price et al. 1994). Deprez et al. (2005) give distributional data for European *Erythroops erythrophthalma*, which is found off Greenland and Svalbard, down the Norwegian coast and around the British Isles, off western France and along the shelf and slope of the northern Mediterranean. The species is found southward along the U.S. east coast as far as Delaware, peaking in abundance at 60–100 m depth in evidence from the NMFS collection (Wigley & Burns 1971), and is widespread in the Arctic basin (Petryashev 2002a,b).

All three of the most abundant mysid species in the NMFS collection showed high abundance on Georges Bank, with *E. erythrophthalma* most abundant on its southern flank, just above the 100-m isobath. *Erythroops erythrophthalma* is found primarily on the middle and outer shelf (Wigley & Burns 1971, Petryashev 2002a). Both *Neomysis americana* and *Americamysis bigelowi* are abundant in estuaries (e.g., Herman 1963, Allen 1984). In the NMFS survey, peak abundances on the shelf for *A. bigelowi* were at 30–60 m depth (Wigley & Burns 1971). The bathymetric distribution of *Neomysis americana* is unusual. In grab samples from the Gulf of Maine, Wigley and Burns (1971) found this species at highest abundance from 30 to 60 m depth, noting its more common presence in grabs taken during daylight. Within Cape Cod Bay, however, *N. americana* apparently has a shallower abundance peak at 10–29 m depth (Maurer & Wigley 1982). In the southern United States, the species rarely is captured in benthic samples offshore (Wigley & Burns

1971), occurring more frequently in the lower, middle and upper reaches of estuaries (e.g., Williams 1972, Zagursky & Feller 1985). This onshore shift, opposite in direction to that of many other species with temperature or latitude, led Williams et al. (1974) to suspect (sub)speciation, but morphological evidence did not support this interpretation, although the issue now merits re-examination with molecular methods (Audzijonyte & Väinölä 2005, Remerie et al. 2006). Over both the shelf and offshore shoals, within coastal embayments and near inlets, abundance peaks of *N. americana* are reported in winter-spring, consistent with an overwintering generation breeding then, although overwintering is not excluded as a possibility within estuaries as well (Carter & Dadswell 1983). Estuarine abundance of *N. americana* generally peaks in summer from the mid-Atlantic states northward, and the number of generations per year can increase to three in the southern part of the species range (Cowles 1930, Whiteley 1948, Hulbert 1957, Herman 1963, Hopkins 1965, Williams 1972). In South Carolina, *N. americana* is found year-round in subtidal estuary channels and in shallow ocean waters, and its peak populations in estuaries are shifted earlier in the year (DeLancey 1987, Johnson & Allen 2005, D.M. Allen, personal communication).

Northeast Pacific shelves

Elsewhere, information is much more fragmentary. In his classic study of nearshore mysids in the surf zone of southern California, Clutter (1967) found the two most abundant mysids to be *Metamysidopsis elongata* Holmes, 1900 (up to about 2000 ind. m⁻³ at 6 m below MLLW (mean lower low water)) and *Neomysis kadiakensis* Ortmann, 1908 (up to about 180 ind. m⁻³ at 8 m below MLLW); both are swarming species. Clutter (1969) reported only a subtle upward shift in median population position of *Metamysidopsis elongata* at night, and he reported no observations on *Neomysis kadiakensis* at night. Little more has been written after Clutter's studies about the behaviour and distribution of *Metamysidopsis elongata* except its essential fatty acid requirements (Kreeger et al. 1991) and its role as a prey species for juvenile white seabass (*Atractoscion nobilis*) (Donahoe 1997). A few observations on abundance patterns and laboratory culture of its Atlantic subspecies have appeared (Tararam et al. 1996, Gama et al. 2002, and references therein).

Neomysis kadiakensis appears to follow an analogous pattern to the European *Mesopodopsis slabberi* in abundance along the west coast of the United States. Clutter described *Neomysis kadiakensis* as occurring in kelp beds as well as over open sand. This species can reach higher abundances in estuaries. Dean et al. (2005) in a salt marsh within the San Francisco estuary noted that it dominated mysid abundance there over the full year, with a spring peak in abundance at 244 ind. m⁻³. They measured a large net import of *N. kadiakensis* into the salt marsh, where instantaneous mortality was calculated as 0.29 day⁻¹. Kringel et al. (2003) in northern Puget Sound over a muddy bottom at 20 m water depth observed coherent emergence and re-entry events of *N. kadiakensis* associated with estimated biovolumes of 4–5 × 10³ mm³ m⁻³. Moreover, these nocturnal emergence events appear to have dominated the holoplankton in abundance (Kringel et al. 2003). Vertical migration of this species is widespread in Puget Sound, but in the deeper reaches individuals do not appear to migrate all the way to the sea bed (Thorne 1968). It seems unlikely that Clutter (1969) could have missed such strong nocturnal emergence, so *N. kadiakensis* likely differs in diel migration patterns along its range. *Neomysis kadiakensis* is distributed from the Gulf of Alaska to southern California (Petryashev 2005).

Kim & Oliver (1989) specifically studied schooling crustaceans in regions where gray whales (*Eschrichtius robustus*) fed in the Bering and Chukchi Seas. In diving observations concentrated in the Bering Sea, they reported swarms of *Xenacanthomysis pseudomacropsis* Tattersall, 1933, *Neomysis rayii* Murdoch, 1885 and *Exacanthomysis arctopacifica* Holmquist, 1981 and sampled them with various means at depths from 3 to 24 m. Petryashev (1992) regarded *E. arctopacifica*

as a junior synonym of *Acanthomysis stelleri* Derzhavin, 1913. In Kim & Oliver's study, *Xenacanthomysis pseudomacropsis* usually dominated and reached abundances of 600 ind. m⁻³. *Acanthomysis stelleri* was one to two orders of magnitude less abundant, and *Neomysis rayii* was reported only from two sites at the southeast extreme of the Bering Sea, where it reached intermediate abundances between those of the other two species. Direct observations of diel migration apparently are lacking, but Wing & Bar (1977, quoted in Mauchline 1980) captured *Xenacanthomysis pseudomacropsis*, *Acanthomysis* sp. and *Neomysis rayii* in mid-water trawls from the Chukchi Sea. *Neomysis rayii* is a known winter diet component in common murrelets (*Uria aalge*) and marbled murrelets (*Brachyramphus marmoratus*) off southeast Alaska (Sanger 1987, DeGange 1996) and *Acanthomysis* spp. are listed as additional diet components of the latter (DeGange 1996), although it is not clear how far the birds make excursions toward the bottom or mysids make excursions off the bottom to effect their encounters. *Neomysis rayii* and *Acanthomysis* spp. are also taken by gray whales (*Eschrichtius robustus*) further to the south, off Vancouver Island (Darling et al. 1998). *Neomysis rayii* must have been caught often enough in plankton samples to be considered a pelagic crustacean by some (McConnaughey & McRoy 1979), but simultaneous benthic and pelagic samples over diel cycles would do much to clarify these issues for all three of the Alaskan species. *Xenacanthomysis pseudomacropsis* occurs from central Japan to British Columbia, *Neomysis rayii* shares that range and extends it to southern California, and *Acanthomysis stelleri* has the narrowest geographic range from northern Japan to the easternmost portion of the Aleutian peninsula. All three species extend into the Chukchi Sea but not above the latitude of Wrangel Island (Petryashev 2002a).

Northwest Pacific shelves

Takahashi & Kawaguchi (1995, 1997) on the Pacific coast of northern Honshu, Japan, took isobath-parallel, epibenthic sledge samples from the shallowest submerged station they could sample at the lowest level of the spring tide out to 100 m from the tide line, to about 5 m water depth. Tows were stratified by distance from shore in 10-m increments and were repeated monthly between March 1992 and January 1993. Three species clearly dominated, with the dominant varying with season and depth: *Archaeomysis kokuboi* Ii, 1964, *A. japonica* Hanamura, Jo & Murano, 1996 and *Iiella ohshimai* (Ii, 1964). *Archaeomysis kokuboi* moved with the tide to stay in the shallowest position, barely immersed, and showed a peak abundance of 511 ind. m⁻² in 31 July in the 0- to 10-m range from the water's edge. (The areal abundance estimate in the present review includes no correction for sampling efficiency but simply divides the number in the tow by its 60-m² area.) *Archaeomysis kokuboi* emerged at night, expanding its distribution offshore, with the reproductively most valuable members of the population showing less tendency to do so. *Archaeomysis japonica* occupied the next depth stratum and did not migrate with the tides but also emerged at night. The species reached peak abundance in the 10- to 20-m interval from the tide line in June at 60 ind. m⁻². *Iiella ohshimai* was found primarily in the deepest samples as juvenile stages but showed some shoaling of its distribution in summer and also emerged at night. *Iiella ohshimai* reached peak abundance of 1.3 ind. m⁻² in the 20- to 30-m distance from the shoreline in August, but in other months more than half of the captured individuals were found further offshore. All three species spent daytime hours buried in the sand, and all three species showed depth segregation of life stages. The *Archaeomysis kokuboi* population had breeding females as its shallowest members, whereas the other two species' populations had juveniles as their shallowest members. *Archaeomysis kokuboi* and *A. japonica* are extensively exploited as food by surf-zone fishes and, as expected from their burrowing behaviour during the day, are taken mostly at night by both benthic and pelagic fishes that converge on this environment (Takahashi et al. 1999). Moreover, adult females of *A. kokuboi* find spatial refuge in the extremes of shallow water (Takahashi et al. 2004).

Yamamoto & Tominaga (2005) took epibenthic sledge samples by boat from the shallow surf zone of the Seto Inland Sea three times a month from May to August in three successive years. *Iiella ohshimai* and *Nipponomysis ornata* Ii, 1964 co-dominated, with mean densities of 1.38 and 1.28 ind. m⁻², respectively. One of the three dominant fish species fed primarily on the (daytime) epibenthic species *N. ornata*, whereas the other two ingested *Iiella ohshimai* more frequently, based on gut contents of daytime-collected fishes (Yamamoto & Tominaga 2005). In a separate study of Japanese flounder (*Paralichthys olivaceus*) from the same region, Yamamoto et al. (2004) found them to prefer the epifaunal *Nipponomysis ornata*. In another site in the same general region of the Seto Inland Sea, sampled monthly by epibenthic sledge between May and October for two of the same years, *N. ornata* showed much greater dominance over *Iiella ohshimai*, and mysid abundance peaked at 250 ind. m⁻² in May–June (Hanamura & Matsuoka 2003).

Of the four mysid species that dominated the nearshore subtidal in these Japanese studies, only *Archaeomysis kokuboi* is listed by Petryashev (2005) in his biogeographic summary. He listed it as being West Pacific, low boreal. Hanamura (1997) described its geographic limits as being from central Hokkaido to Honshu in northern Japan and those of *A. japonica* as being shallow subtidal to 50 m from Kyushu to Hokkaido. Suh et al. (1995) described an offshore migration in *A. kokuboi* in eastern Korea in the afternoon, with onshore migration in the morning, but their study was done before Hanamura (1997) resolved differences between some closely related species of *Archaeomysis*. Hanamura et al. (1996) also confirmed the emergence of *Archaeomysis japonica* at night. It appears that no information on diel migration of *Nipponomysis ornata* is available.

Other regions

In other regions, it was not possible to attempt the two-step methodology for lack of comparable abundance estimates or information on migratory behaviour or lack of both, but it is clear that mysids are ubiquitous at and beyond the range of latitudes considered here. Patagonian fjords, as but one example, contain a rich mysid fauna (Brandt et al. 1997), with evidence of diel migrations (Antezana 1999), and merit more intensive study. In many cases, neuston or plankton samples confirm a pelagic phase, but neither the connection to benthic populations nor phasing of migrations is known (e.g., Sawamoto 1987). A few more of these geographically scattered reports are mentioned in the following discussions of particular issues of ecological roles of mysids and drivers of their vertical migrations.

Mysid 'umwelt'

Information in the three databases used is clearly biased geographically toward Europe and North America, but where data are available on all three aspects, there is strong association among diel migration by a mysid species, its high relative abundance among mysids in the same habitat and its use as food by fishes and other animals. There is no reason to doubt that additional data would add additional species to this list or that it could already be enlarged through other databases, but some trends already are apparent. The clear risk during migration in species with this syndrome must clearly be accompanied and outweighed by substantial fitness gains in nutrition, dispersal, reproductive encounter and other aspects of life in order for these species to be among the most abundant mysids. As but one example of these 'other' potential gains or reduced losses, mysids living in macrophyte beds or over dense diatom mats may be driven out by low oxygen concentrations at night (Ledoyer 1969). One other pattern is apparent immediately from the data: many of the abundant shelf species of mysids show even higher abundances in the convergence zones at estuary mouths (Figure 1) than they do on shelves, with varying seasonal penetrations and population irruptions into polyhaline, mesohaline and even oligohaline reaches of estuaries.

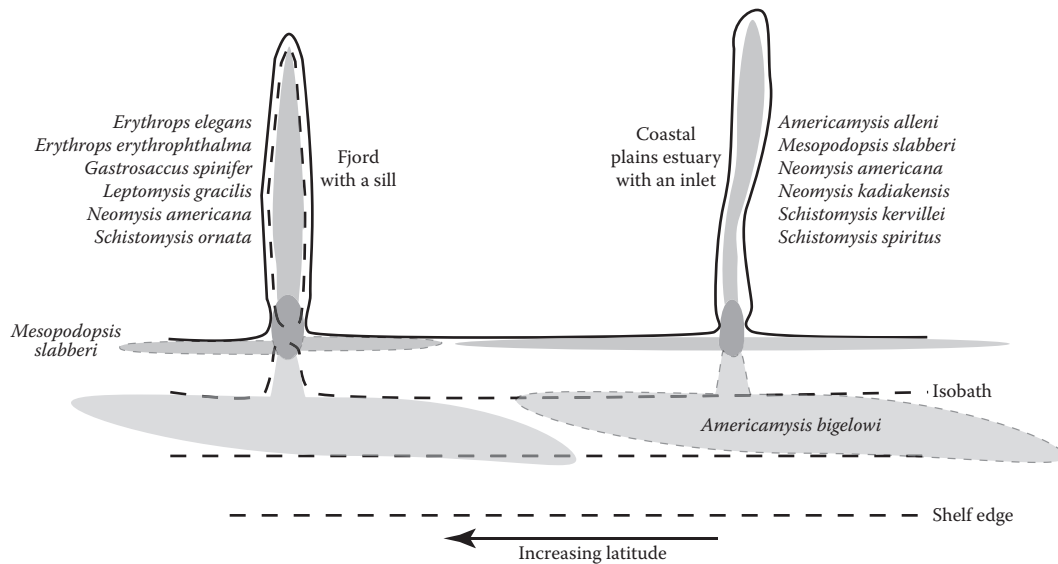


Figure 1 Species that meet abundance criteria in the text and that occur either in the surf zone and estuaries or on the mid-shelf and in fjords or show both patterns (*Neomysis americana*). *Mesopodopsis slabberi* apparently also invades fjords from the surf zone, whereas *Americamysis bigelowi* apparently invades estuaries from the mid-shelf as surmised from seasonal abundance patterns.

Multiple drivers of emergence and their differing relative importance among species, locations and times are as certain for mysids as they are for holoplankton (Pearre 2003), but strong involvement of visual predators is clear from the characteristic pattern of emergence near dusk and re-entry near dawn. What makes the emergent lifestyle unique is relative, Eulerian immobility during the benthic phase, during which overlying waters are replaced. Holoplankton arguably can get a similar subsidy in regions of high vertical shear, and euphausiids are routinely captured in epibenthic sledge samples from mid-shelf depths and deeper (e.g., Cunha et al. 1997), but it will take a particular combination of vertical shear and migration timing to remain in a region of high horizontal velocity (e.g., Barber & Smith 1981). Daytime location of mysids under the surf zone, under inlets, on sills (Figure 1) and under particular portions of estuaries (e.g., Kaartvedt 1989, Cunha et al. 1999) attests to mysid virtuosity in utilising horizontal fluxes and resisting displacement. Horizontal subsidy has been easiest to visualise over abrupt changes in topography such as seamounts (reviewed by Genin 2004). The zooplankters that happen to occur over seamounts and shoals as their downward diel migrations begin are subject to intense predation. In the mysid case, the topography can be less steep, but the process is analogous and it is the mysids rather than their food taxa that do the migrating; the large phytoplankton, other protists and small zooplankton that chance to be advected above a mysid-rich area at night are subject to intense predation. Just as predators resident on seamounts can produce patches of reduced zooplankton abundance in those waters that passed over a seamount at night (Haury et al. 2000), nocturnal, pelagic patches of high mysid abundance of diel migrators can be predicted to produce patches of reduced abundance in their holoplanktonic prey. Preferred daytime mysid habitat underlies wave-driven currents, coastal currents, tidal currents, buoyancy-driven currents and topographically driven flow convergences over shoals, narrows and sills, where resultant flows replace overlying waters at high frequency. The contrast between mysids and euphausiids in fjords (Kaartvedt et al. 1988, Kaartvedt 1989) illuminates the benefits of the mysid lifestyle. Euphausiids are clearly less capable of maintaining or returning to horizontal

co-ordinates of high horizontal flux or of high utility as refuge from predators and so are less able to profit from them than are mysids.

Mysids thus fit into a broader pattern of horizontal import subsidy but have some special adaptations that enhance their gains. Genin (2004, his 'feed-rest' hypothesis) noted that fishes on seamounts can rest in the bottom boundary layer or behind flow obstructions when they are not feeding. Mysids as omnivores can improve on feed-rest by feeding in the pelagic environment and both feeding and resting on the bottom. They can cause 'trophic focusing' (Genin 2004) even where topography is not steep. The reason that this focusing is not as evident as it could be, in turn, is that mysids clearly suffer extensive mortality from mobile decapod and fish predators that horizontally export much of the horizontal import subsidy that they gather. If mysids fed only on locally produced prey and on a narrower range of resources, or if they were not fed on as heavily, their impacts would be far easier to detect but they would be less important as stabilisers in the context of new food-web theory (Montoya et al. 2006, Rooney et al. 2006). The likelihood that they return to similar habitat but not the same location when they re-enter the benthic habitat suggests that they also lend dynamic stability to benthic community structure; a local disturbance in terms of mortality of mysids can recover literally overnight compared with the need in many other benthic species for larval recruitment to occur.

Besides the typical pattern of daytime re-entry and nighttime emergence, a second indication of the importance of visual predation as a driver of emergence is release from re-entry in especially turbid waters (Carter & Dadsell 1983, Castel 1993) and association of high mysid abundances with high turbidity zones of estuaries (e.g., Kimmerer et al. 1998b, Roast et al. 2004, Schiariti et al. 2006), which often leads to shoaling of populations in upper, more turbid reaches (e.g., Hulbert 1957). This association with and benefit from turbidity may underlie the paradoxical southward shoaling of peak abundances of *Neomysis americana* on the continental shelf. South of Cape Cod, particularly where barrier bars and islands develop along this passive continental margin, most fine material delivered by rivers is trapped inside estuaries, and what little does get delivered has a short residence time on the shelf. Dependence by juveniles on macrophyte detritus (either algal or angiosperm) may also contribute to this southward shoaling because macroalgal substrata become scarcer southward and plant and macroalgal fragments are among the particles largely trapped in estuaries. Mysids are not absent from shallow or clear waters, but generally adopt one or more of three strategies where they cannot hide within or below turbid waters: burying themselves in the bottom, hiding in vegetation or other cover or schooling. If the reaction is to visual predation and not turbidity per se, other optical phenomena that impede image formation will also benefit mysids (e.g., image distortion through salinity or thermal microstructure) (suggested by M.J. Perry, personal communication) and wave speckle and bubble clouds in the surf zone. Some mysids do congregate at salinity fronts (Kotta & Kotta 2001b, Schiariti et al. 2006). Of course there are other potential reasons, such as enhanced resource concentrations from electrostatically induced coagulation, from salting out of organics or from frontal circulation patterns.

Day-night shifts in activity level (frequency and duration of movement) and height above the bottom occur even in those species not known to migrate to surface waters, with increases typical of nighttime (Fosså 1986). In the lowermost bottom boundary layer, because of the rapidly increasing horizontal velocity and hence fluxes with increasing distance from the sea bed, even modest changes in height above the bottom can yield large differences in exposure to resources. Coming out of the sediments (for the mysid species that bury) as well as activity and height changes can also produce major changes in encounter rates with predators. Saigusa (2001) provided a high-resolution method for examining activity cycles, that is, by pump sampling from a depth 50 cm below the water surface simultaneously with pump sampling 50 cm above the bottom and collecting sequential 30-min samples from both streams. Saigusa (2001), at Akkeshi on the Pacific Coast of

Hokkaido in water ~3 m deep at high tide, *Nipponomyis toriumi* (Murano, 1977), in 25 days of continuous sampling, showed a strong nocturnal periodicity in capture 0.5 m off the bottom, whereas the surface pump showed weak or no diel periodicity. Both sampling streams showed tidal periodicity in capture rates. At Ushimado on the Seto Inland Sea, in water of similar depth, where only surface water was sampled, an 18-day time series showed *Siriella japonica* Ii, 1964 to have distinct nocturnal periodicity in capture, again modulated by tides. A great deal of diversity in tidal and diel periodicity and height of emergence above the bottom is expected of mysids across species, locations and times as there is ample modulation of both risks and benefits on diverse scales. Particularly striking in the time series analysis by Saigusa (2001) is the ubiquity of periodicity in pump capture of potential prey of mysids and thus, in potential, for their capture by mysids.

An appreciation of mysids

Further evidence of mysid importance in the coastal marine economy

Food-web roles

Roles that mysids play in feeding their predators are increasingly recognised. A search on ‘mysid*’ and ‘feeding’ in ASFA currently returns about 900 citations of which >90% concern mysids in diets of other animals. Mysids constitute particularly large fractions in the diets of many fishes in the 3–15 cm length category. In a collection of nearly 500 beam trawl samples from the Westerschelde estuary (Hostens & Mees 1999), mysids occurred in >50% of the (mostly juvenile) fish stomachs analysed and constituted >10% of the diets of two goby species (*Pomatoschistus lozanoi* and *P. minutus*), garfish (*Belone belone*), two gadids (bib, *Trisopterus luscus*, and whiting, *Merlangius merlangus*), two flatfish species (*Pleuronectes platessa* and *Platichthys flesus*), herring (*Clupea harengus*), seabass (*Dicentrarchus labrax*), sea snail (*Liparis liparis*), hook-nose (*Agonus cataphractus*) and tub gurnard (*Trigla lucerna*). Beach seining in the southern Sea of Japan produced similar dietary prominence in the 19 fish species recovered, with 67% of individuals feeding on mysids (Inoue et al. 2003). As other prominent examples of mysid dominance in gut contents, juvenile cod (*Gadus morhua*) <10 cm long in one study from the northwest Atlantic feed almost exclusively on mysids (Link & Garrison 2002), and European hake (*Merluccius merluccius*) show similar dietary preference (Papaconstantinou & Caragitsou 1987, Bozzano et al. 1997). Plummer et al. (1983) examined gut contents of California halibut (*Paralichthys californicus*) trawled from 6–30 m depths off southern California and found *Neomysis kadiakensis* to dominate the diets of fish <25 cm long. Patterns inside estuaries are similar (e.g., Nemerson & Able 2004). Particularly when locally dominant mysid species bury themselves during the day and the water column is shallow, bottom fishes may show higher feeding rates on mysids at night for simple encounter-rate reasons (e.g., Hirota et al. 1990, Takahashi et al. 1999). Even mysids that stay near the bottom in deeper water may become more active at night than during the day (Fosså 1986), increasing their encounter rates with demersal fishes.

As an example of pelagic fish diets, mysids are important items in the nighttime diets of European anchovies (*Engraulis encrasicolus*) (see Tudela & Palomera 1997), emphasising the role of migration in encounter. In the Baltic, where the interaction of mysids and herring (*Clupea harengus*) has been studied most extensively, herring feed on mysids primarily as medium to large fish during winter (Möllmann et al. 2004). Whereas herring are widely regarded to be primarily visual feeders and thus unlikely to eat nocturnally emerging mysids (Flinkman et al. 1992), other clupeids do not necessarily follow this pattern. Alewives (*Alosa pseudoharengus*) use the lateral line to locate mysid prey in the dark (Janssen et al. 1995) and in their sometimes-turbid marine and estuarine habitats, specialise on mysids, crangonids and amphipods (Stone & Daborn 1987).

Moreover, gut contents analysis underestimates mysid contribution to assimilation because mysids are more digestible than are many other taxa (Lankford & Targett 1997). The high dietary value of mysids, based on richness in polyunsaturated fats (Navarro & Villanueva 2000, Richoux et al. 2004), has also been recognised in aquaculture feeds (e.g., Takeuchi et al. 2001). A particularly clever application of stable carbon and nitrogen isotopic methods to flounders that eat mysids permits estimation of their cumulative food consumption after release from a hatchery and documentation of their competition with natural stocks (Tominaga et al. 2003, Tanaka et al. 2005).

Another line of evidence for food-web significance comes from estuarine and coastal habitat changes that have gone beyond their 'normal' limits through interannual variability (e.g., in freshwater runoff) or through habitat expansion of invasive species. A notable example is invasion of the San Francisco Bay estuary system by the overbite clam (*Potamocorbula amurensis*), which appears to have greatly reduced phytoplankton and small zooplankton stocks available to benthos and plankton alike. Mysid stocks have plummeted to 10% of previous levels (Kimmerer & Orsi 1996), apparently as a result of food limitation (Orsi & Mecum 1986, Kimmerer 2002). Eight of 13 fish species showed declines in apparent response to this reduction, and only striped bass (*Morone saxatilis*) contained more than traces of mysid remains (Feyrer et al. 2003) after the invasion.

Other vertebrates also utilise mysid prey. Notably, gray whales (*Eschrichtius robustus*) are observed to feed on mysids both on shallow shelf feeding grounds (Kim & Oliver 1989) and along the coast of British Columbia (Darling et al. 1998, Dunham & Duffus 2002, Stelle 2002, Patterson 2004). Bowhead whales (*Balaena mysticetus*) also take mysids (Lowry & Burns 1980). Seabirds also utilise mysid populations (e.g., Moran & Fishelson 1971, Divoky 1978, Sanger 1987, DeGange 1996), and some species of polar seals (i.e., crabeater seals, *Lobodon carcinophagus*, and Weddell seals, *Leptonychotes weddellii*) also have been found to eat mysids (Green & Williams 1986, Lake et al. 2003). Seals at lower latitudes appear more commonly to have a less-direct dietary interaction with mysids, experiencing parasitism by nematodes that use mysids and the fish predators of mysids as intermediate hosts (Jackson et al. 1997). Humans also harvest mysids and do so on a commercial scale (2000–3000 tons of one species per year) in Japan (Omori 1978).

Mysids are also substantial dietary components of many invertebrates. They appear critical, for example, to diets of the smallest juvenile cuttlefish (*Sepia officinalis*) <2 cm long (Le Mao 1985) and are substantial components in diets of many cephalopods (e.g., Aronson 1989, Huang 2004). Many decapod shrimp species routinely prey on mysids, but among the most interesting couplings is the frequent association of species of *Crangon* with vertically migrating mysids. Although it is clear that *Crangon* spp. are not obligate feeders on mysids, where mysids are abundant local *Crangon* species appear to specialise on them (e.g., Price 1962, Sitts & Knight 1979, Siegfried 1982, Pihl & Rosenberg 1984, Wahle 1985, Hong & Oh 1989, Oh et al. 2001, Hanamura & Matsuoka 2003). *Crangon septemspinosa* emerges on a diel cycle with or shortly after *Neomysis americana* according to Taylor et al. (2005) and broadly overlaps its habitat and geographic ranges. On Georges Bank, catches of the two species in macrozooplankton samples are highly correlated (Brown et al. 2005). Taylor et al. (2005) pointed out that mysid emergence in their system is also associated with copepod emergence. This copepod-mysid-crangonid emergence combination (Figure 2) greatly expands the size spectrum of prey available in this movable feast, and some fish species use a substantial fraction of the total range at one time or ontogenetically (e.g., Stone & Daborn 1987, Gatlin 1997, St.-Hilaire et al. 2002, Yamamoto et al. 2004, Yamamoto & Tominaga 2005). Other invertebrates may also follow the migration (e.g., Matsumoto 1995). It is also clear that the depth limits and sensory postures of some benthic invertebrate predators are tuned to the arrival of vertical migrants (Lagar-dère 1977). Mysids are both preyed upon and parasitised by protists (Buchanan & Hedley 1960, Shields 1994). Mysids may also be eaten by other mysids of the same (Johnston & Ritz 2001, Quirt & Lasenby 2002) or different species (Jerling & Wooldridge 1995). Mysid-mysid predation

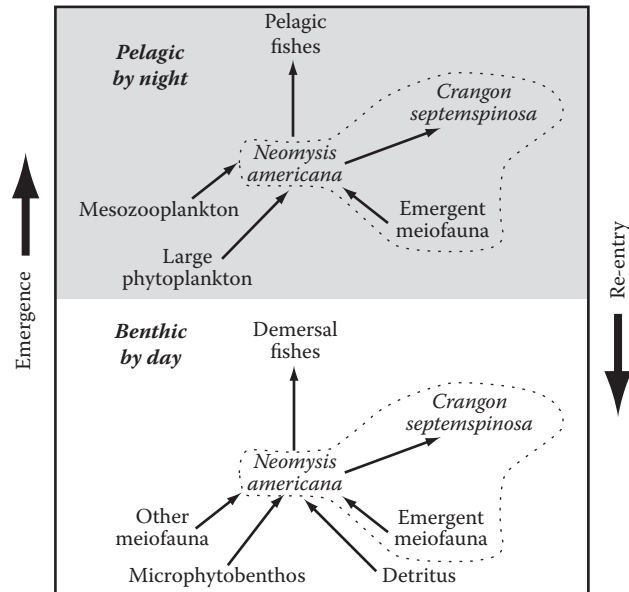


Figure 2 The immediate food web of *Neomysis americana*, showing changes and some surprising constancy over the diel cycle. The components within the dotted line all migrate, providing a much larger size spectrum for encounter by larger decapods and fishes than would a single migrant. Mysids are extremely omnivorous and are consumed by many species; the non-migrating part of this web is highly aggregated in the diagram.

is a function not only of size, but also of behaviours and abundances of the predator and prey mysids as well as of alternative prey (Winkler & Greve 2004).

Because mysid diets have recently been reviewed by Takahashi (2004), present comments are limited to a short summary. He pointed out that carnivory on holozooplankton is typical of later juvenile and adult stages of mysids. In coastal and poly- to mesohaline estuarine environments, prey are often copepods ingested at roughly 3–30% of mysid body carbon day⁻¹. In oligohaline and freshwater environments, cladocerans are often preyed upon heavily, probably because they can be filtered in bulk (Viitasalo et al. 2001) and digested readily, and are ingested at 24–300% of mysid body carbon day⁻¹. The carnivorous component of the diet appears to be especially important for growth and reproduction (Viherluoto et al. 2000). Smaller, younger juveniles that migrate eat smaller holozooplankton, detritus and phytoplankton, but rarely ingest cells or chains <10 mm long, often selecting diatoms in preference to other phytoplankton taxa. When large diatoms are scarce, diets of juveniles may shift to microzooplankton (Jerling & Wooldridge 1995). The smallest mysid individuals often do not migrate off the bottom and thereby may focus even more strongly on a detrital or microphytobenthic diet. The potential dietary role of benthic diatoms for multiple life stages of mysids bears emphasis (Mauchline 1968, Perissinotto et al. 2003). Takahashi (2004) usefully described the trend of increasing carnivory with size and maturity as life-history omnivory, supporting the generality of the stable isotope-based conclusions and terminology of Branstrator (2000) for *Mysis relicta* Loven, 1862. The same term has been applied to fishes (Montoya et al. 2006), but mysid omnivory brackets a larger range of food types closer to the base of the food web, yet spans more than one habitat. Mysid life-history omnivory is particularly well documented by analysis of fatty acids (Richoux et al. 2005), and lipid accumulation in mysids from nighttime predation on holozooplankton is probably enhanced by post-feeding migration to cooler waters (Chess & Stanford 1999). Benthic phases may also span the entire gamut of diets from detritus to microphytobenthos to heterotrophic protists and rotifers to larger meiofauna and even macrofauna

(Johannsson et al. 2001, Albertsson 2004), but all sizes of many species are more prone to ingest detritus during the benthic phase than during the pelagic (Table 2 of Takahashi 2004). It seems very likely that benthic-phase mysids are able to take advantage of the much greater food value of suspended detritus (Mayer et al. 1993) either by direct suspension feeding from material already suspended in the bottom boundary layer or by resuspending it from the bottom and then filtering it (Mauchline 1980, Viherluoto et al. 2000).

Cellulases that are apparently endogenous have been reported in *Mysis stenolepis* S.I. Smith, 1873 by Friesen et al. (1986), and macrophyte detritus appears to be particularly important in the winter diet of *Neomysis americana* in salt marshes in the southern part of its range (Zagursky & Feller 1985). Stable isotopic data also support a winter shift toward a greater contribution from refractory terrestrial, angiosperm detritus to mysid diets in coastal British Columbia (Mulkins et al. 2002). Froneman (2001), however, found no seasonality in the isotopic signature of *Mesopodopsis wooldridgei* Wittman, 1992 in the temperate Kareiega estuary of South Africa but did find evidence of likely contribution to its nutrition from eelgrass. All these studies contrast with the stable isotopic results of Dauby (1995) for four species of *Leptomysis* that, contrary to the diel migrators focused on in this review, school near the bottom during the day, remaining largely immobile relative to the bottom and not feeding, and migrate down to feed on detritus at night; he found only minor dietary influence from seagrass, with much greater reliance on micro- and macroalgae. Dauby's results, in turn, are compatible with those of Metillo & Ritz (2001), who found seasonal laminarinase activity cycles in three Tasmanian mysid species, which imply a winter reliance on macroalgal detritus. In summary, reliance on detritus of varied sources depends on species and perhaps on location.

One point to emphasise is that most species of mysids, although they tend toward carnivory as late juveniles and adults, do not appear to become exclusively carnivorous in the field (Hansson et al. 1997, Branstrator 2000). Adults of some species, however, move very much toward that extreme (Jerling & Wooldridge 1995, Kouassi et al. 2006). The vertically migrating species tend to show increases in the fraction of detritus and sediments as gut contents during their benthic phases (e.g., Lasenby & Shi 2004). On a diel timescale, they are sequential omnivores, alternating between daytime diets rich in nitrogen and worth substantial digestive time and detrital diets that yield higher net rate of gain at higher throughput rates (Zagursky & Feller 1985, Penry & Jumars 1987, Jumars 2000). Eating food of different qualities in sequence allows tailoring of gut retention time to day-night change in diet quality (Penry & Jumars 1987, Jumars 2000), which can provide much higher assimilation efficiency than optimising retention time on a complete mixture of daytime with nighttime diets. Mysids in general have complex masticatory and digestive structures that not only admit broad diets but also make ingestion of organisms that have no hard parts (e.g., many protists and larval stages) difficult to identify (e.g., Brunet et al. 1994, De Jong-Moreau et al. 2001).

Mysids can be sufficiently abundant to influence prey community structure (e.g., Fulton 1983). Both in the surf zone and in the plankton, larger diatom cells and chains experience the greatest grazing pressure from mysids (e.g., Webb et al. 1987, 1988, Linden & Kuosa 2004). In a particular interesting migratory role reversal from the typical offshore or estuarine scenario, *Gastrosaccus psammodytes* Tattersall, 1958 feeds on surf-zone diatoms during the nighttime, benthic phase of the diatoms (Webb et al. 1988), and *Mysidopsis wooldridgei* may consume up to 70% of surf-zone diatom primary production (Webb & Wooldridge 1990). David et al. (2006b) found that juvenile *Mesopodopsis slabberi* could account for the vast majority of herbivory in some settings. In fresh water, daphnid populations can be severely reduced by mysids, defeating the purpose of mysid introductions into lakes as food for salmonids (Spencer et al. 1999). In one shallow, tropical lagoon, a population of mysids appeared to explain the low zooplankton:phytoplankton biomass ratio and potentially could have consumed the entire holozooplankton production (Kouassi et al. 2006). In that particularly carnivorous role, mysids can contribute substantially to phytoplankton nitrogen

requirements through excretion (Kouassi et al. 2006), but more typically the effect of feeding on a combination of phytoplankton and zooplankton is expected to produce subtle shifts in size structure of phytoplankton with little net effect on standing stocks (e.g., Linden & Kuosa 2004).

In estuaries, grazing pressure by mysids on holozooplankton varies among locations and seasons but can be substantial (e.g., Fulton 1983, Aaser et al. 1995, Kibirige et al. 2003, Winkler et al. 2003). Early results with *Americamysis bigelowi* showed substantially reduced feeding on copepods in the dark versus the light (Fulton 1982). Contrary to expectations from their well-developed eyes, from the results of Fulton (1982) and from the observation by Clutter (1969) of more polarised schooling in the light, more recent experimental data do not support the idea that most mysids are primarily visual feeders. One migrating species showed higher ingestion rates on copepods in the dark, whereas a non-migrating species showed no difference in light versus dark (Viherluoto & Viitasalo 2001). Different mysid species apparently rely to differing degrees on tactile and visual cues, and likely on chemical ones as well. It seems likely that species risking vertical migration will have means to feed efficiently in the dark, that is, to obtain net gain during that migration risk by ingesting large, lipid- and protein-rich prey. Moreover, mysids are capable of predation on relatively large prey on the bottom as well (e.g., Wilhelm et al. 2002). One particularly interesting observation is that, given a choice, some mysid species prefer meroplankton (David et al. 2006a). Mysids thus have the potential to cause large mortality of meroplanktonic recruits in the plankton or when they are settling. This potential coastal filter of larvae in both habitats (pelagic and benthic) merits attention.

Habitat alteration and coupling

Roast et al. (2004) documented a significant role for mysids in resuspension of sediments underlying the turbidity maximum of an estuary. Acoustic experiments with artificially emplaced sediments (C.D. Jones & P.A. Jumars in preparation) in 20 m water depth off the Friday Harbor Laboratories pier in the San Juan Islands, Washington, strongly implicated emergent *Neomysis kadiakensis* in rapid microtopographic roughening of the sediment-water interface. Because the sediment surface at steady state is already rough, this interaction of mysids is normally difficult to detect but likely contributes to the erodibility effects documented by Roast et al. (2004), and attacks by predators of mysids add further to it. Less obviously, mysids also have the potential to alter the lowermost chemical boundary layer above the sediment-water interface, both through this roughening (e.g., Figure 1 of Jumars & Nowell 1984) as well as through movement over the bottom. The diffusive sublayer in smooth-turbulent flow over the sea bed is typically on the order of 1 mm thick. Diffusion time over that distance, calculated at time = distance²/(2D), where *D* is the molecular diffusion coefficient (typically $\geq 2 \times 10^{-9} \text{ m}^2 \text{ s}^{-1}$), is 4 min. Thus disruption of the lowermost 1 mm every 4 min or less by mobile animals could appreciably increase benthic-pelagic fluxes by producing unsteady diffusion through frequent sharpening of the diffusion gradient.

In terms of habitat coupling, diel migrations of holoplankton that feed closer to the surface than where they spend other parts of the day result in net downward fluxes of nitrogen in the form of excretion and carbon as respired dioxide (Longhurst & Harrison 1988, Longhurst et al. 1990) in addition to the downward advection of particles as gut contents and faeces. Mysids returning toward the seabed transport materials downward in all these ways. Unlike holoplankton, however, emergent mysids also transfer material upward by feeding on the bottom and excreting and respiring in surface waters. Net nitrogen flux is almost certainly downward because of the generally high C:N ratios in benthic detrital foods, but where most carbon is obtained and carbon dioxide released is less clear because swimming activity and temperature on average are both higher during the pelagic phase. For materials highly concentrated in sediments, such as hydrophobic contaminants and certain valence states and compounds of rare-earth elements and metals, mysid migrations and

food-web concentration conceivably could result in net upward transport (Evans et al. 1989, Neff 1997, Song & Breslin 1999).

Interesting potential exists for an interaction of habitat coupling and habitat modification by dense, migratory swarms of mysids. Kunze et al. (2006) have documented a significant contribution to turbulence and water-column mixing by coastal euphausiids during periods of stratification; similar effects can be expected from mysids. One reason that diel migrants may be especially effective at cross-isopycnal mixing is that, unlike shear-driven turbulence in the stratified ocean, swimming is directed in the vertical, causing downward inertial jets during the upmigration and vice versa.

A particularly tractable system for estimating, through daytime-collected egesta, the mysid contribution to habitat coupling was identified by Carola et al. (1993), who worked with mysids that migrate horizontally out of a submarine cave at night and return during the day, allowing collection of faecal pellets in simple sediment traps set in the cave. Such submarine caves are shut off from normal vertical particulate fluxes as well as being sheltered from normal horizontal particulate fluxes through the obvious flow obstruction. They are generally considered oligotrophic. Coma et al. (1997) estimated that the 756-m³ cave during the day housed 1–12 million mysids over the seasons of their year-long study (peaking in spring). They estimated that the population's *daily* import to the cave through faecal deposition varied seasonally between 20 and 407 g dry wt of particulate organic matter, 2–21 g C and 0.5–2.7 g N. Most pellets were released within 4.5 h after the mysids' sunrise return. The pellets are remarkably labile, with 20–50% of both C and N released in dissolved form within 2 h after egestion, and they account for previous inability to reconcile biological oxidation demand in such caves. Although it is a wonderful demonstration of intense habitat coupling between the pelagic environment of the nearshore Mediterranean and a cave environment, the results are difficult to generalise to sediment-dwelling mysids and their benthic-pelagic coupling. The cave dwellers apparently do not feed during the day, and their nightly diet remains obscure. Scanning electron microscopic examination of the pellets revealed no animal and few phytoplankton remains, prompting Coma et al. (1997) to consider them to be detritivores, but the lability of the pellets is then particularly puzzling. Possibilities compatible with the observed detrital remains in the pellets are a diet rich in soft-bodied protists captured by feeding on marine snow or rich in soft-bodied meroplankton (David et al. 2006b).

Dominating the holoplankton

Recent acoustic estimates of abundance call for renewed attention to mysid migrations. Two geographically widely separated studies (Kringel et al. 2003, Taylor et al. 2005) found that the water column during emergence was completely dominated by mysids, that is, that the mysid contribution to nighttime standing stock exceeded daytime standing stocks of macrozooplankton by an order of magnitude (Figure 3). Although widely separated, the environments share many similarities. Both are in productive, shallow (10- to 20-m) regions of fjords that experience little dilution by freshwater runoff, so whether and how deep these kinds of abundances extend over the continental shelf is an obvious question. Another issue is whether acoustic methods would reveal much higher abundances in those estuarine environments where high mysid abundances are already known.

Midnight sinking was noted in many of the contour plots of abundance versus depth and time made by Macquart-Moulin & Ribera Maycas (1995) for pelagic mysids. Midnight sinking in mysids has been observed at least since the classic study of *Neomysis americana* in Narragansett Bay by Herman (1963). Often but not always, mysids that emerge tend to be less abundant in near-surface layers near the middle of the night than just after sunset or just before dawn. In some cases, a clear mid-depth concentration accounts at least in part for this change (e.g., Herman 1963, the second

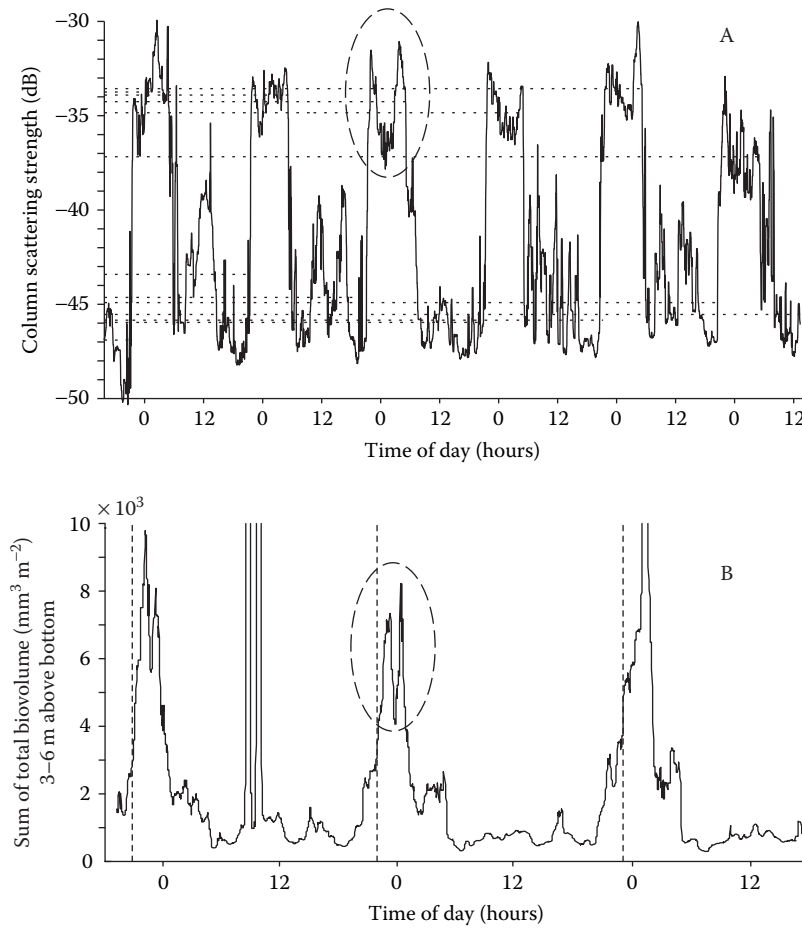


Figure 3 Changes in integrated water-column abundance derived from acoustic backscatter showing overwhelming dominance by emergent animals. (A) Column scattering strength at 265 kHz from West Sound, Orcas Island, Washington, in ~20 m of water. (From Kringel et al. 2003. With permission from the American Society of Limnology and Oceanography, Inc.) Horizontal dotted lines connect median column scattering strengths between and during emergence events, showing a 14-fold increase during emergence. The dashed oval shows apparent midnight sinking (higher scattering strengths on both sides of a local minimum during emergence). The first full day of the data record was 27 August 1995. (B) Column-integrated biovolumes derived by acoustic inversion for the Damariscotta River estuary, mid-coast Maine, a shallow fjord. Bottom depth is approximately 10 m, and the large emergence events that begin at the vertical dashed lines are cued by the tides. (From Taylor et al. 2005, their Figure 3. With permission of the Estuarine Research Federation.) Column-integrated standing stocks here also often display the molar- (tooth-) shaped structure with a local minimum (dashed oval) and are 6-fold higher during emergence than during the day (Taylor et al. 2005). The first full day of this record was 15 August 2002.

depth interval in the 4–5 April samples of his Figure 7; Macquart-Moulin & Ribera Maycas 1995, bottom panel of their Figure 5 for *Anchialina agilis*). *Anchialina agilis* generally shows dusk and dawn capture peaks in epibenthic sledge samples as well, but no evidence of a midnight return all the way to the sea bed (Dauvin et al. 2000). Drivers of midnight sinking in mysids are not well known, but satiety and predator evasion have been suggested in other taxa, and more recently midnight sinking has been shown to promote retention of *Calanus* spp. in model results for one inland sea

(Emsley et al. 2005). It is worth remarking again that navigation through use of the polarised light field should be most reliable both near the surface and near dawn and dusk, as one potential contributor to surface congregation at those times.

Lending trophic and dynamic stability

Although they once were thought to have a destabilising effect on communities, recent and more realistic, non-linear, non-equilibrium theory suggests an important stabilising role for omnivores (McCann & Hastings 1997, Emmerson & Yearsley 2004) that has been confirmed in experiments (Holyoak & Sachdev 1998). Omnivory is an obvious advantage when a favoured resource becomes scarce, and multiple advantages accrue from eating one's competitors for limiting resources. Less obviously and more paradoxically, species that are eaten by many predators may suffer lower total predation intensity (Montoya et al. 2006). The shelf ecosystems in which mysids participate have high connectance (Link 2002, Dunne et al. 2004), but mysids have more connections over more trophic levels than does the average member of even those highly connected food webs. In shallow water, mysids contribute in a major way to multichain omnivory, linking organic matter that originates from benthic and pelagic primary production; theory originally developed for lakes suggests that this linkage is particularly stabilising (Vadeboncoeur et al. 2005). By being food for pelagic as well as benthic fishes and by consuming both planktonic and benthic primary and secondary production and detritus, mysids not only link benthic and pelagic food webs but also link resources with different inherent timescales. The latter linkages reduce synchrony and overshoot in the populations constituting those resources, identifying another of the mechanisms through which omnivores stabilise food webs (Rooney et al. 2006).

The northwest Atlantic shelf ecosystem has been disturbed at such high frequency and high intensity for so long that it has not remained stable, with the notable crash of the groundfish fishery (Link 2002, Choi et al. 2004). Although offshore banks have shown recovery of herring (*Clupea harengus*) from about 1993 (Fogarty & Murawski 1998), some coastal spawning stocks have not recovered from overfishing or environmental degradation (Smedbol & Stephenson 2001). Cascading trophic effects from the groundfish collapse have been observed, with northern shrimp (*Pandalus borealis*) and snow crab (*Chionoecetes opilio*) apparently experiencing release from predation (Frank et al. 2005). A hint of the potentially stabilising effect of mysids comes from the conjecture that they likely experienced a release from predation by benthic predators during the infamous cod (*Gadus morhua*) crash in 1993 (Choi et al. 2004) and may have experienced some release from herring predation as well. Juvenile cod captured in the southern Gulf of St. Lawrence shifted after 1990 from feeding on euphausiids to feeding on mysids, perhaps reflecting population expansion in mysids, and as of 2000 had not shifted back (Hanson & Chouinard 2002).

Reasons why mysids have been underappreciated

Problems of sampling

The most obvious reason why mysids are not better understood is the difficulty of making total areal (m^{-2}) abundance estimates. It is a problem greatly compounded by simultaneous and (or) sequential occupation of multiple habitats by mysids. Clutter & Anraku (1968) published a photograph showing that information can be transmitted through a mysid school to turn it away from an approaching plankton net. Lasenby & Sherman (1991) invoked the same explanation for greater capture in vertically operated traps than in trawls. Fleminger & Clutter (1965) took oblique plankton tows through a laboratory tank containing mysids ($\geq 95\%$ *Metamysidopsis elongata*) and captured significantly more individuals in the dark than in the light. They noted, however, that they lacked

observations to distinguish whether the difference was due to visual avoidance by the mysids or to their potentially broader vertical distribution in the dark (the latter documented by Clutter 1969 in the field). Eleftheriou & Holme (1984) suggested that a 10% sampling efficiency is a reasonable estimate for total macrofauna captured by epibenthic sledges. Emergence traps (e.g., Kringel et al. 2003) may also be biased to an unknown degree. Traps designed to catch emergent individuals alter cues and may induce greater or lesser emergence than would occur in the absence of the trap. Capture efficiency of emergent individuals is also unknown. Ribes et al. (1996) compared abundance estimates based on faecal recovery in the aforementioned cave setting with net tows by divers and found a 10-fold difference, with the net-based estimates being lower. A rare estimate of mysid sampling efficiency based on independent sampling with several methods was that of Carlton & Hamner (1987) from a coral reef lagoon. They found epibenthic sledge efficiency (relative to the most efficient sampler, a trap operated by divers) for mysids to be between 1% and 10%. Because nocturnally emerging mysids in coastal waters stay in the relative dark around the clock, often in turbid waters, it is difficult to imagine how to undertake a complete census of a population analogous to that carried out by Carlton & Hamner (1987).

Capture efficiency is certain to vary with life stage and species of mysid and likely with whether they are schooling at the time of sampling, so the purpose of this short review of net and trap sampling clearly is not to find or endorse a fixed estimate of sampling efficiency but rather to indicate that most mysid sampling based on nets is likely to provide gross underestimates. One underlying reason is high burst-swimming speed (caridoid escape reaction) and intermediate size (order of 1 cm): fast nets in order to achieve reasonable filtration efficiencies typically use meshes too large to capture mysids, whereas fine-meshed nets to achieve reasonable filtration efficiencies are typically towed too slowly to capture mysids efficiently. For species that release eggs or weakly swimming larvae into the plankton, slowly towed nets or plankton recorders will still reveal the presence of large populations (e.g., Sameoto 2001). For mysids and other peracarids that brood young, such gear will not sample adequately, especially if newly released juveniles initially are benthic. When most places contain few individuals and a few places contain many mysids, a small number of samples is unlikely to encounter the high concentrations of mysids. Although precise estimates of mysid mean areal abundance would still be useful in evaluating their importance in the ocean economy (e.g., in determining whether they must be included in estimates of secondary production, nutrient regeneration and vertical fluxes), the more aggregated a population is, the less relevance mean abundances have to issues such as encounter rates and behaviours (Omori & Hamner 1982). Direct observations by divers find mysid swarms up to densities of nearly 600 l⁻¹ (6 × 10⁵ m⁻³). Such dense swarms are usually dominated by a single species but may be joined by several (Ohtsuka et al. 1995). Instead of focusing on mean abundance it may make more sense to be concerned about the fraction of space occupied by swarms and the frequency with which any given place is occupied by a swarm.

A simple exercise demonstrates several aspects of the mysid-sampling problem. For *Anchialina agilis*, because the entire population appears to emerge at night, it would appear to be feasible to estimate total areal abundance by vertically integrating depth-specific abundance estimates. For the points near 2020 h on 11 December for male *A. agilis* in the 60-m water column as depicted by Macquart-Moulin & Ribera Maycas (1995, their Figure 4) integrating by linear interpolation between the four depths sampled yields an areal abundance of ~15.4 males m⁻². For females plus juveniles on the same night, two sections are plotted (their Figure 5) that show peak abundances at about 0500 h of ~3 and ~15.4 ind. m⁻², respectively, for an average areal estimate for females and juveniles of ~9 ind. m⁻². The sum (total of males plus females and juveniles) exceeds typical, sledge-estimated abundances for the species, and itself is likely an underestimate because of net avoidance by pelagic *A. agilis*, but could be an overestimate of local benthic areal abundance during the day if there is significant local horizontal convergence during emergence.

Acoustic estimates of abundance based on vertically integrated biovolumes and of migration rates based on changes in vertically resolved biovolumes are also underestimates of unknown severities. A continuing issue with acoustic estimates of organism abundance is individual target strength, particularly for elongate organisms with complex morphologies, because their target strengths vary with orientation relative to the transducer, greatly increasing the uncertainty of abundance estimates made through acoustic inversion (e.g., Amakasu & Furusawa 2005, Lawson et al. 2006). Time-varying polarizations and direction changes of swarms and schools clearly compound this problem, but acoustic methods are more robust in biological application than some of the complexities in acoustic inversion might suggest (Benoit-Bird & Au 2002).

A more fundamental problem, often opined (Pearre 2003), is that methods that infer migration from changes in spatial distributions are unable to detect migrations that do not cause net change (Figure 4). Thus it is not known to what extent acoustic observations of *Neomysis kadiakensis* (e.g., Kringel et al. 2003) or *N. americana* (e.g., Abello et al. 2005, Taylor et al. 2005) reflect individuals staying in the water column for hours at a time versus frequently exchanging places with benthic members of the same population, and it is not known what fraction of the total population fails to migrate at all. Mysid species and life stages differ in this regard, as reflected in near-surface and near-bottom or nearshore and offshore samples taken at different times of day. Acoustic methods based on backscatter intensity in principle could be used to obtain data fairly close to the bottom by burying an upward-looking device. Besides the logistical problems, however, most transducers have non-ideal near-field effects, and TAPS (Tracor Acoustic Profiling System, now under the auspices of BAE Systems, San Diego, California) on this account does not collect data closer than 37.5 cm from its transducers. Conversely, down-looking geometries (e.g., Greenlaw et al. 2004) are effectively 'blinded' in the lowermost one or two range bins by the high backscatter intensity from the bottom. Use of split-beam, dual-beam and multibeam acoustics, generating the acoustic equivalent of binocular vision and giving some capability of tracking individuals, promises at long last to reveal individual zooplankton behaviours (Smith et al. 1992, Kaufmann et al. 1993, De Robertis et al. 2003). These methods do not overcome interference from strong bottom scattering, but they should allow individual acoustic target strengths and trajectories of individuals to be determined from stable bottom platforms, at least when current speeds are small and acoustic sampling intervals are short. Each sampling method will need to be used for its strengths and to remedy the weaknesses of others. Acoustics have the clear advantage in spatial and temporal resolution (e.g., Figure 5), but have the generic problem of being poor at resolving identities. When species diversity is low, however, acoustic methods can be sufficient for discrimination (David et al. 1999), and shape and biomechanical properties that are detectable acoustically show promise of providing better discrimination in the future. Acoustic methods excel with their high resolution in both space and time at pinpointing locations and times of interest for sampling by other means (e.g., Figure 6).

Difficulty in modelling

Whereas high, flow-driven horizontal flux over the bottoms they inhabit is an important component of the 'umwelt' of mysids that emerge in coastal environments, it compounds the difficulties of simulation. It is no accident that many of the citations given here are for studies done in closed systems (lakes) and semi-enclosed systems (estuaries) where effects are much easier to calculate and model, rather than the nominal coastal environments of primary interest. Open-shelf systems are more difficult to constrain in both measurements and models. Further, the same infidelity to habitat that makes abundance estimates difficult also complicates study in analog laboratory systems. Although smaller tanks have yielded valuable observational data on taxa without extensive migrations (Fosså 1986), a much larger system (e.g., Conover & Paranjape 1977) would be needed to

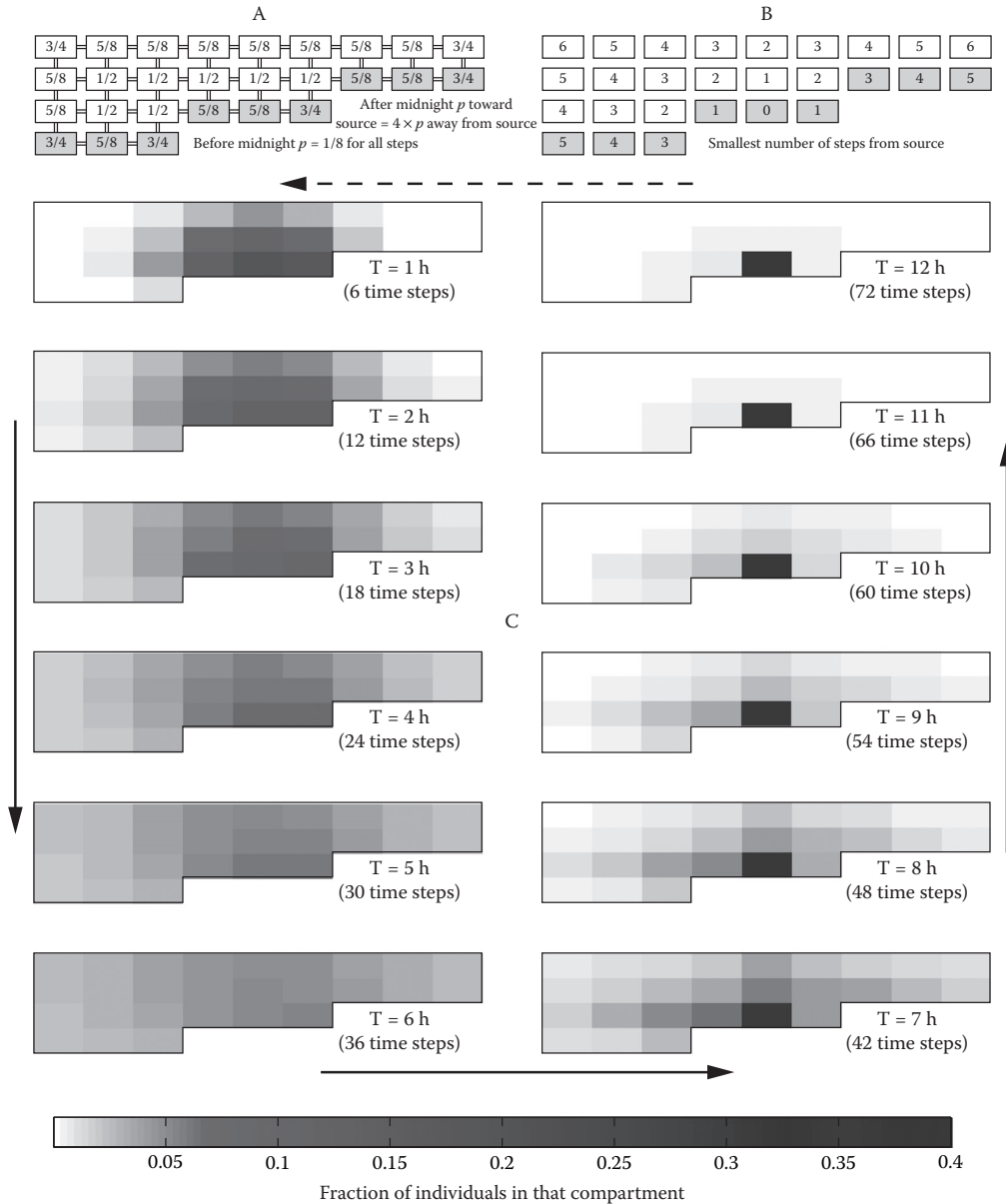


Figure 4 A simple demonstration of the potential for radically different mysid behaviours to produce similar patterns of vertical change in abundance over large regions of the habitat and the consequent need to develop methods for tracking individuals during migration. Simple, heuristic Markov models (cf. Kemeny & Snell 1960, Jumars et al. 1981) were set up under two different sets of hypothetical behaviours. The boxes in panels A and B represent a 2-dimensional section in the onshore–offshore direction, shoaling to the right. Greyed boxes (A, B) represent a hyperbenthic environment, with white boxes being in the water column. In both model runs (see also next page), all animals began in the box labelled 0 in panel B. Time steps were 10 min. In the first run, all transition probabilities were set to 1/8; that fraction of individuals in each box moved to the adjacent box, and the fractions in (A) represent the proportion that stayed in the box during one time step. After a long time with this transition matrix, individuals would become uniformly distributed. At $T = 6$ h, however, the original source box became an absorbing state (transitions out were prohibited) representing recognition of the habitat by the model animals. In addition, all transition probabilities that reduced the number of steps back to the original source box were made five times larger than those leading away. (*Continued on next page.*)

HABITAT COUPLING BY MID-LATITUDE, SUBTIDAL, MARINE MYSIDS

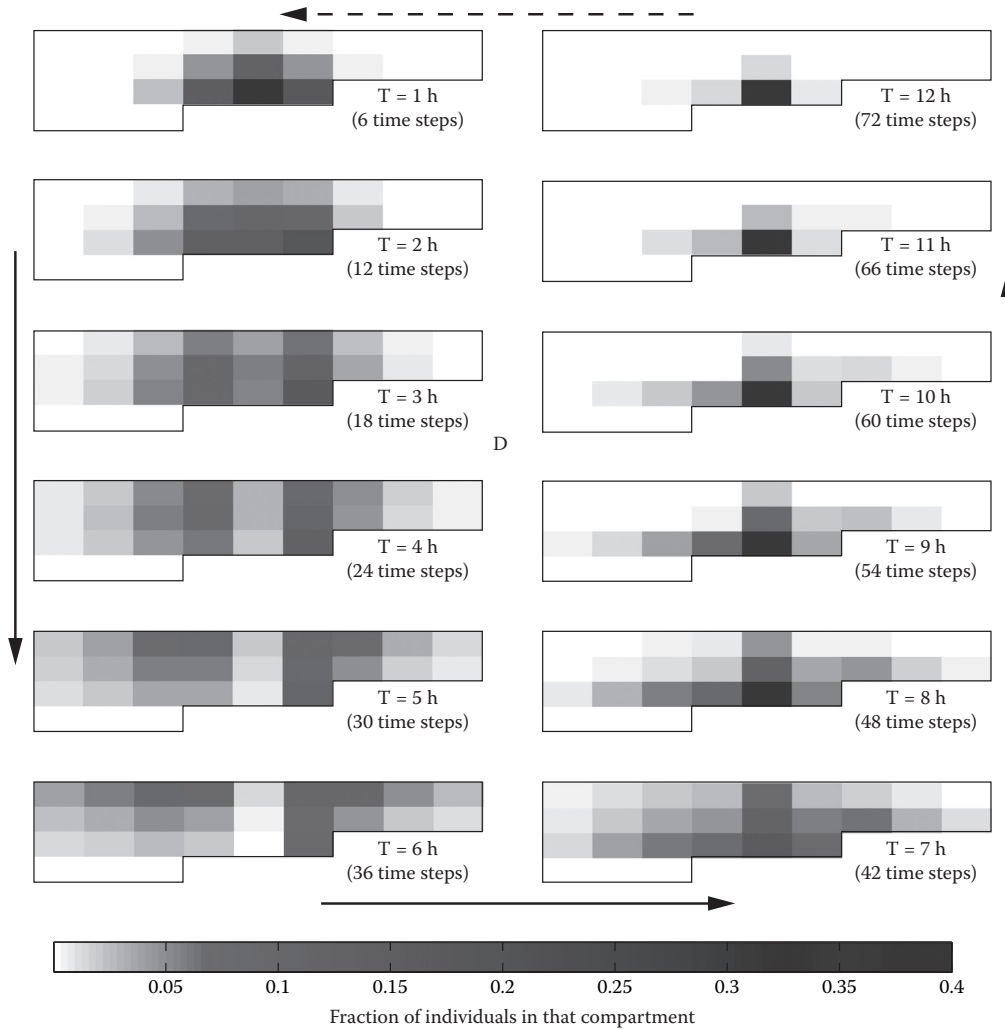


Figure 4 (continued) That process led to the return of 95% of all individuals in 6 h. This first scenario can be construed as a broadening of the depth distribution through very active random transfer among compartments, with a biased random walk bringing the animals back. Arrows in panel C represent the cycle that emergence would follow from start to finish. If the cycle is repeated (dashed arrow), results of the slightly different starting condition are not perceptibly different. In the second scenario (D) the same fractions remained in each compartment as shown in (A). Initially, all transitions moving a greater number of steps away from the same source box were set at 1/20 (with zero probability of moving toward the source), except that downward transitions were ruled out (also set at zero) and the model was run for 6 h before reversal of behaviour (moving away from the original source set to zero probability and moving toward set to 4/25). In this phase, the initial source compartment was again made perfectly absorbing. The second scenario can be construed as much slower, deliberate navigation to and from nighttime feeding areas. Because *net* movement among boxes is not radically different between the two scenarios (except for deep regions in panel D that are effectively unreachable), neither is the depth-time distribution of individuals. Again 95% of individuals returned after 72 time steps, and running the cycle again with this starting condition produces results that are not perceptibly different from starting all individuals in the original source compartment. Animals in the first scenario do a great deal more moving among locations per unit of time and therefore would likely have much higher encounter rates with predators. Future methods need to differentiate net from gross migration rates. Note that while neither scenario includes any sinking at all, the pattern of abundance in the surface compartment above the source shows what might be interpreted as midnight sinking, that is, higher abundances early and late in the migration cycle than in its middle.

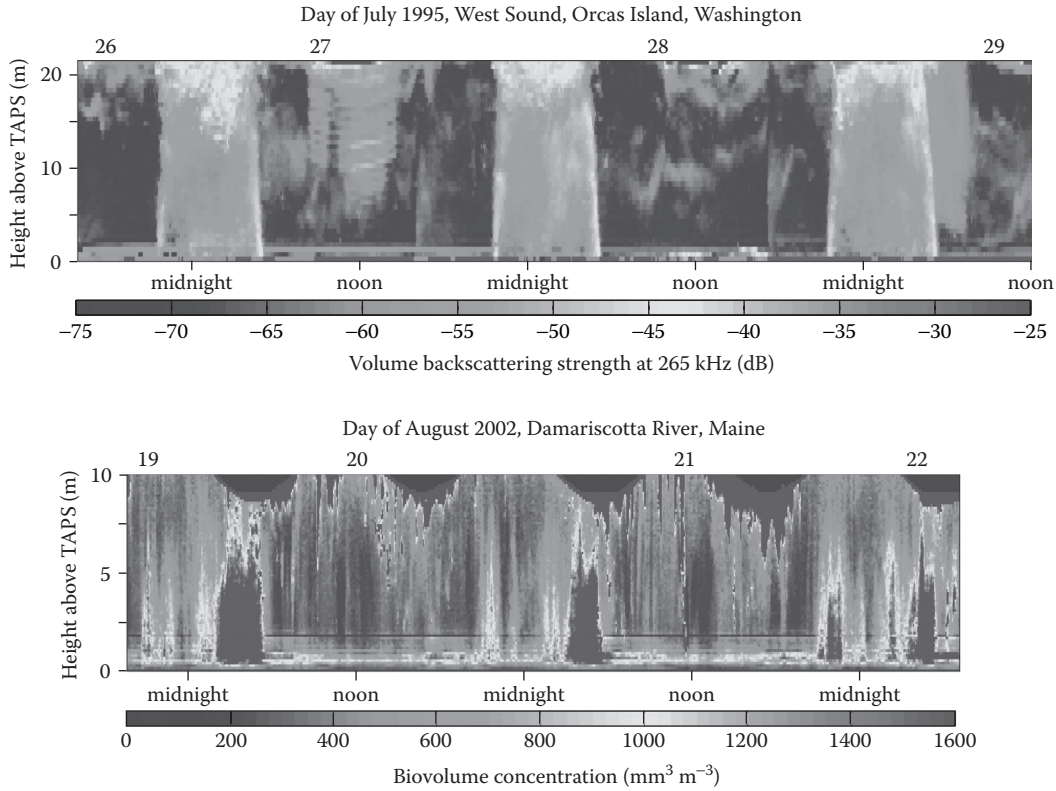


Figure 5 (See also Colour Figure 5 in the insert following page 344.) Resolution achievable acoustically without resolving individual mysids, showing some of the diversity that can be encountered in emergence. The two time series have been aligned so that midnight occurs in both at the same location on the abscissa. Regularity of nightly emergence in the West Sound time series (formed from data taken every 2 min in 25-cm range bins; top panel from Kringel et al. 2003. With permission of the American Society of Limnology and Oceanography, Inc.) is stunning, and the descents are often more organised than the initial ascent, a phenomenon herein called the Dracula effect (Abello et al. 2005). The data from the Damariscotta estuary have even higher resolution (taken every minute with 12.5-cm spatial resolution). Low tides occurred near noon in the West Sound series, and the reflection from the water surface is evident as bright red patches of high backscatter. The Damariscotta time series shows both low tides of the day, with the red extensions from the surface being a combination of fish aggregations and bubbles injected by breaking wavelets from the afternoon sea breeze. The Damariscotta series shows multiple emergence events per night. The first emergence events after dark are light cued (Abello et al. 2005), whereas the largest events begin at peak tidal flow speed after dark (Taylor et al. 2005). (Bottom panel from Taylor et al. 2005. With permission of the Estuarine Research Federation.)

Figure 6 (opposite page; see also Colour Figure 6 in the insert.) Acoustic methods that do not resolve individual mysids can also be used to gather information on group ascent and descent velocities and times of departure from and return to the sea bed. (After Kringel et al. 2003, from the same 1995 dataset presented at the top of Figure 5. With permission of the American Society of Limnology and Oceanography.) Leading edges of the ascent can be recognised as the first and the last pixels above background backscattering levels at each height above bottom (white circles). Slopes of the linear regressions yield ascent and descent velocities, and intercepts provide objective start and stop times of emergence. Modal abundance values (blue X marks, colour version) represent the behaviours of a larger fraction of the emergent population, but again only net migration rates can be visualised from measures of total backscatter.

HABITAT COUPLING BY MID-LATITUDE, SUBTIDAL, MARINE MYSIDS

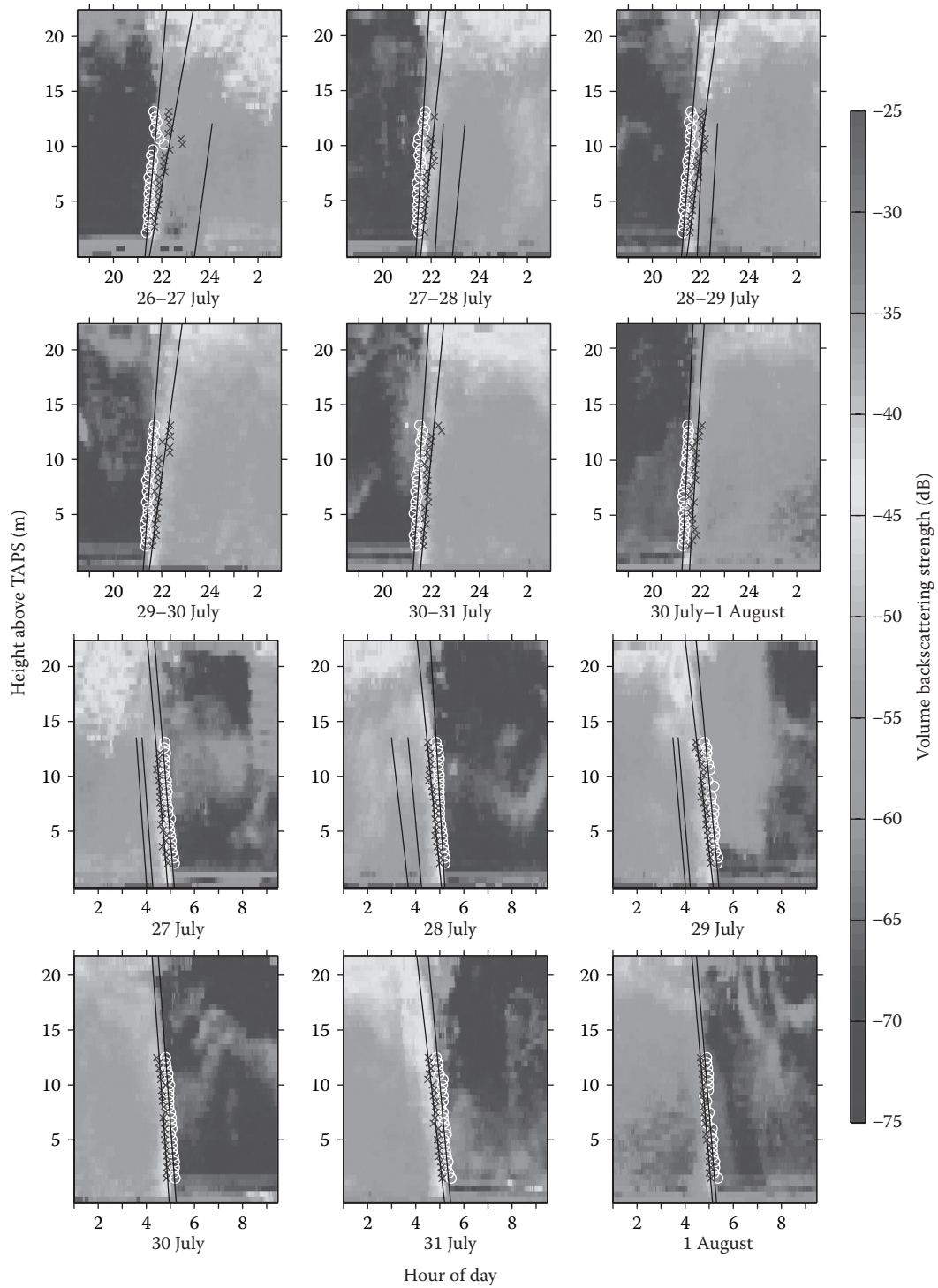


Figure 6 (See facing page for caption.)

provide realistic prey distributions and allow migration. Moreover, mysids are notoriously sensitive to light exposure and take considerable time to recover physiologically, and presumably behaviourally, from unnatural levels (e.g., Attramadai et al. 1985, Lindström et al. 1988). Red-light viewing to avoid light-induced artifacts (e.g., Fosså 1986) rapidly becomes less practical at long range because red light has a high absorption coefficient in water.

Challenges and opportunities

A continuing challenge is to produce an effective, convincing census of shelf mysid populations (abundance versus location versus time) that misses neither migrating nor non-migrating members. No one method yet attempted appears to be a panacea in this regard because different methods have different strengths and weaknesses in different habitats.

In this review, emphasis has been placed on the challenges in measuring the vertical component of migration and the coupling of benthic with pelagic habitats because enough data can be gathered to review them. The horizontal component provides many additional challenges and opportunities. It is obviously a key feature of mysid migrations in and out of caves (e.g., Carola et al. 1993, David et al. 1999) and vegetation (e.g., Wittman 1977, Mattila et al. 1999). Whereas organisms with clear structural, spatial refuges from predation can return to them when risk is high, organisms without a structural spatial refuge adopt other means of reducing risk. Besides the obvious tactic of staying in the dark, emergent mysids can alter schooling patterns and (or) reduce their feeding rates to reduce risk by evading pursuit or detection, respectively (Ritz 1994, Hamren & Hansson 1999). Mysids are documented to change behaviour via both visual and chemical cues from predators (Hamren & Hansson 1999, Cohen & Ritz 2003, Linden et al. 2003). Schooling for mysids that have evolved schooling behaviours may be more effective at predator evasion than is their entry into vegetation because such entry breaks up schools into more easily taken, smaller groups (Flynn & Ritz 1999), and swarm-formers versus species using structural refugia show the expected responses (Linden et al. 2003). Burrowing or burying during the day by emergent mysids appears to be an intermediate solution, providing mechanical, optical and perhaps chemical refuge from sensory detection by predators, but it probably has costs of reduced feeding capabilities relative to mysids feeding at the sediment-water interface. Mysid schooling may be less effective against predators that themselves school (Foster et al. 2001) and may incur greater risk from suspension-feeding animals that do not pursue individual prey but filter them in bulk, such as gray whales (*Eschrichtius robustus*). School size appears to depend on a dynamic optimum solution between reduction of risk and enhancement of feeding success (Ritz 1994). Among questions that merit attention are whether mysids by schooling during emergence and re-entry enhance their mean individual rates of capture of emergent and holoplanktonic copepods and whether those in poorest nutritional status take greater risks by emerging earlier in the night as has been demonstrated for some diel migrators among the holoplankton (Hays et al. 2001).

Near shore, where physical gradients in nearly all directions and over time are usually strong, gradients in risk and potential gain run in all directions but certainly covary strongly with distance from shore, water depth and time of day (e.g., Takahashi et al. 2004). Diel horizontal migration has not received much recent attention in shallow-water biological oceanography, whereas diel horizontal differences in abundance are so commonly documented among freshwater crustaceans and rotifers that the term 'shore avoidance' was coined when the behaviour of swimming toward open water in the morning and a putative orientation mechanism in the form of polarised light were reported (Siebeck 1968a,b). Curiously, marine mysid capability to detect polarisation was documented a decade earlier (Bainbridge & Waterman 1957), but early marine work focused more on physiology than on ecological implications. More recently, Goddard & Forward (1991) documented

grass shrimp orientation mediated by polarisation and aiming them away from shore during daylight, likely avoiding littoral predators. Test results are consistent with several predictions based on predator avoidance in fresh waters (e.g., Wicklum 1999). Recent experimental verification of homing capabilities in marine mysids (Twining et al. 2000) and clarification of submarine polarisation showing potential utility for orientation to >200 m depth (Waterman 2005) promise renewed interest. Notably, horizontal tilt of the polarisation e-vector is greatest near dawn and dusk, giving the best onshore–offshore information then. Benefits of homing to particular reef, cave or macrophyte sites are obvious, but information on relocation of mysids from horizontally (alongshore) more uniform environments is scarce. Wittman (1977), however, painted mysids in his diving study and remarked that he could find them up to 12 days later (the intermolt period for one of the dominant species). Further mark-recapture results might be particularly informative about homing and might also be revealing about population sizes if the relevant parameters can be estimated.

In terms of risks, many also vary over timescales beyond the diel. Over 6 yr of observation, we have observed *Neomysis americana* to be present in our local, shallow fjord (Damariscotta River estuary, with little freshwater input) weeks before any appreciable vertical migration begins. Nocturnal emergence does not start until late May or early June, coincident with the termination of the annual alewife (*Alosa pseudoharengus*) run upstream (P.A. Jumars, personal observations). A mechanistic relationship remains to be established, but a time-varying predation risk at mid-latitudes from seasonal cycles of clupeids is nearly universal.

In terms of spatiotemporal gradients of predators, recent acoustic results document that, in a setting with a narrow shelf, many mid-water animals migrate strikingly close to shore at night, with onshore–offshore speeds exceeding those of their vertical excursions by three orders of magnitude (Benoit-Bird et al. 2001, Benoit-Bird & Au 2004). Although wider shelves will impede mid-water participants in diel migration, analogous phenomena in diel predator movements are expected even on broad shelves. For emergent mysids that time-share food resources and predation risks between pelagic and benthic habitats, the likelihood that optimal benthic and pelagic habitats occur in the same depth of water seems remote. What is perhaps the greatest animal migration on the planet has recently been revealed acoustically and comprises horizontal movements of great shoals of fishes over the continental shelf (Makris et al. 2006); diel patterns are not yet established. It is easy to predict with confidence that the horizontal and coastal equivalent of Vinogradov's ladder (Vinogradov 1962) will be documented in the observatory era of oceanography and that mysids will constitute several rungs.

Combined gradients in predation risk and resources can produce confusing patterns of resource use when interpreted according to resource availability alone, particularly for omnivores that have multiple feeding options (Morris 2005). In an innovative and ambitious contribution, Speirs et al. (2002) predicted and dissected the movements of intertidal mysids as functions of both resource and predator effects and time, through population-level modelling of distributions. It could be useful to repeat their measurements of response to sediment organic quality using a method more sensitive to the labile, digestible component of sediments (Mayer et al. 1995), which in general is not well correlated with total organic carbon (Dauwe et al. 1999) and using only the surficial and resuspendable materials (Mayer et al. 1993) to which epibenthic mysids are exposed.

A quickly advancing, alternative approach to modelling organisms that use multiple habitats also appears to merit closer examination for potential application to mysids. Given the long history of research on diel vertical migration in zooplankton, prospects for rapid advance to predictive understanding of emergence by reductionist testing of the same or variant collections of hypotheses on mysids or other emergers appear bleak. As an alternative, IBM is a subset of agent-based modelling within complexity theory (Auyang 1998) and has several characteristics that distinguish it from classical reductionist or holistic approaches (Grimm & Railsback 2005, p. 55):

- “Theory is neither holist (system-level) nor reductionist (individual-level). We do not assume that ecological systems can be understood from only the system level, but we also do not assume that a system is simply the sum of its individual parts. Systems have properties of completely different types than the properties of individuals, and theory must explain these system properties.
- Theory must therefore be multilevel, linking traits of individuals to properties of the system. We are not interested in understanding all aspects of individual behavior but instead are interested in developing models of individuals that explain important system properties.
- Observational and experimental science at both the individual and system level is the basis for theory development. Such empirical science is important both for discovering the phenomena driving the system and for testing theories.”

IBM is also an obvious approach toward understanding of emergence because the constellation of traits associated with emergent mysids overlaps so broadly with published success stories of IBM in explaining and predicting schooling and foraging behaviours under varying risks, dispersal, habitat usage and local reproductive success (Grimm & Railsback 2005, Chapter 6). What is particularly promising about this approach is that it frequently predicts very different consequences in different environments, as would appear necessary in the case of *Neomysis americana*. IBMs have already been used in other marine applications (Miller et al. 1998, Grimm et al. 1999, Crain & Miller 2001, Leising 2001). The variety of IBM that would appear appropriate to mysids assumes that individuals choose behaviours that on average enhance their fitness, and those behaviours are termed ‘adaptive traits’ (Zhvotovsky et al. 1996). A successful IBM is generally recognised through correct prediction of often-subtle spatial patterns of distribution and habitat usage (Dieckmann et al. 2000, Grimm & Railsback 2005). Both from the standpoint of understanding observations and making models, the words of Pearre (2003) resonate: “Without knowing the actual movements of individuals it seems unlikely that we will be able to understand their causes, nor the effects of vertical migrations on the environment or on the migrators themselves”.

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HABITAT COUPLING BY MID-LATITUDE, SUBTIDAL, MARINE MYSIDS

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HABITAT COUPLING BY MID-LATITUDE, SUBTIDAL, MARINE MYSIDS

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HABITAT COUPLING BY MID-LATITUDE, SUBTIDAL, MARINE MYSIDS

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