Chapter 1

Neomysis integer: a review

ABSTRACT

The present chapter aims to be a literature review on the brackish water mysid *Neomysis integer*, with focus on its feeding ecology, life history aspects, behaviour, physiology, biochemical composition, bioenergetics and ecotoxicology. All records on the species, available from literature, are listed as an appendix. The review aims to identify the state-of-the-art and the gaps in our knowledge on the species.

Abundant information is available on the distribution patterns of *Neomysis integer* in enclosed brackish waters and estuaries, although on has to keep in mind that the swarming behaviour, vertical and horizontal migration, segregation of life stages and escape behaviour of *N. integer* (all not fully understood yet) can handicap the quantification of the density and biomass, and may hamper the calculation of the production and the study of the life history of the species.

There is a great need for the description of the feeding ecology of key species – like *Neomysis integer* – in estuarine environments for the development of accurate C-flux models and the description of detritus based food web patterns, including the quantification of transfer coefficients. Although *N. integer* is described as an important food item for many demersal and pelagic fish, larger epibenthic crustaceans and wading bird species, quantitative information is still lacking on its own diet, feeding rates, feeding patterns and selectivity (especially for populations living in estuarine conditions).

Numerous data are available on the life history of *Neomysis integer* over a wide geographical and habitat range, although southern populations (< 51°N) are more poorly known. Variations are observed between these populations in the number of cohorts, size-at-maturity, fecundity and growth rate. Growth and reproduction are affected by prevailing environmental conditions as generally observed in Crustacea. However, in the eurythermic and euryhaline *Neomysis integer*, typically living in the highly dynamic estuarine environment, this is not thoroughly studied yet. Details on how intra- and post-marsupial development, moulting processes and reproduction are affected by a wide range in salinity, temperature, food quantity and quality are still lacking.

The biochemical composition and the ecophysiology of *Neomysis integer* are well known and several methodologies to calculate the energy budget have been applied to the species.

There has been an increasing interest in using the brackish water mysid *Neomysis integer* as a toxicological test species for Western European estuarine systems. Mortality, respiration, swimming behaviour, testosterone metabolism and energy budgets are well established endpoints for bioassays with the species. However, more data on its growth, moulting and development are needed (at the individual- and population-level). The influence of prevailing environmental variables on these processes, as well as their optimal range have to be known in order to develop optimal laboratory cultures and to differentiate between chemically-induced variability and natural variability in toxicity testing.

Because *Neomysis integer* is often used as a model species to study the ecology of brackish water crustaceans, and because the species is easy to sample qualitatively in shallow water and easy to keep in the laboratory, many studies and data are available concerning the species. The older studies (< 1980) are often superficial or based on a limited number of observations; many data are often unpublished (as Ph.D. theses or reports) or published in local journals. Information extracted from this *'grey'* literature has been integrated in the review. In the last 10 years, more in-depth studies have been published concerning aspects of the feeding ecology, population dynamics, physiology, bioenergetics, behaviour, and ecotoxicological use of the species, as well as on molecular work.

One should consider this chapter as a reference work, to refer to when specific information on one of the topics is needed. Reading of the review is **not** necessary to understand the context of the following chapters. Since its content differs from the remainder of the thesis, the chapter has a separate reference list and font. It has a separate table of contents to help to navigate through the text. The author's contributions (results presented in this thesis and some unpublished work) are highlighted in the text.

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1 INTRODUCTION

1.1 Taxonomy

The order Mysidacea (Crustacea: Peracarida) includes species that inhabit most aquatic environments from the open sea to inland water bodies, and from strictly marine to freshwater conditions. At present 1065 species of mysids have been described, distributed over 170 genera (Deprez *et al.*, 2004; http://www.vliz.be/vmdcdata/nemys). The genus *Neomysis* (Czerniavsky, 1882) consists of 17 species, of which at least 10 are confined to brackish water conditions (Mauchline and Murano, 1977; www.iorbis.org). The only European representative is *Neomysis integer* (Leach, 1814).

Phylogenetic discussion: MYSIDA - MYSIDACEA

In the 80 – 90's of the 20th century the phylogenetic relationship of the constituent taxa of the Order Mysidacea were discussed in literature. Watling (1981; 1999) suggested that the Lophogastrida and the Mysidacea could not be considered as sister groups and that they both were rather related to the Eucarida than to the other orders of the Peracarida. The family Mysidae (to which Neomysis integer *belongs) was considered to be part of the order Mysida (e.g. http://tolweb.org/tree?group=Peracarida; Kobusch, 1998).*

However, based on a complex of 93 morphologic, anatomic and embryonic characters, Richter and Scholtz (2001) recently concluded that the taxa Mysida and Lophogastrida are indeed sister-groups within the monophyletic Order Mysidacea and that they are not separated from the other peracarid orders (Amphipoda, Mictacea, Spelaeogriphacea, Cumacea, Tanaidacea, Isopoda and Thermosbaenacea). The discussion continues … In the present work we use the term Mysidacea.

1.2 External morphology

Mysidacea are shrimp-like animals that are characterized by a marsupium within which the entire larval development takes place (*cfr.* opossum shrimps). The brood pouch is composed of two, three or seven pairs of lamellae (oostegites) attached to the thoracic limbs. The uropods consist of lamellar endopods and exopods forming a tail fan with the telson. The endopods usually possess a statocyst. The telson is always wider at the base than at the apex. The abdominal legs never have chelae. The shield-like carapax covers the greater part of the cephalothorax, but is not attached to it in the last thoracal segments. For a more detailed definition of the order we refer to Tattersall and Tattersall (1951).

Neomysis integer (Leach, 1814) has a slender habitus and grows up to about 17 mm in length (Figures 1, 2). Its transparent body has occasional brown pigmentation. The large, stalked eyes are conspicuous. The well developed carapax, protecting the head and thorax, leaves the 7th and 8th thoracic somites uncovered and has a short rostrum. The two pairs of antennae are long and biramous. In adult males, the peduncle of the first antennae (antennule) bears a setose lobe (lobus masculinus) between the flagellae. The outer extension (exopod) of the second pair of antennae, takes the form of a flattened plate, known as the antennal scale. It is an important diagnostic characteristic for the species. The antennal scale of *N. integer* is very long and narrow, tapering to a point. It is bordered along its margins with setae and has a distinct distal suture.

The thoracopods are well developed and biramous, but lacking branchiae. The exopods are fringed and look feather-like. The adult female has a marsupium consisting of two pair of brood lamellae (oostegites) present on the 7th and 8th thoracopods. The lamellae are thin-walled, transparent concave plates fringed with strong, short setae that interlock ventrally to form a closed chamber below the thorax. Typical for the genus *Neomysis* are the two pairs of median finger-like processes extruding from the sterna of the last 2 thoracic somites into the marsupial cavity.

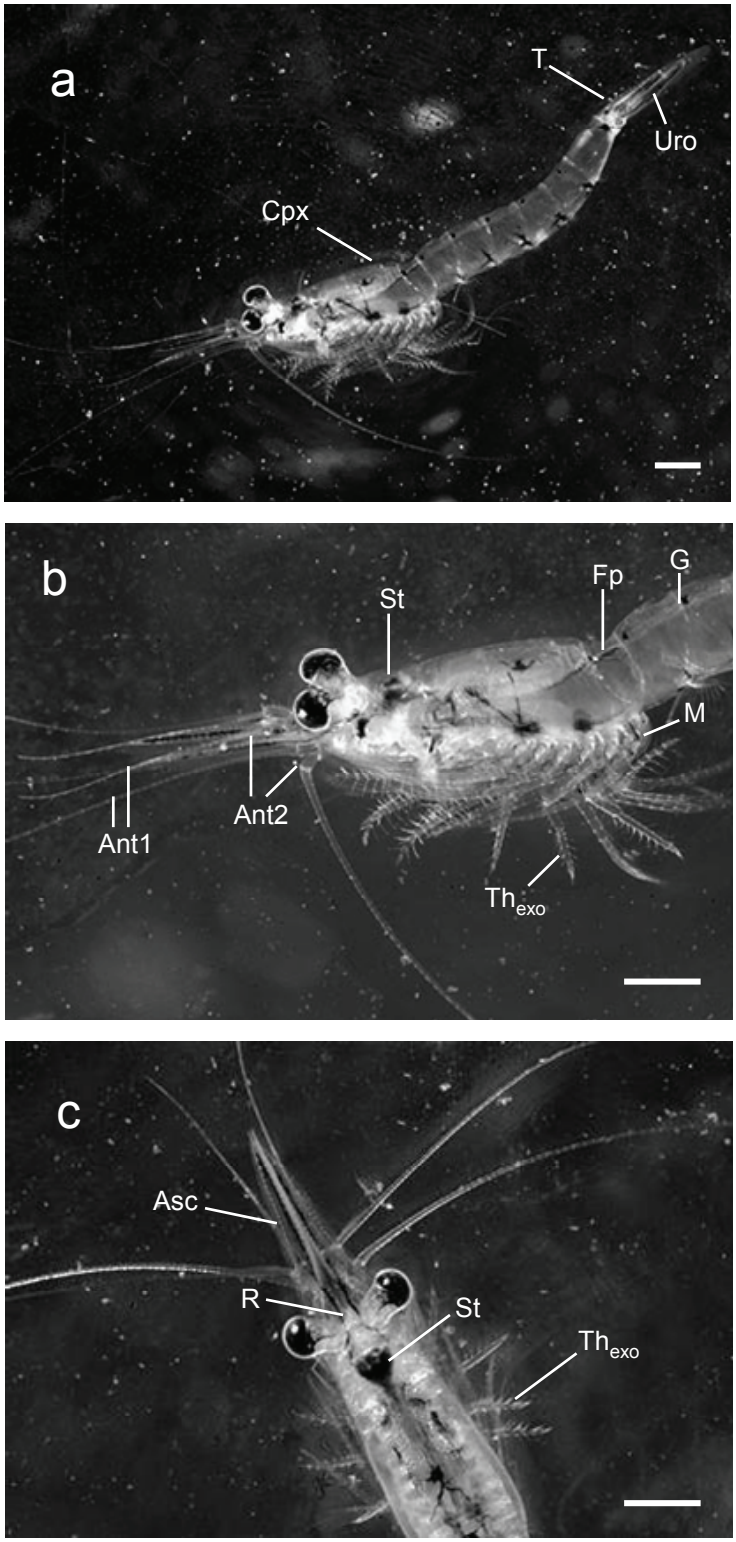


Figure 1: (a) habitus of the brackish water mysid *Neomysis integer*; (b) Cephalothorax in lateral view; (c) Cephalothorax in dorsal view. Ant1: 1st antennae (antennules), Ant2: 2nd antennae, Asc: Antennal scale, Cpx: Carapax, Th_{exo}: exopodite of thoracopod, Fp: faecal pellet, G: gut, M: (developing) marsupium, R: rostrum, St: Stomach, T: Telson, Uro: Uropods. Scale bar: 1 mm (Pictures: Offermans, R.)

The abdominal limbs (pleopods) are less developed, with the exception of 4th pair in adult males. They have an elongated 4th pleopod with a terminal pair of barbed setae. The last pair of pleopods is biramous and flattened, and forms the tail fan (uropods). The endopods of the uropod are as long as the telson, and have a statocyst at their basis. The two endopods are armed with a dense row of comb-like spines on their ventral surface near the inner margin. The exopods are one and a half times as long as the telson. They are not armed with spines but do have setae all round. The telson is long, triangular in outline with a narrow, uncleft apex (*cfr. integer*). Short spines border the lateral margins, while the apex has two pairs of spines of which the outer are twice as long as the inner.

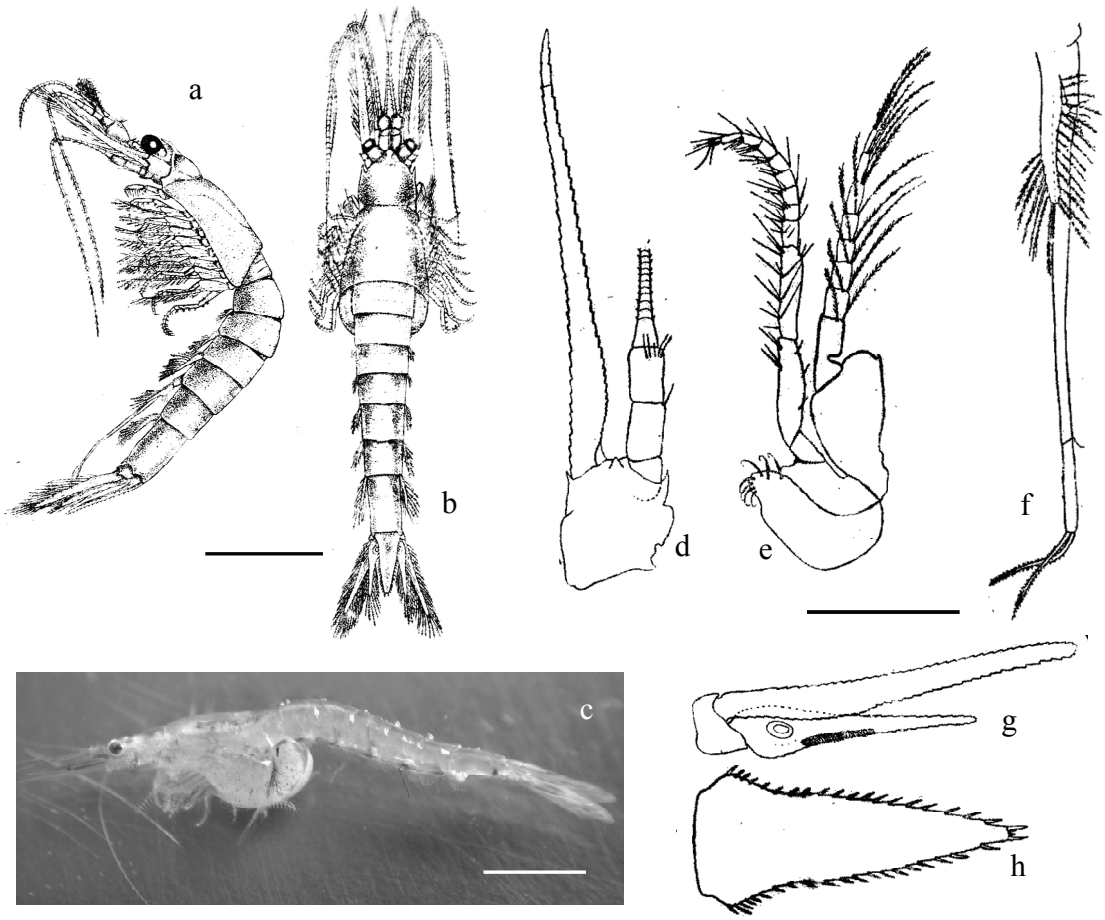


Figure 2: Habitus of adult male (a), female (b) and ovigerous female (c) *Neomysis integer* (scale bar 5 mm). Details on antennal scale (d) , 8th thoracic limb of male (e), 4th pleopod of male (f), uropod (g) and telson (h); scale bar 500 µm. (Drawings from: Tattersall and Tattersall, 1951).

The morphology of the feeding appendages and the intestine of *Neomysis integer* are treated in paragraphs 3.7 and 3.8. The description is adapted from Tattersall and Tattersall (1951), Mauchline (1980), Hayward and Ryland (1995), http://www.marlin.ac.uk/species/taxon_Neomysisinteger.htm and http://ip30.eti.uva.nl/bis/crustacea.php. The telson and antennal scale, important diagnostic characteristics for the species, are particularly susceptible to injury, causing atypical morphology which may lead to misidentification (Hayward and Ryland, 1995).

1.3 Geographical distribution and habitats

Neomysis integer is one of the most common mysids along the Atlantic coast of Western Europe. It is a hyperbenthic, euryhaline and eurythermic species, confined to the brackish environment within estuaries (Tattersall and Tattersall, 1951). It is also abundant in brackish (oligohaline to freshwater) inland water bodies, which were connected to the sea in recent geological history, *i.e.* brackish water ponds, lakes, ditches and canals (Tattersall and Tattersall, 1951; Bremer and Vijverberg, 1982). Occasionally, the species is reported for the open sea in British and Belgian continental waters (Kramp, 1910; Makings, 1977; Dewicke, 2002), but it is very uncommon there. *N. integer* is also reported as a resident species in the Belgian surf zone water (Lock *et al.*, 1999, Beyst, 2001; Beyst *et al.*, 2001), although with low densities (< 1 ind m^{-2}).

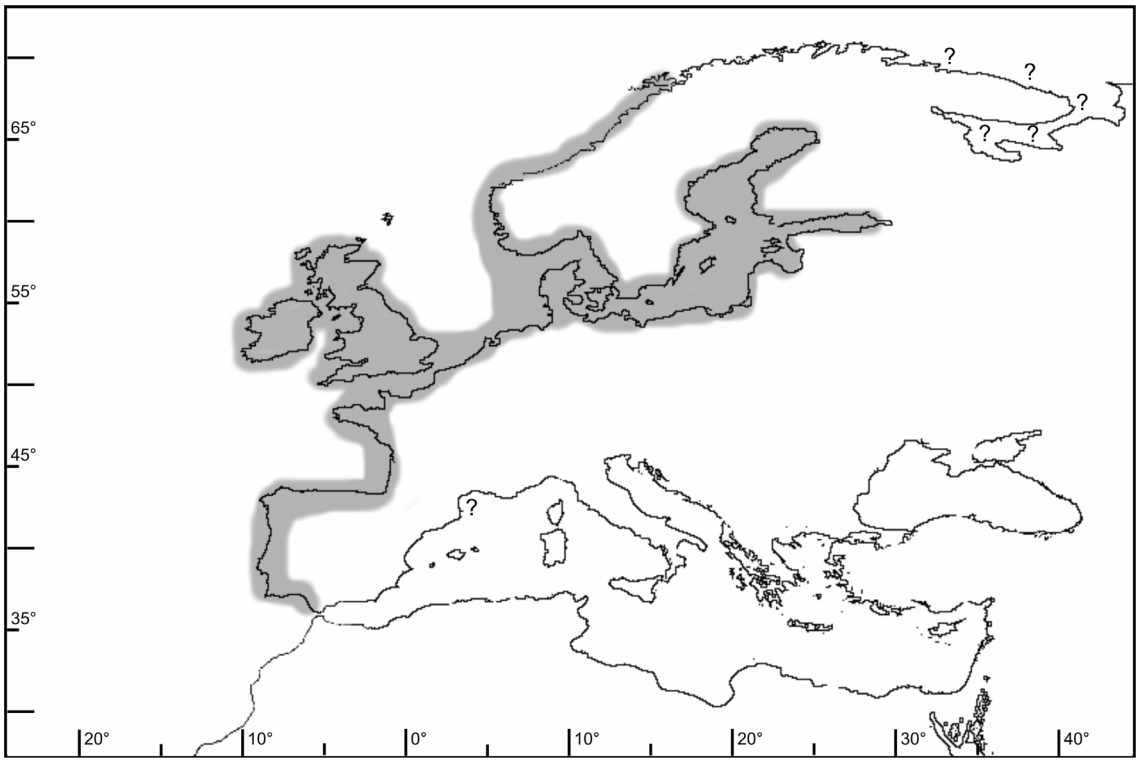


Figure 3: Distribution of *Neomysis integer* based on records in literature (Based on: Remerie, 2005).

Neomysis integer is commonly recorded along the Atlantic coastline and Britain between the longitudes 68°N (coast of Norway, Lofoten) and 36°N (South coast of Spain) and in the Baltic Sea (Figure 3, Appendix 1). The species is reported to occur more to the North (68 to 71°N), up till the Murman coasts of the Barents Sea and the White Sea (Wagner, 1885 referring to Jarzynsky), but recent observations do not confirm this (Väinölä, personal communication). Also, the two records of *N. integer* along the Mediterranean coastline in the canal d'Arlès and the mouth of the Rhone estuary (Bacescu, 1941) have not been confirmed since (Wittmann and Ariani, 2000).

1.4 Sampling

Mauchline (1980), Janssen (1985) and Mees and Jones (1997) summarize the different quantitative sampling techniques that can be applied to catch *Neomysis integer* in a variety of habitats. One should keep attention to the fact that the swarming behaviour, the vertical and horizontal migration, the often apparent segregation of the life stages and the escape behaviour of *N. integer* can handicap the exact estimation of their abundance and biomass, and hampers the calculation of the production and the study of the life history of the species (Mauchline, 1980; Arndt and Jansen, 1986; Thiel, 1992; Mees *et al.*, 1994).

2 Distribution patterns

2.1 Density, biomass and associated species in estuaries

Because of its sediment affinities (Hough and Naylor, 1992; David *et al.*, 2005), *Neomysis integer* can be considered as an element of the hyperbenthos (syn. suprabenthos), *i.e.* the fauna living in the lowest meter of the water column. Baseline studies on the spatial and temporal patterns in the estuarine hyperbenthic community, and on the contribution of *N. integer*, have been published for several NE Atlantic estuaries (Table 1).

Table 1: Available studies on the spatial and/or temporal distribution of *Neomysis integer* in the hyperbenthos of western European estuaries.

Latitude	Estuary	Source	Max density (biomass)
53°N	Elbe	Bernát et al., 1994; Köpke and Kausch, 1996	210 m^{-3} (bottom) 4-360 m^{-3} (surface)
53°N	Weser	Schuchardt et al., 1989; Haesloop, 1990	-
53°N	Jade Bay	Apel, 1992	-
53°N	Eems	Mees et al., 1995	22 m^{-2}
53°N	Conwy	Hough and Naylor, 1992	-
52°N	Shannon	O'Sullivan, 1984	-
51°N	Severn	Bamber and Henderson, 1994; Moore et al., 1979	-
51°N	Schelde	Subtidal: Mees and Hamerlynck, 1992; Mees et al., 1993; 1993b; 1994; 1995	160-190 m^{-2} (225mgADW m^{-2})
		Marshes: Cattrijsse et al., 1994; Hampel et al., 2003; 2003b	240 m^{-3} (840mgADW m^{-3})
50°N	Tamar	Milner, 1986 Moffat and Jones, 1992; Moffat, 1996	1400 m^{-3} 200 m^{-3}
49°N	Seine	Zouhiri et al., 1998; Mouny et al., 1996; 1998, 2000; Dauvin et al., 2000	667 – 2160 m^{-3} (200mgADW m^{-3})
45°N	Gironde	Sorbe, 1980; Mees et al., 1995; David et al., 2005	26 m^{-2}
43°N	Ria Deba	San Vicente, 1993; 1996	< 0.5 m^{-2}
43°N	Ria Urola	San Vicente, 1993; 1996	< 0.5 m^{-2}
43°N	Ria Oria	San Vicente, 1993; 1996	< 0.5 m^{-2}
43°N	Ria Uremea	San Vicente, 1993; 1996	< 0.5 m^{-2}
43°N	Ria Bidasoa	San Vicente, 1993; 1996	Absent
40°N	Ria de Aveiro	Cunha et al., 1999	-
37°N	Ria de Alvor	Rodriguez and Dauvin, 1987	-
36°N	Bay of Cádiz	Drake et al., 1997	-
36-37°N	Guadalquivir	Drake et al., 2002	9 m^{-3} (59mgWW m^{-3})

The hyperbenthic fauna in the upper reaches of European estuaries is dominated by the mysids *Neomysis integer* and *Mesopodopsis slabberi* (Sorbe, 1980; Mees *et al.*, 1993; 1993b; 1994; 1995; Moffat and Jones, 1992; 1993; Moffat, 1996; Köpcke and Kausch, 1996; Drake *et al.*, 2002; David *et al.*, 2005). In winter, the latter species is virtually absent in the estuary (*e.g.* Schelde, Tamar, Jade). Throughout the year *N. integer* occupies the upper, oligohaline zone (*e.g.* Moffat and Jones, 1992; Mees *et al.*, 1994; 1995), both in the subtidal and the adjacent marshes (Ralph, 1965; Mees *et al.*, 1993b). It is generally found in lower saline water than *M. slabberi* and recorded right up to the point at which the high-tide salinity is 0.1 psu (Percival, 1929; Sorbe, 1980; Zouhiri *et al.*, 1998).

Neomysis integer is typically associated with the zone of highest suspended matter concentrations (Bernát *et al.*, 1994; Mees *et al.*, 1995; Moffat, 1996; Köpcke and Kausch, 1996; Fockedey, unpublished).

The (daytime) vertical distribution of *Neomysis integer* in and around the maximum turbidity zone of the Elbe, Schelde and Gironde estuaries was studied by Fockedey (unpublished – EU project MATURE). By sampling a shallow system in two depth strata (near the surface and near the bottom) with a High Speed Plankton Sampler (mesh size 1 x 1 mm), the entire water column (generally < 10 m) was considered to be sampled and the relative abundance of *N. integer* in the two layers was compared.

In turbid waters, *i.e.* when suspended particulate matter concentrations were higher than 200 mg l^{-1}, the *Neomysis integer* population was evenly distributed over the water column, as was the case for the maximum turbidity zone of the Elbe and along the entire longitudinal transect of the Gironde. In the Schelde estuary, *N. integer* was predominantly present near the bottom during daytime, as turbidity is relatively low compared to the two other estuaries.

In many estuaries this zone of maximal turbidity at the fresh-water/brackish-water interface (maximum turbidity zone MTZ or estuarine turbidity maximum ETM) is associated with low dissolved oxygen levels (Costa and Elliott, 1991; Baeyens *et al.*, 1998; Mouny *et al.*, 2000; Roast *et al.*, 2002), especially in summer periods. These low dissolved oxygen levels cause problems for metazoan life. Concentrations lower than 40 % oxygen saturation level (*i.e.* 3.3 – 5.1 mg l^{-1} at 5 – 25 °C) are limiting for *N. integer* (Mees *et al.*, 1995), while concentrations lower than 7 mg l^{-1} produce a barrier for upstream migration of estuarine fish (Costa and Elliott, 1991). *N. integer* is found in the Schelde at a much higher salinity (10 – 15 psu) than in other, less organically polluted estuaries where the population maximum is found at around 3 – 5 psu. In the polluted Schelde, the maximal population densities are found near the limit of viable oxygen concentrations regardless of salinity (Mees *et al.*, 1993, 1993b, 1994; 1995), where no adverse oxygen conditions hamper their development.

In shallow estuarine water, *Neomysis integer* is often associated with the coexisting mysid *Praunus flexuosus* (Muus, 1967; Mauchline, 1971; Välipakka, 1992). *P. flexuosus* is more restricted to intertidal areas and occurs in much lower numbers in comparison with *N. integer*. Other typical associated hyperbenthic species in the subtidal are Gammarids (*Gammarus zaddachi*, *Gammarus salinus*), the isopod *Eurydice pulchra*, shrimp (*Crangon crangon*, *Palaemonetes varians*, *Palaemon longirostris*) and fish (*Pomatoschistus microps*, *P. minutes, Pleuronectes flesus* and larvae and juveniles of clupeids) (Moore *et al.*, 1979; Sorbe, 1980; Rudstam *et al.*, 1986). Typical associated zooplankton species are the calanoid copepods *Eurytemora affinis* and *Acartia* spp. (Moore *et al.*, 1979; Castel, 1993; Soetaert and Van Rijswijk, 1993; David *et al.*, 2005). The endobenthic fauna of the oligohaline zone of the estuary is impoverished (mainly *Corophium* sp., oligochaetes, and chironomids), due to the high turbidity clogging their feeding mechanisms, salinity stress and pollution, in addition to possible regular dredging of the upstream shipping channels (Pearson and Rosenberg, 1987; Ysebaert *et al.*, 1993; Mouny *et al.*, 1998).

Densities

Most authors (*e.g.* Moore *et al.*, 1979; Mees *et al.*, 1994) report distinct peaks of density (and biomass) of *Neomysis integer* in spring and summer, while densities generally drop in wintertime. Seasonal fluctuations in the densities can be partially explained by periods of active breeding when the population increases in size or by predation and increased winter mortality when the densities drop (Mauchline, 1971c; Gameson, 1982), although migration can also take part in explaining variable densities (Schuchardt *et al.*, 1989). The geographical position of the population within the estuary shows tidal variation due to advection within the tidal cycle and shows seasonal variation due to the freshwater discharge, with a more downstream position in winter and a more upstream position in summer and autumn (Sorbe, 1980; Schuchardt *et al.*, 1989; Hough and Naylor, 1992; Köpcke and Kausch, 1996; Mouny *et al.*, 1996).

In the subtidal of the **Schelde estuary**, the peak densities were 160 – 240 ind m^{-2} in spring and summer (Mees *et al.*, 1994; 1995; Mees and Jones, 1997). In the marshes of this estuary, maximal densities of 240 ind m^{-3} were recorded in early summer (Cattrijsse *et al.*, 1994; Hampel *et al.*, 2003; 2003b). In the bottom waters of the main channel in the **Elbe estuary**, the densities of *N. integer* were more or less constant during the day (210 ind m^{-3}), while at the surface densities fluctuated between 4 and 360 ind m^{-3}, with maximal values at the beginning of the ebb tide, especially at night (Bernát *et al.*, 1994; Köpcke and Kausch, 1996). Moffat and Jones (1992) and Moffat (1996) reported maximal *N. integer* densities of 200 ind m^{-3} in the **Tamar estuary** in late spring. Their value is considered to be an underestimate due to inefficient sampling of the larger immatures and adults with fine meshed plankton nets. In the same estuary, Milner (1986) reported a density of up to 1400 ind m^{-3} during summer. For the meso-oligohaline area of the **Seine estuary**, maximal densities of 667 and 2160 ind m^{-3} were reported for spring and autumn respectively (Zouhiri *et al.*, 1998; Dauvin *et al.*, 2000). In the **Gironde and Eems estuaries**, maximum densities were much lower in summer, respectively 26 and 22 ind m^{-2} (Mees *et al.*, 1995). In the **Guadalquivir**, mean density of *N. integer* was 9 ind m^{-3} in the surface water (Drake *et al.*, 2002). In the small **Rias Deba, Urola, Oria and Uremea** the estimated densities never exceeded 0.5 ind m^{-2} (San Vicente, 1993). See Table 1.

Neomysis integer is the most widespread mysid species in the **Baltic Sea** (Köhn, 1992). It is a typical species of very shallow waters (Välipakka, 1992) with densities of 100, 10 and 1 ind m^{-3} at respective depths of 0.5, 2 and 5 metres (Weslawski, 1981). In shallow Danish estuaries and lagoons the maximal densities of *N. integer* can amount to 3000 – 4000 ind m^{-2} (Muus, 1967). Rasmussen (1973) even reported 50000 ind m^{-2}. In open water, the species is far less abundant than the co-occurring *Mysis mixta* and *Mysis relicta* (Margonski and Maciejewska, 1999). Generally, the densities of *N. integer* are higher along the southern coasts of the Baltic Sea in comparison with the more northern areas (Thiel, 1992). In the northern Baltic region, with low densities of 24 ind m^{-2} (Hansson, 1990) *N. integer* contributes only 3 % of the total mysid biomass (Rudstam *et al.*, 1992). In the South, densities between 160 ind m^{-2} (Arndt and Jansen, 1986) to more than 600 ind m^{-2} (Thiel, 1992) were reported for shallow stations, while in open waters the densities reported by Margonski and Maciejewska (1999) were only 15 ind m^{-2}. In the middle reaches of the Baltic, along the Swedish coast of the Baltic proper, maximal densities of *N. integer* were 24 ind m^{-2} (Rudstam *et al.*, 1986) and in the Gulf of Riga (eastern Baltic, Latvia) maximal densities were 20 – 40 ind m^{-2} (Kotta and Simm, 1979).

Biomass

The standing stock available at a certain moment is usually estimated by calculating the available biomass per surface or volume unit (in dry weight or ash free dry weight) using the length frequency distributions and a length-dry weight regression (Table 2). These regressions do not show significant differences between males and females (Beattie and de Kruijf, 1978; Mees *et al.*, 1994). The relationship shows no variation with the time of the year (Beattie and de Kruijf, 1978; Mees *et al.*, 1994), although Aaser *et al.* (1995) constructed separate regressions for winter and summer. When formalin-preserved animals are used for the biomass determination, some authors (*e.g.* Bremer and Vijverberg, 1982) use a correction factor for the weight loss and add 10 % to the calculated dry weight (Beattie, 1982). Some studies directly weigh the total biomass available as wet weight. The (dry weight) standing stock is then calculated as 22 % of the wet weight for *Neomysis integer* (Maciejewska and Opalinski, 2002). The ash weight amounts approximately 10 % of the dry weight of *N. integer* (Astthorsson, 1980). The ash free dry weight thus is 90 % of the dry weight. Biomass can also be expressed as volume through the water-displacement method based on the principle that an immersed mass displaces its own mass of water (Margonski and Maciejewska, 1999).

In the **Schelde estuary**, the standing stock biomass of *Neomysis integer* peaked in late spring with 225 mgADW m^{-2} (Mees *et al.*, 1994). In the marshes along this estuary, maximal biomass values of 840 mgADW m^{-3} were measured in the same period (Cattrijsse *et al.*, 1994). In the **Seine estuary**, the biomass of the species peaked in September with 200 mgADW m^{-3} (Dauvin *et al.*, 2000). In the **Guadalquivir**, the mean biomass of *N. integer* only amounted to 58 mgWW m^{-3}, *i.e.* 13 mgDW m^{-3} (Drake *et al.*, 2002). In the southern **Baltic** the maximal biomass was estimated as 620 (Arndt and Jansen, 1986) and up to 9.5 g WW m^{-2} (*i.e.* 2100 mgDW m^{-2}) in the shallow areas (Thiel, 1992). See table 1.

Table 2: Length – weight regressions available for *Neomysis integer*.

lnADW = -5.539 + 2.267 lnSL	n=100; r^2=0.997	Mees et al., 1994
lnDW* = 1.432 + 2.853 lnSL	n=9, r^2=0.99, p<0.001	Irvine et al., 1995
Log DW = 2.7847 log TL – 2.5229	N=132; r=0.99, p<0.01	Astthorsson, 1980
DW = 0.00391 $TL^{2.48}$	n=15; r^2=0.998	de Kruijf, 1977
DW = 0.0041 $SL^{2.78}$	n=51; r^2=0.97, p<0.0001	Gorokhova and Hansson, 1999
DW = 0.00254 $TL^{2.7676}$	r=0.99	Jansen, 1985c; Arndt and Jansen, 1986
DW = 0.00638$TL^{2.435}$	n=100; r^2=0.98; p<0.0001	Aaser et al., 1995
DW = 0.00347 $TL^{2.7046}$ (winter)	n=50; r^2=0.98; p<0.0001	Aaser et al., 1995
DW = 0.00621$TL^{2.4873}$ (summer)	n=50; r^2=0.98; p<0.0001	Aaser et al., 1995
DW = 0.0016 $TL^{3.086}$	n=201; r^2=0.97	Winkler and Greve, 2004
$\log_{10}$DW = -0.58 + 2.64 $\log_{10}$TL	N=45; r=0.99	Summers, 1980
WW = 0.0022715 $TL^{3.46}$	r=0.996	Jansen, 1985c; Arndt and Jansen, 1986

With **DW**: dry weight (in mg); **DW***: dry weight (in µg); **WW**: wet weight (in mg); **ADW**: ash free dry weight (in mg); **SL**: Standard length, *i.e*. from the front of the eyes to the last abdominal segment (in mm); **TL**: Total length, *i.e.* from the front of the eyes to the end of the telson or the end of the uropods excluding the setae (in mm) TL= 1.165 SL - 0.080 (n = 112; r^2 = 0.997; p < 0.001; Mees et al., 1994); TL = 3.78 CL (Schuchardt et al., 1989); **CL**: Carapax length, from the basis of the eyed to the median end of the carapax, in lateral view (in mm); CL= 0.266 SL + 0.439 (n = 112; r^2 = 0.908; p < 0.001; Mees et al., 1994).

2.2 Brackish ponds and lakes

Neomysis integer is common in brackish lakes and ponds which were once connected to the sea until recent historical times. In those enclosed brackish water bodies, the *N. integer* population can undergo blooms and crashes (*e.g.* Barnes *et al.*, 1971; Parker and West, 1979; Fockedey and Remerie, unpublished). Its abundance and biomass can vary considerably between years and between lakes within the same district (Bremer and Vijverberg, 1982; Aaser *et al.*, 1995). In the Frisian brackish lake district, the peak densities reported for the Bergumermeer were 1000 ind m^{-2} in one year and 5800 ind m^{-2} in another year (Beattie and de Kruijf, 1978) or 6 ind m^{-2} in the Tjeukemeer in one year and 110 ind m^{-2} in another year (Vijverberg, unpublished). In the pond Galgenweel (Belgium) maximal densities of 1100 ind m^{-2} were recorded in the 90's (Soselisa, 1994; Fockedey, unpublished), but since 2002 densities dropped to < 1 ind m^{-2} (Verslycke *et al.*, 2000; Fockedey and Remerie, unpublished). The factors controlling these large population fluctuations remain to be determined. Annual variations in densities can be caused by adverse winter conditions (*e.g.* low oxygen concentrations due to ice cover). Another reason for a low standing stock in some years might be due to varying levels of predation by young and larval fish. Also, high summer temperatures, combined with the low salinity of these lakes, might cause a population crash due to physiological constraints of *N. integer*. In deeper lakes the colder, but often anoxic, hypolimnion is not a refuge from the warm surface layers (Parker and West, 1979). The decline of a *N. integer* population in the Belgian pond Galgenweel might be related to the invasion of the Pontocaspian invader *Hemimysis anomala* (Verslycke *et al.*, 2000).

Some lakes can support this very high density and biomass, while other lakes sustain a significantly lower order of densities. A high density of 1100 – 10400 ind m^{-2} was reported for *Neomysis integer* in Danish, Belgian and English brackish lakes (Irvine *et al.*, 1993; 1995; Jeppesen, *et al.*, 1994; Soselisa, 1994; Aaser *et al.*, 1995), while maximal densities of 6 ind m^{-2} are registered in the Slotermeer (Bremer and Vijverberg, 1982) or 0.5 ind m^{-2} in Lake Grevelingen (Platenkamp, 1983). The species is mainly abundant in those ponds or lakes with poorly developed submerged vegetation. According to Espeel (1982), wave action in these ponds is stronger due to the absence of macrophytes and more detritus is brought into suspension, providing a food resource for *N. integer*.

High densities of *Neomysis integer* in brackish lakes are often associated with a low predation pressure by fish. High densities of 3000 – 13000 *N. integer* ind m^{-3} are present in Danish brackish lakes with low fish biomass (Aaser *et al.*, 1995; Jeppesen, *et al.*, 1994) and a removal of 75 % of the fish stock in a Dutch Lake resulted in a major increase in *N. integer* density (Hosper and Meijer, 1993; Meijer *et al.*, 1994). When fish predation decreased due to a toxic bloom, the population size of *N. integer* substantially increased in Hickling Broad, a brackish lake in England (Irvine *et al.*, 1993). However, high densities of *N. integer* in brackish lakes may also reflect the hypertrophic character of the water mass (Aaser *et al.*, 1995), where the species even enhances eutrophication, both directly and indirectly (see later paragraph). In the brackish lake Hickling Broad, the *N. integer* population itself was suppressed by toxic algal blooms stimulated by the ingress of black-headed gull guano (Bales *et al.*, 1993).

The maximal biomass of *Neomysis integer* (in summer) in brackish lakes can be less than one mg (Bremer, 1980), several mg (Platenkamp, 1983), around 1g (Soselisa, 1994; Aaser *et al.*, 1995; Irvine *et al.*, 1995) or in the order of several grams DW m^{-2} (Beattie and de Kruijf, 1978).

In brackish lakes and pools, *Neomysis integer* is often associated with *Palaemonetes varians* (Norman, 1892; Kemp, 1910) and *Pleuronectes flesus* (Parker and West, 1979). In the more saline Lake Grevelingen, the species lives together with *Praunus flexuosus*, *Idotea chelipes* and *Gammarus locusta* (Platenkamp, 1983).

2.3 Swarming behaviour

Large line-formed swarms of *Neomysis integer* have been observed in shallow estuarine waters (Percival, 1929; Mauchline, 1971c; Arndt and Jansen, 1986; Walesby, 1973; Köpcke and Kausch, 1996). The shoals are one to two meters across by up to 10 m long and stay approximately at 10 cm under the water surface (Parker and West, 1979). At the turn of the tide at flood and some time afterwards during ebbing, the shallow water along the edge of the estuary and the edges of mud banks can be overcrowded with *N. integer* thus forming a thick 'mysid soup' (Percival, 1929). Köpcke and Kausch (1996) encountered far higher densities (1230 ind m^{-3}) in a shallow area of the upper Elbe estuary as compared to the subtidal (210 ind m^{-3}). Also, in the Baltic and in brackish water ponds the species has an extremely aggregated spatial distribution (*e.g.* Espeel, 1982; Arndt and Jansen, 1986; Rudstam *et al.*, 1986).

Although difficult to sample quantitatively (Mauchline, 1971c; Arndt and Jansen, 1986; Thiel, 1992), Roast *et al.* (2004) made an attempt to realistically estimate the maximal density of *Neomysis integer* swarms present over a subtidal flat at low tide by using a dip net and a Perspex cylindrical drop trap. They obtained densities of 11000 to 27000 ind m^{-2} or 36000 to 89000 ind m^{-3}. The volume taken by the swarms was extremely variable, ranging from 0.07 to 1.1 m^3 and containing from 6000 to 51000 individuals.

Next to creating a protection against predation (see later paragraph), increasing the reproductive success and helping in maintaining position (Clutter, 1969), living in a shoal may improve the filtration of suspended food by creating unidirectional currents (Zelickman, 1974). Individuals in large swarms had a decreased individual respiration rate and saved energy (Ritz *et al.*, 2001). For other aggregating crustaceans like Penaeids (Cortoni Valenti *et al.*, 1993), daphniids (Burns, 2000) and euphausiids (Haywood and Burns, 2003), it has been demonstrated that the cost of forming aggregations lead to a decreased growth rate and a lower asymptotic length (possibly by allelopathy). This is not yet demonstrated for *Neomysis integer*.

2.4 Segregation / Partitioning of the life stages

It has often been observed that juvenile and adult stages of *Neomysis integer* shoal separately (Tattersall and Tattersall, 1951; Kinne, 1955; Milner, 1986). Adults of *N. integer* are frequently found in dense swarms near the shore margins or in tidal marshes at certain phases of the tidal cycle in estuaries, while juveniles stay in deeper water (Välipakka, 1992). Sorbe (1980) described the reverse situation in the Gironde estuary with the juveniles occupying the shore, while the adults prefer the subtidal reaches.

Ralph (1965) noted that females utilize the marsh creeks, while newly released juveniles in the smallest size classes and males did not co-occur there. Cattrijsse *et al.* (1994) observed juveniles to be more present in the marsh than in samples from the subtidal of the Schelde estuary. Kinne (1955), Parker and West (1979) and Platenkamp (1983) did not find the early post-marsupial juveniles (2 – 4 mm total length) in bottom samples. This segregation of juveniles from the adults can help to prevent cannibalism (Välipakka, 1992). The swimming speed of adults and juveniles of a species can differ considerably, with the result that a mobile shoal or school becomes a self-sorting mechanism, separating age groups and so producing swarms of individuals of similar body size (Clutter, 1969). Differential swimming speed of juveniles and adults has not been investigated yet for *Neomysis integer*.

Some authors found the larger *Neomysis integer* situated more upstream along the subtidal, longitudinal estuarine gradient than the juveniles. In the Tamar estuary, there is some evidence that the mature and immature mysids move upstream to occupy the lower salinity zones during some periods of the year (spring and September), while juveniles are fairly evenly distributed along the salinity gradient (Moffat, 1996). Smaller juveniles were found in higher salinities than the larger size classes of juveniles (Milner, 1986; Moffat, 1996). In the Conwy, Gironde and Weser estuaries, males occurred more commonly down-estuary, and gravid females and juveniles more upstream (Sorbe, 1980; Schuchardt *et al.*, 1989; Hough and Naylor, 1992). Also, Astthorsson (1980) observed a geographical segregation between the sexes in the Ythan. The different life stages must be able to select particular physico-chemical regimes (mainly temperature, salinity and current speed) in order to achieve the partitioning seen in the population along the gradient. The occurrence of ovigerous females higher up the estuary may relate to the selection of optimal salinity for embryonic development (Hough and Naylor, 1992). Small sexual and/or ontogenic differences in the substrate preference might also be the cause of this segregation in brackish lakes (Beattie and de Kruijf, 1978).

2.5 Position maintenance in the estuary

In estuaries, *Neomysis integer* faces the problem of retaining its position against conditions of net seaward transport (Hough and Naylor, 1992; Roast *et al.*, 1998). In general, there are three main control mechanisms for the positioning of invertebrate populations in estuarine systems: (1) reproductive compensation of seaward losses, (2) behavioural adaptations like alterations in swimming activity at different tidal phases, and (3) use of hydrodynamic processes within the estuary (*e.g.* Siegfried *et al.*, 1979; Wooldridge and Erasmus, 1980; Wooldridge and Bailey, 1982; Moffat and Jones, 1993; Schlacher and Wooldridge, 1994).

Position maintenance has a high environmental relevance, as the mysids have to maintain in areas of optimum feeding conditions, lowest competition and lowest vulnerability to predation. However, due to the position maintenance, the animals experiences tidal and seasonal salinity and temperature fluctuations (Roast *et al.*, 1998). In the Looe estuary for example, *Neomysis integer* is exposed to daily temperature fluctuations of 5 to 15 °C and daily salinity fluctuations of 1 to 34 psu (Roast *et al.*, 1998). In the Schelde the daily and seasonal fluctuations are smaller (Mees *et al.*, 1993), while in other estuaries like for example Elbe, Weser, Conwy and Gironde the tidal variations are notable (Sorbe, 1980; Schuchardt *et al.*, 1989; Hough and Naylor, 1992; Köpcke and Kausch, 1996; Mouny *et al.*, 1996).

Neomysis integer maintains its position in estuaries by a combination of the three previously described factors: by a reproductive compensation through the production of relatively large numbers of juveniles per brood, by using hydrodynamic processes within the estuary (Moffat and Jones, 1993) and by an adapted swimming behaviour (Roast *et al.*, 1998). It migrates during the ebbing tide laterally out of the main channel towards the shallow areas with lower current velocity. By horizontal lateral movements prior to low water tide, *N. integer* can take advantage of the upstream transport provided by the subsequent flood tide and thereby compensates for the downstream drift (Köpcke and Kausch, 1996). The mysids stay predominantly close to the bottom during the peak ebbing tide. At the low tide and the beginning of the flood tide, *N. integer* undertakes vertical and lateral migration to reach the surface of the water in the channel of rapid current flow in order to be transported upstream (Köpcke and Kausch, 1996; Fockedey, unpublished).

In laboratory experiments, Hough and Naylor (1992) demonstrated a maximum swimming activity by *Neomysis integer* after the time of the expected high tide, which indicates that there is an endogenous ebb-phased circa-tidal rhythmicity. This result contrasts with the above described field data to prevent displacement of the animals out of the estuary. In general, mysids (also *N. integer*) exhibit positive rheotactic behaviour and swim forward into the current at low current velocities (Parker and West, 1979; Hough and Naylor, 1992; Roast *et al.*, 1998). At velocities greater than 12 cm s^{-1}, position maintenance of *N. integer* breaks down (Roast *et al.*, 1998) and animals are displaced by the current. In the East Looe river estuary (UK), *N. integer* is generally only present in areas where current velocities do not exceed 15 cm s^{-1} (Roast *et al.*, 1998; Lawrie *et al.*, 1999). Persistent swimming throughout the ebb tide under endogenous control, coupled with the rheotactic behaviour prevents the *N. integer* individuals occupying shallow zones of stranding in a pool in the intertidal. Aggregations of *N. integer* in imminent risk of stranding initially head into the current, but as the water level drops, and before a pool is completely cut off, the species swims with the current draining from the pool and enters the stream before finally re-orientating and swimming into the current (Hough and Naylor, 1992). In the inner part of Arcachon Bay near the mouth of the l'Eyre river, a substantial part (12 %) of the macrobenthic community of intertidal mudflats sampled during ebb consisted of (stranded) *N. integer* (Bachelet and Dauvin, 1993).

As swimming speed is an important factor in the position maintenance of the species, it is likely to be beneficial for the mysid to utilize any available shelter in order to conserve energy (Roast *et al.*, 1998b). The species aggregates in shallower water with low current velocity (Roast *et al.*, 1998; Lawrie *et al.*, 1999) and in the lee of rocks and macroalgal clumps where water flow rates were less than 10 cm s^{-1} (Hough and Naylor, 1992; Lawrie *et al.*, 1999). In experimental conditions, Roast *et al.* (1998b) observed *Neomysis integer* to enter the boundary layer where lower velocity flows are experienced. This corresponds with field studies, where *N. integer* is generally caught in greatest abundance in near-bottom samples (Hough and Naylor, 1992; Bernát *et al.*, 1994; Köpcke and Kausch, 1996; David *et al.*, 2005; see earlier remark of Fockedey, unpublished). Attachment to the substratum and even shallow burrowing into the sediment are also common means of position maintenance in moving waters (Roast *et al.*, 1998b).

A decreased swimming activity of *Neomysis integer* was demonstrated under conditions of hypoxia and pollution with heavy metals and pesticides (Roast *et al.*, 2000b; 2000c; 2001b; 2002; 2002b). *In situ* this alteration in the swimming activity may be reflected in an altered position maintenance of the population in the estuary (cfr. Schelde?).

2.6 Vertical and horizontal migration

Vertical migration

Diel and tidal vertical migration and distribution patterns of *Neomysis integer* in **estuaries** were described for populations in the Elbe (Bernát *et al.*, 1994; Köpcke and Kausch, 1996; Fockedey, unpublished – EU project MATURE), Severn (Moore *et al.*, 1979), Schelde (Mees, unpublished – EU Project JEEP; Fockedey, unpublished - EU project MATURE), Seine (Zouhiri *et al.*, 1998; Dauvin *et al.*, 2000) and Gironde (Fockedey, unpublished - EU project MATURE). A considerable amount of the *N. integer* population is distributed all over the water column in the turbid reaches of the estuary, especially at the beginning of the flooding tide (just after low water) when the current velocity is low (Köpcke and Kausch, 1996; Fockedey, unpublished). In the Elbe, the animals showed a pronounced day-night rhythm in their vertical distribution pattern (Bernát *et al.*, 1994; Köpcke and Kausch, 1996; Fockedey, unpublished). During daylight hours the mysids remained near the bottom, while during the night equally high numbers were found in bottom and surface waters. In the Seine estuary, the mysids were sampled near the bottom in high abundance only during the day at low tide. At high tide and during the night the densities in the benthic boundary layer were up to seven times lower, due to dispersal into the water column (Zouhiri *et al.*, 1998; Dauvin *et al.*, 2000). In the Westerschelde and Gironde estuaries, *N. integer* did not show a diurnal vertical migration pattern (Fockedey, unpublished).

Diel vertical migration of *Neomysis integer* in the **Baltic** is well documented (Jansson and Källander, 1968; Jansen, 1985; Arndt and Jansen, 1986; Rudstam *et al.*, 1986; Debus *et al.*, 1992). In deeper stations of the Baltic *N. integer* stays near the sediment during daytime and migrates to the surface with the beginning of the evening twilight (Rudstam *et al.*, 1986; Debus *et al.*, 1992).

Also the diurnal vertical migration patterns of *Neomysis integer* in shallow **brackish lakes** are well described (Beattie and de Kruijf, 1978; Bremer and Vijverberg, 1982; Irvine *et al.*, 1993; Aaser *et al.*, 1995). From noon until sunset, virtually 100 % of the population is living near the bottom. At midnight the animals are more or less evenly distributed over the water column. At sunrise a substantial part of the population is still present in the water column. Densities of *N. integer* caught at the bottom (with bottom traps) during daytime can be 2 to 3-fold greater than at night, while daytime densities based on vertical hauls are 4-fold less than at night (Aaser *et al.*, 1993). There are no evident differences in the population structure over the water column at night, indicating that all stages and both sexes perform the vertical migration to the same extent (Beattie and de Kruijf, 1978). The vertical migration is more pronounced in summer than in late autumn and winter (Beattie and de Kruijf, 1978). Through their vertical migrations *N. integer* is considered to form a direct link between the benthos and the pelagos (Elliott *et al.*, 2002).

Horizontal migration and distribution patterns

The **longitudinal distribution** of the population of *Neomysis integer* along the estuary can change in response to seasonal changes in the position of the salinity gradient and the maximum turbidity zone, which in turn are influenced by the long-term seasonal cycle of freshwater run-off (Moore *et al.*, 1979; Sorbe, 1980; Eisma, 1986; Köpcke and Kausch, 1996; Allen *et al.*, 2003). In winter and spring, during high run-off, the *N. integer* population of the Elbe estuary was geographically situated more downstream than in summer. However, the salinity range where the species is present varied from 1.2 – 27.7 psu in winter to a more compressed salinity zone at 0.6 – 3.4 psu in summer (Köpcke and Kausch, 1996). In the Schelde, however, the salinity zones are relatively stable and the *N. integer* population remained in a narrow zone of 20 km close to the Dutch-Belgian border due to adverse oxygen conditions more upstream, regardless of salinity (Mees *et al.*, 1994). Hough and Naylor (1992) designated the middle part of the Conwy as a distribution centre for *N. integer*, from which the species spread upstream and downstream in the estuary as their numbers increased during summer. *N. integer* is also reported to perform active seasonal migration along the longitudinal axis of the estuary (Kühl and Mann, 1969; Schuchardt *et al.*, 1989).

In the estuarine environment, *Neomysis integer* actively migrates during certain periods of the **tidal** cycle from the subtidal channel towards the sheltered shores with low current velocities (Astthorsson, 1980; Hough and Naylor, 1992; Mees *et al.*, 1993b; Köpcke and Kausch, 1996; Speirs *et al.*, 2002; see former paragraphs). Speirs *et al.* (2002) could demonstrate that the high numbers of *N. integer* over the immersed intertidal mudflats were not the result of a passive diffusion process, nor the result of an attraction to the organically rich sediments as feeding grounds, nor a predator avoidance response, but were the result of an active migration to areas with a low current velocity.

Neomysis integer is known to make extensive use of **salt marshes** on the margins of estuaries (Ralph, 1965; Jansen, 1985; Mees *et al.*, 1993b; Cattrijsse *et al.*, 1994; Hampel *et al.*, 2003; 2003b). The non-vegetated subtidal channels of European marshes do not provide shelter to predation. On the contrary, migration into the intertidal marsh is associated with an increased predation pressure on the mysids by juvenile and adult fish and shrimp, using the marsh respectively as a nursery and feeding ground (Cattrijsse *et al.*, 1994; Dean *et al.*, 2005). In the Schelde estuary, *N. integer* follows the edge of the tidal cycle and makes maximal use of the salt marsh from the first hour to the last hour of the high water period (Cattrijsse *et al.*, 1994; Hampel *et al.*, 2003). Migration in and out of the marsh is maximal when current velocities are minimal, and is considered to be an – at least partly – active process (Cattrijsse *et al.*, 1994). Possibly, the marshes of the Schelde estuary serve as areas favoured by *N. integer* for reproductive purposes. Smaller individuals were more frequently found in the marsh area and peak abundance of juveniles occurred earlier in the season than in the subtidal channels of the estuary (Cattrijsse *et al.*, 1994; Mees *et al.*, 1993). Probably the large amount of detritus inside the marsh creeks attracts the mysids as well (Zagursky and Feller, 1985; Cattrijsse *et al.*, 1994).

Neomysis integer living in the coastal waters of the Baltic Sea performs **seasonal horizontal migrations** from the shallow littoral zone to deeper water when temperatures became too low (< 2 °C) or too high (> 20 °C) (Kinne, 1955; Muus, 1967; Jansen, 1979; Arndt and Jansen, 1986; Rudstam *et al.*, 1986; Thiel, 1992; Välipakka, 1992; Jansen, 1993). Similar observations were made for *N. integer* inhabiting brackish lakes and ponds (Vorstman, 1951; Barnes *et al.*, 1977).

Part of the latter populations can make seasonal horizontal migrations towards almost freshwater environments in the connected ditches and channels. However, *N. integer* is dependent on higher saline waters to complete its reproductive cycle and is not present all year in these fresh water bodies (Haesloop and Scheffel, 1991).

Neomysis integer living in the Baltic performs additional **daily horizontal migrations** from the shallow shores towards the central part of the water body at night. In the daytime, *N. integer* forms large shoals (up to 600 ind m^{-2}) in the shallow nearshore regions of the Baltic Barther Bodden to reduce the danger of predation by visually predating fish. At that moment the organisms are restricted to feed on detritus. At night, when young and small fish do not feed, the swarms break up and *N. integer* migrates to the offshore region to search actively for zooplankton (Debus *et al.*, 1992).

In the stagnant water of brackish lakes and ponds, large variations in the horizontal distribution pattern of *Neomysis integer* are described. These result from the swarming behaviour and the **bottom substrate preferences** of the species (Beattie and de Kruijf, 1978; Bremer and Vijverberg, 1982). In the Slotermeer (The Netherlands), *N. integer* preferred sand substrates with a thin layer of fine mud on top over mudless sand or peat substrates (Bremer and Vijverberg, 1982). In Bergumermeer (The Netherlands), the densities of *N. integer* were on average 3 times higher on the hard sandy bottoms in comparison with the bottoms of soft mud or peat (Beattie and de Kruijf, 1978). In loch Furnace (Ireland), *N. integer* forms 1 metre wide and 1 metre deep band at a few decimetres from the water surface above steep bouldery shores (Parker and West, 1979). Where the bottom was weedy the shoals tend to be more concentrated, while in more exposed areas the shoals tend to be deeper. In shallow parts with stands of *Phragmites* the distribution of *N. integer* is patchier, being associated with bottom features like occasional stones or plants.

3 ROLE OF *Neomysis integer* IN THE FOOD WEB

In the brackish part of estuaries, the high standing stock of many functional units (hyperbenthos, but also epibenthos, mesozooplankton, and both demersal and pelagic fish) is explained by the import of large quantities of allochtonous organic matter (natural inputs and discharges from various effluents). The food web has been described as heterotrophic, *i.e.* respiratory processes exceed the *in situ* autotrophic production and the food web tends to be based on detritus (Hummel *et al.*, 1988; Hall and Raffaelli, 1991; Hamerlynck *et al.*, 1993; Heip *et al.*, 1995). This compares with the autotrophic food chain in the mouth of the estuary, where primary production lies at the basis of the food web (Hamerlynck *et al.*, 1993). Heterotrophic bacteria are not only responsible for the remineralisation of the nutrients (Goosen *et al.*, 1992); they simultaneously constitute the basis of the food web for higher trophic levels (Azam *et al.*, 1983; Sherr and Sherr, 1988; Billen *et al.*, 1990). Detritus and/or their associated bacteria are consumed, directly or indirectly, by the microzooplankton, the mesozooplankton and the hyperbenthos (Fenchel, 1988; Hamerlynck *et al.*, 1993). Fish and epibenthic macro-invertebrates can then feed at this 'secondary energy level'. There is a great need for the description of the feeding ecology of key species in estuarine environments.

3.1 Predators

Mysids are important food items for many demersal and pelagic fish, larger epibenthic crustaceans and wading bird species (Mauchline, 1980). In particular environments, where mysids are present in large numbers (e.g. coastal and estuarine waters), they form an important link in the food web. Often they replace copepod prey progressively in the diet of fish during ontogenic development from the postlarval to juvenile stages (Sorbe, 1981). In estuaries, the hyperbenthos, and mysids in particular, often dominate in the diet of 0-group individuals of commercially important fish and also sustain high densities of non-commercial demersal fish (e.g. gobies), which are an important prey for the larger size classes of the commercial species (Elliott *et al.*, 2002). Despite the differences in the species composition of the fish fauna between estuaries, similar feeding guilds can be distinguished over a wide geographical range. Each estuary has a dominant food web that relies on small detritivore epibenthic crustaceans; in some cases this can be mysids, while in others it relies on gammaridean amphipods or even isopods (McLusky and Elliott, 2004). A mysid feeding guild is described for several estuaries (Costa and Elliott, 1991; Mees and Jones, 1997; Hostens and Mees, 1999; Elliott *et al.*, 2002), although it is replaced by a gammaridean feeding guild in e.g. the Humber (Elliott, personal communication) and in Scottish Loch systems (Kislalioglu and Gibson, 1977), despite the presence of large densities of *Neomysis integer* (Mauchline, 1971; Budd, 2002). Next to these small epibenthic crustaceans, larger epibenthic crustaceans (like *Crangon crangon* or *Palaemonetes varians*) and mesozooplanktonic calanoid copepods (like *Eurytemora affinis*, *Acartia* spp.) also play an important role in the food web of the upper part of estuaries (Costa and Elliott, 1991; Maes *et al.*, 2003). Burke (1995) even suggested that the gradient in mysid densities in North-Carolina estuaries (*Neomysis americana*) can act as a guide for the migration of flounder to their nursery grounds.

The low-salinity reaches of **estuaries**, around the turbidity maximum, have proved their role as a nursery for larval and juvenile stages of marine and freshwater fish species and epibenthic crustaceans (Elliott and Hemingway, 2002). A large biomass of food must be available to sustain the populations of these rapidly growing individuals. In turbid waters, the number of sessile macrobenthic species generally decreases due to burial and/or clogging of their feeding apparatus; macrobenthic prey being largely ignored by fish predators in the upper reaches of the Schelde (Maes *et al.*, 2003). Hyperbenthic animals, like *Neomysis integer*, are present in high densities all over the year (Mees *et al.*, 1994) and certainly contribute to the nursery function of the area (Maes *et al.*, 2003; Hostens and Mees, 1999). Some examples of quantitative studies are available (Table 3) for the estuaries of the Schelde (Hostens and Mees, 1999; Maes *et al.*, 2003), Darss-Zingst (Thiel, 1996), Medway (Van den Broek, 1978), Tagus (Moreira *et al.*, 1992) and Loch Etive (Kislalioglu and Gibson, 1977). Qualitative studies are available for the upper Elbe (Thiel, 2000) and the Forth (Costa and Elliott, 1991).

In the mesohaline part of the **Schelde** estuary (The Netherlands), *Neomysis integer* is preyed upon by at least 15 fish species (Hostens and Mees, 1999). It is a dominant prey item in the stomachs of bib (*Trisopterus luscus*), sand goby (*Pomatoschistus minutus*), Lozano's goby (*P. lozanoi*) and herring (*Clupea harengus*). *N. integer* is also a numerically important food item for whiting (*Merlangius merlangus*), tub gurnard (*Trigla lucerna*), intertidally caught plaice and flounder (*Pleuronectes platessa* and *P. flesus*), sea bass (*Dicentrarchus labrax*), sea snail (*Liparis liparis*), pipefish (*Syngnathus rostellatus*) and hook-nose (*Agonus cataphractus*). For the common goby (*P. microps*), sprat (*Sprattus sprattus*), sole (*Solea solea*) and subtidally caught plaice (*P. platessa*) *N. integer* was only supplementary food. In contrast to the intertidal, the stomachs of subtidally caught flounder never contained *N. integer*. In the upper reaches of the Schelde estuary (power plant of Doel, Belgium) the diet of *Pomatoschistus minutus*, *Anguilla anguilla* and pike perch (*Stizostedion lucioperca*) was dominated all over the year by the mysid species (Maes *et al.*, 2003). *N. integer* and *Mesopodopsis slabberi* are important food supplements for young clupeids (*Clupea harengus* and *Sprattus sprattus*), sea bass (*Dicentrarchus labrax*) and *Pomatoschistus microps* in the Schelde estuary, especially in autumn (Maes *et al.*, 2003).

Next to fish, the very abundant caridean shrimp and prawn (*Crangon crangon*, *Palaemonetes varians* and *Palaemon longirostris*) are also important predators of the estuarine *Neomysis integer* population (Kemp, 1910; Marchand, 1981; Sorbe, 1983b; Mouny *et al.*, 1998; Hostens and Mees, 1999; Maes *et al.*, 2003; Hostens, 2003). They compete for the same resources (mainly *N. integer*) with the 0-group fish in the upper reaches of the estuary (Maes *et al.*, 2003).

In the southern **Baltic Sea** (Darss-Zingst estuary, Germany) *Neomysis integer* is dominant in the diet of pike-perch (*Stizostedion lucioperca*), perch (*Perca fluviatilis*), smelt (*Osmerus eperlanus*), pleuronectids and the sand goby (*Pomatoschistus minutus*), while it is an addition to the diet for the common goby (*Pomatoschistus microps*), roach, three-spined stickleback and herring (Arndt and Jansen, 1986; Thiel, 1996 and references therein).

In **inland water bodies** the typical predators of *Neomysis integer* are three-spined stickleback (*Gasterosteus aculeatus*), smelt (*Osmerus eperlanus*), perch (*Perca fluviatilis*), juvenile pike-perch (*Stizostedion lucioperca*), ruffle (*Gymnocephalus cernua*) and palaemonid shrimp (Bremer and Vijverberg, 1982; Irvine *et al.*, 1993; Søndergaard *et al.*, 2000). Occasionally eel (*Anguilla anguilla*) feeds on *N. integer* when its densities are high and chironomid larval densities are rather low (Bremer and Vijverberg, 1982).

Neomysis integer is also described to be an important prey for birds (Patterson, 1905; Cramp, 1977; 1983; Van De Vijver, 1983): a.o. avocet (*Recurvirostra avosetta*), common goldeneye (*Bucephala clangula)*, common and red-breasted merganser (*Mergus merganser* and *M. serrator)*, black-legged kittiwake (*Rissa tridactyla*), little tern (*Sterna albifrons*), tufted duck (*Aythya fuligula*), shoveler (*Anas clypeata*), green sandpiper (*Tringa ochropus*), common sandpiper (*Actitis hypoleucos*), eared grebe (*Podiceps nigricolli*), and non-specified wading birds. The low density of *N. integer* populations in several brackish inland waters was significantly related to the high density of foraging birds (Van De Vijver, 1983).

In laboratory feeding experiments, Winkler and Greve (2004) demonstrated the intraguild predation of the mysid *Praunus flexuosus* on juvenile (< 4 mm) *Neomysis integer*. However, *P. flexuosus* preferred calanoid copepods over *N. integer* in mixed prey conditions since they were easier to catch. In the Baltic the isopod *Saduria entomon* predates on *N. integer*, but laboratory and field experiments demonstrated that the large isopod caught more efficiently its own juveniles compared to the juvenile mysids (Leonardsson, 1991).

Estuaries are believed to provide non-limiting resources to the level of consumers (Barnes, 1974). As a result, estuarine fish often feed opportunistically on copepods, mysids and caridean shrimp (Hostens and Mees, 1999). The high productivity and standing stock of invertebrate prey may cause high niche overlap between the species since there is no need to partition the available food resources (Pianka, 1982).

Table 3: Some studies demonstrating the role of *Neomysis integer* as food for estuarine macro-invertebrates and fish. For the quantitative studies the degree of dominance (including a measure indicating the importance in the diet) is given.

Scientific name	Common name	Estuary	Country	Dominance in diet	Measure of importance	Scource
Crangon crangon	Brown shrimp	Schelde – subtidal	The Netherlands	D+	%O=50%	Hostens, 2003
		Schelde - march	The Netherlands	0 (<10mm SL)	-	Cattrijsse et al., 1997
Palaemon longirostris	Delta prawn	Seine	France	D+ (spring)	%N= 24-27%	Mouny et al., 1998
Pomatoschistus microps	Common goby	Darss-Zingst	Germany	S	RI_i = 6%	Thiel, 1996
		Schelde – subtidal	The Netherlands	S	%O=16%	Hostens and Mees, 1999
		Schelde – marsh	The Netherlands	D-	%N= 15%; %G= 39%	Hampel and Cattrijsse, 2004
		Schelde – power station	Belgium	S (esp. autumn)	%O=3%; %W=7%	Maes et al., 2003
		Seine	France	D+ (esp. 39-50 mm)	%N=57%	Mouny et al., 1998
		Ythan	UK, Scotland	S (mainly in summer)	%O=9%	Healey, 1972
		Tagus	Portugal	D+	no information	Moreira et al., 1992
Pomatoschistus minutus	Sand goby	Darss-Zingst	Germany	D	RI_i = 13%	Thiel, 1996
		Schelde	The Netherlands	D- (SL>30mm)	%O=59%	Hostens and Mees, 1999
		Schelde – power station	Belgium	D	%O=33%; %W=38%	Maes et al., 2003
		Tagus	Portugal	D+	no information	Moreira et al., 1992
Pomatoschistus lozanoi	Lozanoi's goby	Schelde – subtidal	The Netherlands	D+	%O=57%	Hostens and Mees, 1999
Dicentrarchus labrax	Sea bass	Schelde – subtidal	The Netherlands	D-	%O=22%	Hostens and Mees, 1999
		Schelde – salt marsh	The Netherlands	D	%A=40%; %G=70%	Cattrijsse, 1994
		Schelde – power station	Belgium	S	%O=14; %W=13%	Maes et al., 2003
		Tagus	Portugal	D+	no information	Moreira et al., 1992
Osmerus eperlanus	Smelt	Darss-Zingst	Germany	D	RI_i = 13%	Thiel, 1996
Pleuronectes flesus	Flounder	Medway – power station	UK	0	%O=0%	Van den Broek, 1978
		Schelde – subtidal	The Netherlands	0	%O=0%	Hostens and Mees, 1999
		Schelde – intertidal	The Netherlands	D-	%O=35%	Hostens and Mees, 1999
		Schelde – power station	Belgium	S	%O=21%; %W=38%	Maes et al., 2003
		Ythan	UK, Scotland	S	%N=<5%	Summers, 1980
Pleuronectes platessa	Plaice	Medway – power station	UK	0	%O=0%	Van den Broek, 1978
		Schelde – subtidal	The Netherlands	S	%O=4%	Hostens and Mees, 1999
		Schelde – intertidal	The Netherlands	D+	%O=21%	Hostens and Mees, 1999
Solea solea	Sole	Schelde	The Netherlands	S	%O=3%	Hostens and Mees, 1999
Clupea harengus	Herring	Darss-Zingst	Germany	S/D	RI_i = 9%	Thiel, 1996
		Schelde	The Netherlands	D-	%O=62%	Hostens and Mees, 1999
		Schelde – power station	Belgium	S (esp. autumn)	%O=24%; %W=25%	Maes et al., 2003
Sprattus sprattus	Sprat	Schelde	The Netherlands	S	%O=10%	Hostens and Mees, 1999
		Schelde – power station	Belgium	S (esp. autumn)	%O=17%; %W=2%	Maes et al., 2003

Table 3 (cont.)

Scientific name	Common name	Estuary	Country	Dominance in diet	Measure of importance	Scource
Anguilla anguilla	Eel	Schelde – subtidal	The Netherlands	0	%O=0%	Hostens and Mees, 1999
		Schelde – power station	Belgium	D	%O=57%; %W=68%	Maes et al., 2003
Gasterosteus aculeatus	Threespined stickleback	Darss-Zingst	Germany	S (not for O-group!)	RI_i = 3-4%	Thiel, 1996
Spinachia spinachia	Fifteen-spined stickleback	Loch Etive	W Scotland, UK	S	%N=12%	Kislalioglu and Gibson, 1977
Liparis liparis	Sea snail	Schelde	The Netherlands	D-	%O=31%	Hostens and Mees, 1999
Stizostedion lucioperca	Pike-perch	Schelde – power station	Belgium	D	%O=40%; %W=63%	Maes et al., 2003
Perca fluviatilis	Perch	Darss-Zingst	Germany	D	RI_i = 15-30%	Thiel, 1996
Rutilus rutilus	Roach	Darss-Zingst	Germany	S	RI_i = 1%	Thiel, 1996
Syngnathus rostellatus	Pipefish	Schelde	The Netherlands	D	%N=80%; %G=90%	Delbaere, unpublished
Syngnathus typhle	Pipefish (deep-nosed)	Tagus	Portugal	D+	no information	Moreira et al., 1992
Syngnathus abaster	Pipefish	Tagus	Portugal	D-	no information	Moreira et al., 1992
Syngnathus sp.	Pipefish	Tagus	Portugal	D-	no information	Moreira et al., 1992
Merlangius merlangus	Whiting	Medway – power station	UK	D- (< 80mm SL)	%O=21%; %A=12%	Van den Broek, 1978
		Schelde	The Netherlands	D-	%O=19	Hostens and Mees, 1999
Trisopterus luscus	Bib	Medway – power station	UK	D- *(< 100 mm SL)*	%O=22%; %A=19%	Van den Broek, 1978
		Schelde – subtidal	The Netherlands	D+ (SL: 50-130mm)	%O=57%	Hostens and Mees, 1999
Trigla lucerna	Tub gurnard	Schelde – subtidal	The Netherlands	D+	%O=33%	Hostens and Mees, 1999
Agonus cataphractus	Hook-nose	Schelde	The Netherlands	D-	%O=25%	Hostens and Mees, 1999
Ciliata mustela	Five-bearded rockling	Schelde	The Netherlands	S	%O=14%	Hostens and Mees, 1999

D+: Dominant food item (>50%); **D-**: Subdominant (10-50%); **S**: Supplementary food item; **0**: absent; **%W** = annual average of percentage biomass of the stomach content; **%A** = annual average of percentage abundance; **%N** = numerical abundance; **%O** = frequency of occurrence; **%G** = gravimetrical abundance; **RI_i** = relative importance index according to George and Hadley (1979)

E.g. while the feeding niches of *Pomatoschistus minutus* and *P. lozanoi* in the coastal zone are spatially segregated through interspecific competition, this is not the case in the brackish water zone, where mysids are highly abundant and food is unlikely to be a limiting factor. Here both species prefer to feed on *Neomysis integer* (Hostens and Mees, 1999). Although the resources meet the annual food demand of the dominant fish species in the Schelde estuary, Maes *et al.* (2003) found some degree of trophic segregation between the dominant members of the estuarine fish assemblage.

For some predators, like gadoids, *Neomysis integer* is only a preferred food item during a particular period in the life cycle. As the fish grow larger, an ontogenic shift from calanoid copepods to *N. integer* and amphipods has been described for bib (*Trisopterus luscus*) and whiting (*Merlangius merlangus*) (Van den Broek, 1978; Hostens and Mees, 1999). Later in their life they shift their diet to shrimp and small fish. Simultaneously the gadoids migrate out of the estuary to spend the rest of their lives in coastal areas and the open sea. Mysids are still encountered in stomach contents, but only the more marine species *Schistomysis spiritus* and *S. kervillei* (Hamerlynck and Hostens, 1993).

3.1.1 Predation pressure on *Neomysis integer*

A comparison between the annual consumption of the dominant fish species (610 mgADW m^{-3} y^{-1}) and the annual production of estuarine copepods (1600 mgADW m^{-3} y^{-1}; Escaravage and Soetaert, 1995) and *Neomysis integer* (300 mgADW m^{-2} y^{-1}; Mees *et al.*, 1994) in the Schelde **estuary,** suggest that food is not in short supply for the predators (Maes *et al.*, 2003). *N. integer* is consumed throughout the year by estuarine fish (Maes *et al.*, 2003). The impact of fish and macro-invertebrates on the local *N. integer* population is considerd to be rather low (1 % of the annual standing stock) and top-down control is unlikely (Hostens and Mees, 1999). Maes *et al.* (2003), on the other hand, found maximal consumption by fish on *N. integer* to coincide with minimal production and standing stock of the prey item (autumn-winter) in the upper Schelde estuary and concluded that predation sometimes may lead to a rapid depletion of the resources (a.o. *N. integer*), especially in years of high fish recruitment.

The impact of predation by young and small fish on the population of *Neomysis integer* in the Barther Bodden (southern **Baltic Sea**) is high and the mean annual consumption of *N. integer* mounts up to 9 gWW m^{-2}. This corresponds to 94 – 99 % of the total annual production of *N. integer* population (Thiel, 1992; 1996). In summer, *Clupea harengus* and *Osmerus eperlanus* consumed more than 5 times the local production of *N. integer* (Franek, 1988; 1989).

3.1.2 Predator avoidance mechanisms

For small aquatic invertebrates, predation is an important mortality pressure. The ability to detect the presence of predators and to adjust behaviour accordingly is a major advantage (Lindén *et al.*, 2003). The following abilities help *Neomysis integer* to diminishing the predation risk: vertical and horizontal migration patterns, swarming behaviour, well developed visual cues, mechanical and chemical predator detection, adapted feeding and swimming behaviour, and a direct escape response by tail flipping.

In brackish lakes and the Baltic, *Neomysis integer* performs diel vertical migrations (see before) to decrease the predation risk. They live in the dark, near bottom layers at daytime to avoid visual predators, and rise to the surface to feed at night time (Mauchline, 1980). In the daytime, *N. integer* is known to form large shoals in the shallow nearshore regions (Mauchline, 1971c) to reduce the danger of predation by visually predating fish. In the night time, when young and small fish do not feed, these swarms break up and *N. integer* migrate to the offshore region to search actively for zooplankton (Debus *et al.*, 1992).

The schooling behaviour of mysids is considered to be an effective anti-predator mechanism (Clutter, 1969; O'Brien and Ritz, 1988). If schools are attacked, the confusion effect serves to protect individual members and reduces the capture efficiency (Magurran, 1990). Information about approaching predators can be obtained through other school members, without each mysid needing to individually confirm the extent of the danger (Magurran, 1990).

In the littoral, mysids (like *Neomysis integer*) can use their good visual abilities (Fulton, 1982) in the well-lit shallow water to detect predators and derive an optimum escape direction. In darker or turbid waters, mechanical reception (Rademachers and Kils, 1996) and chemical reception of kairomones excluded by predators (Lindén *et al.*, 2003) are relatively more important. The eye function of *Neomysis integer* is studied by Hallberg *et al.* (1980) and Lindström (1992, 2000).

Another reaction described for *Neomysis integer* to a predator attack, is the direct escape response by tail flipping in which *N. integer* escapes at a high speed (796 mm s^{-1} or 80 body lengths s^{-1}) by flexion of the 3rd abdominal segment (Kaiser *et al.*, 1992b; Rademacher and Kils, 1996). Mysids like *N. integer* can be ranked with euphausiids and calanoid copepods as one of the fastest members of the zooplankton (Rademachers and Kils, 1996). The high-speed escape response by tail flipping seems to be very effective and only 25 % of the predator attacks were successful under laboratory condition (Rademachers and Kils, 1996). The tail flip itself seems to expose the telson to the bite of the predator, making it quite vulnerable for mechanical damage, even if the attack is not effective. The presence of *N. integer* individuals with an altered telson morphology (< 1 – 9 %; Holmquist, 1957; Chojnacki and Ciupinski, 1986; Mees *et al.*, 1995b) is considered to be a result of damage due to the unsuccessful predation attacks and subsequent regeneration of the damaged parts. The alternative theory (Norman, 1892; Holmquist, 1957; Chojnacki and Ciupinski, 1986), that the aberrant telson forms would result from mutations resulting from environmental pollution, was refuted by an amputation/regeneration experiment performed by Mees *et al.* (1995b), but cannot be ruled out completely. In contrast to the large escape reaction in the case of a fish predator attack, *N. integer* did not show any escape reaction at all in the case of *Praunus flexuosus* attacking (Winkler and Greve, 2004). Especially the juveniles of *N. integer* are strongly suppressed by this intraguild predation.

3.2 Diet of *Neomysis integer*

There is a great need for the description of the feeding ecology of key species (like *Neomysis integer*) in estuarine environments for the development of accurate C-flux models and the description of detritus based food web patterns, including the quantification of transfer coefficients. To date, few studies have taken hyperbenthos or mysids into account. Notable exceptions are Hall and Raffaelli (1991) and Soetaert and Herman (1995). Hyperbenthic mysids are thought to provide a significant link in the exchange of organic matter between the benthic and pelagic systems of estuaries, however, data on the contribution of *N. integer* to such food fluxes are limited (Roast *et al.*, 2000). The trophic position assigned to mysids and the hyperbenthos in general seems to be guessed rather than derived from field data.

Mysidacea are generally described as omnivores, feeding on detritus, algae and zooplankton (*e.g.* Mauchline, 1980). They can feed selectively on different zooplankton species and size groups (*e.g.* Cooper and Goldman, 1980; Murtaugh, 1981a; 1981b), and thus have the potential of structuring zooplankton communities (Fulton, 1982; Rudstam *et al.*, 1989). The phytoplankton (Kost and Knight, 1975; Siegfried and Kopache, 1980) and tychoplankton (Webb *et al.*, 1987; Wooldridge, 1989) are possibly also influenced through selective grazing by mysids. Mysid predation has even been reported as a possible control on meiofaunal densities (Siegfried and Kopache, 1980; Grossnickle, 1982; Johnston and Lasenby, 1982). Most mysids utilize organic detritus to a considerable extent and they can be responsible for the remineralisation of a substantial proportion of the non-refractory detritus (Kost and Knight, 1975; Jansen, 1985b).

3.2.1 Qualitative diet descriptions

Literature on the diet of the omnivorous *Neomysis integer* is scarce, and often only qualitative information is available. According to Lucas (1936) and Tattersall and Tattersall (1951) the species grazes on suspended organic detritus and/or planktonic diatoms. According to these authors the species only feeds on living copepods, dead mysids or amphipods when concentrations of other suspended food items are too low.

Later studies describe *N. integer* as an omnivore, consuming bottom detritus, organic matter in suspension, phytoplankton (a.o. diatoms), mesozooplankton (rotifers, calanoid and harpacticoid copepods), amphipods, carrion, fragments of leaves and of macroalgae, spores and seeds, insects and insect larvae and sand grains (Vorstman, 1951; Mauchline, 1971; 1980; Sorbe, 1980; Astthorsson, 1980; Jansen, 1985b). *N. integer* however prefers animal food (Kinne, 1955; Uitto *et al.*, 1995). In some locations phyto- and zoobenthos, like benthic diatoms, meiofaunal nematodes, harpacticoids and ostracods, amphipods, chironomids, and oligochaets, are present in stomach contents of *Neomysis integer* (Astthorsson, 1980; Bremer and Vijverberg, 1982; Haesloop, 1990; Speirs *et al.*, 2002; Vilas and Fockedey, unpublished).

In monospecific laboratory cultures, *Neomysis integer* feeds on dead or immobile individuals, just released juveniles, shed moults and faecal pellets (Vorstman, 1951; Molloy, 1958; Raymont and Krishnaswamy, 1960; Parker and West, 1979; Astthorsson, 1980; Sorbe, 1980; Kuhlman, 1982; Weisse and Rudstam, 1989; Roast *et al.*, 2000; Winkler, 2000; Verslycke and Janssen, 2002; Fockedey *et al.*, in press – Chapter 3). It can survive in the laboratory given a monospecific or mixed diet of *Artemia* nauplii, phytoplankton (*Nannochloris* spp.) and Cladocera like *Daphnia* spp. (Kuhlmann, 1984; Roast *et al.*, 1999), but it also effectively feeds on barnacle larvae and harpacticoid copepods (Mauchline, 1971) or oligochaetes (Haesloop, 1990). Astthorsson (1980) sustained the culture with a mixture of ground mussel tissue, *Enteromorpha*, detrital mud and *Artemia* nauplii. Raymont *et al.* (1964; 1966; 1968) kept *N. integer* for several weeks without additional food. They fed on the micro-organisms and detritus present in the water from which they were collected.

3.2.2 Feeding modes

Neomysis integer is a skilful swimmer and gathers small prey items, phytoplankton and suspended detrital material with the endopodites of the thoracopods, while simultaneously generating feeding currents with the exopodites of the thoracopods (Lucas, 1936; Tattersall and Tattersall, 1951; Astthorsson, 1980; Espeel, 1982). Furthermore, *N. integer* feeds raptorially on mesozooplankton and benthic invertebrates (Astthorsson, 1980; Mauchline, 1980; Bremer and Vijverberg, 1982). In brackish lakes the species grazes upon periphyton on the submerged plant (Irvine *et al.*, 1993; Bales *et al.*, 1993).

Neomysis integer feeds on the upper layer of the sediment substratum by stirring it up and feeding, both by filtering and raptorially, in the clouds of particles suspended (Raymont *et al.*, 1964; Parker and West, 1979; Astthorsson, 1980). The species is also able to collect aggregations of surface sediment prior to ingestion (Roast, 1997; Roast *et al.*, 2000; Roast *et al.*, 2004). While feeding according to this mode *N. integer* can actually contribute to the turbidity of its environment (and, more specifically, the maximum turbidity zone), either by de-stabilising the sediment surface by its feeding behaviour and so enhancing erosion rates or, by actively increasing the SPM due to sloppy feeding on sediment aggregates collected at the sediment surface (Roast *et al.*, 2004).

3.2.3 Quantitative diet descriptions

⇨ Stomach content analyses

Performing quantitative stomach content analyses of mysids is the most appropriate way to obtain information of the amount of food ingested in the field. This information is scarce for *Neomysis integer*, and is often missing details on the used methodology and results. Generally, the dietary items present in the gut are simply counted or recorded as present. Often only body parts of the larger zooplankton are found in the stomachs of *N. integer* as well as amorph detrital material, both hampering quantitative analyses. One study expresses the gut content of *N. integer* in terms of biomass (Bremer and Vijverberg, 1982). Biomass of the prey was derived from morphometric and length-wet weight regressions for zooplankton, and biomass of the ingested algal cells was derived from their bio-volume (assuming a specific weight of 1.0). The information available on quantitative stomach analyses of *N. integer* concerns populations from inland water bodies (Bremer and Vijverberg, 1982) and the Baltic Sea (Jansen, 1985b; Arndt and Jansen, 1986). Quantitative diet information is generally lacking for the maximum turbidity zone of estuaries.

Stomach content analyses were performed by Arndt and Jansen (1986) on *Neomysis integer* from the southern **Baltic Sea**. The diet composition was 53 % detritus, 37 % animal food, 6 % phytoplankton and 4 % sand grains. In **brackish lakes** *N. integer* feeds predominantly on zooplankton, plant detritus and algae (Bremer and Vijverberg, 1982; Irvine *et al.*, 1993). In terms of biomass, the diet consisted of more than 95 % detritus and animal food (Bremer and Vijverberg, 1982), mainly *Bosmina* sp., nauplii and copepodites of cyclopoids and calanoids. Rotifers and oligochaetes were taken occasionally. In numerical terms, algae (mainly benthic diatoms) were a very abundant food item, but their share in the biomass of the total gut filling was very small. *N. integer* feeds on filamentous blue-green algae (like *Oscillatoria*) and is capable of actively breaking down the longer algal filaments to smaller bits. Bremer and Vijverberg (1982) analysed only gut contents, *i.e.* faecal pellets; the content of the stomach itself was not included in their analysis.

In the Weser **estuary** *Neomysis integer* preferentially consumes animals prey (Haesloop, 1990). Next to zooplankton (mainly *Eurytemora affinis*), other prey were consumed too (*Corophium lacustre*, small gammarids, oligochaets and chironomids) as well as diatoms, macroalgae (*Enteromorpha* spp.) and macrophyte detritus. Sorbe (1980) described semi-quantitatively, and without giving further details, the diet of *N. integer* in the Gironde estuary. It consisted mainly of macrophytal detritus and benthic diatoms. Zooplankton was not considered important. In the intertidal areas of the Ythan, *N. integer* is a benthic feeder as sand grains, endobenthic harpacticoids (15 – 20 ind mysid^{-1}), nematodes and ostracods were the main dietary components (Astthorsson, 1980; Speirs *et al.*, 2002), while phytoplankton and other plant material (fragments, spores, and seeds) were eaten incidentally (Astthorsson, 1980).

⇨ **Fullness index**

Bremer and Vijverberg (1982) considered the alimentary track of *Neomysis integer* as a tube (without taking the spherical stomach into account) and determined its fullness by estimating the total amount of food (*i.e.* faecal pellets) present in the gut at a certain moment as a percentage of its total volume. Calculated in this way, the fullness index of *N. integer* in the brackish lake Slotermeer was used to monitor feeding intensity over a 24h cycle (see later paragraph). Astthorsson (1980) evaluated the quantity of food in the stomachs of *N. integer* on an arbitrary scale from 0 to 3. Throughout the year the majority of the mysids had a stomach fullness index of 3, reflecting that *N. integer* does not experience food shortage in the Ythan estuary. However, both techniques are subjective and do not deliver firm or detailed results.

A stomach fullness index, as the weight of the stomach relative to the weight of the animal, can give a better indication on the species' feeding periodicity and feeding intensity when studied at regular intervals over a certain time span. One can even calculate the feeding rate or ingestion rate from weight-based fullness index data by taking the gut passage time (*i.e.* gastric evacuation rate, turnover time) into account. An assumption is that animals only feed on one type of food and that they feed continuously. If the animals do not feed continuously, but in discrete meals, it is necessary to know the daily ration and the periods of feeding activity. Different calculation methods are available in fisheries research, but they have never been applied to animals as small as mysids (Eggers, 1977; Elliott and Persson, 1978). Fockedey and Mees (1999 – Chapter 2) applied the fullness index technique for the first time with *Neomysis integer* and used it to describe latitudinal, sexual and ontogenic variation in the diet, as well as seasonal and diurnal variation (Fockedey, unpublished – EU MATURE). By using the same technique, the diet of *N. integer* was compared between species (Remerie, 1999; Vilas and Fockedey, unpublished) and between populations of different habitats (Fockedey, unpublished; Soselisa, 1994; Fockedey, unpublished).

⇨ **Ontogenic shifts and sexual variation**

An ontogenic shift in the diet of *Neomysis integer* was demonstrated for a Dutch brackish lake (Bremer and Vijverberg, 1982), where the species fed intensively on zooplankton. *N. integer* showed no distinct size selective predation on Cladocera, but the larger cyclopoid copepods were only eaten by the larger mysids. Juvenile mysids (< 5 mm TL) fed more heavily on rotifers than the larger mysids. In an English brackish lake, Irvine *et al.* (1993) found that larger *N. integer* individuals had a higher number of *Eurytemora affinis* in their stomachs.

The size of the ingested *E. affinis* was not related to the size of the mysid. Juvenile *N. integer* of the Gironde estuary fed more on benthic diatoms, while adults had a relatively higher proportion of detritus in their stomachs (Sorbe, 1980). No ontogenic variation in the quality of the diet of *N. integer* could be demonstrated by Fockedey and Mees (1999 – Chapter 2), but smaller individuals consumed less items.

Sexual differentiation in the diet of *Neomysis integer* can be expected as well, as females probably need specific nutritional requirement for the development of the ovaries and the production of viable eggs (Kiørboe *et al.*, 1985). Fockedey and Mees (1999 – Chapter 2) could not demonstrate any sexual variation in the diet quality of *N. integer*, but they did not include gravid females in their study.

⇨ **Temporal variation**

The diet of *Neomysis integer* can vary over different time scales due to tidal, diurnal, monthly, seasonal and interannual variation. However, little information is available and is restricted to the study of the relative proportions of the diet constituents of *N. integer* over the course of the year. In the diet of *N. integer* from the southern Baltic Sea, detritus is more important in wintertime, while animal food is more important in summer (Arndt and Jansen, 1986). In an English pond, the number of higher plant remains was large in early spring in comparison to late spring and summer (Irvine *et al.*, 1993). In the Gironde estuary, the diet of *N. integer* shifts from a dominance of detritus in winter, to benthic diatoms in summer (Sorbe, 1980).

⇨ **Feeding periodicity**

The feeding periodicity and the variation in intensity of feeding can be demonstrated through the study of the variability in the gut fullness and from the frequency of occurrence of empty guts. In the brackish lake Slotermeer, *Neomysis integer*'s feeding activity reached a maximal intensity at sunset. It was still high during the first part of the night, but became low towards the morning and reached a minimum just after sunrise (Bremer and Vijverberg, 1982). *N. integer* is the only mysid from the Schelde estuary feeding at night and daytime. The other mysid species (*Schistomysis kervillei*, *Schistomysis spiritus*, *Praunus flexuosus* and *Gastrosaccus spinifer*) are typically night feeders (Remerie, 1999). More detailed patterns in the feeding intensity, coupled to tidal and diurnal rhythms, have not been studied yet for *N. integer*.

Fockedey and Mees (1999 – Chapter 2) developed a method to perform quantitative diet analyses of *Neomysis integer* individuals taken from the field. The method joins two techniques: (1) a microscopic stomach analysis and (2) a fullness index determination based on weight. After the dissection and preparing of the stomach in a semi-permanent slide, the counting and measurement of food items is further performed using image analysis. The technique includes an analysis of the amorph unidentifiable detritus by EDAX (Energy Dispersive Spectroscopy X-ray Microanalysis). The stomach fullness technique is adopted from fish feeding studies and here applied for the first time on small invertebrates like mysids.

Fockedey and Mees (1999 – Chapter 2) compared the diet of *Neomysis integer* collected from the maximum turbidity zone of the Schelde, Gironde and Elbe in spring. *N. integer* was found to be an omnivore which mainly utilizes the mesozooplankton and detritus carbon pools. In all three estuaries, the diet was dominated by calanoid copepod (up to 10 *Eurytemora affinis* ind^{-1}) and was supplemented with rotifers (esp. in Elbe) and cladocers. Phytoplankton, pollen and benthic organisms, though present in the stomachs, were negligible. Macrophytal detritus and amorphous material, originating from sediment macro-aggregates suspended in the water column or deposited on the sediment surface, were very abundant food items. Fullness indices in the Elbe and Schelde were comparable (< 1) and significantly lower than in the Gironde (1 – 4). A higher fullness index in the Gironde reflects the consumption of higher amounts of detritus in this estuary. No sexual, nor ontogenic shifts, could be demonstrated in the diet quality, nor in the prey size, but smaller mysids consumed less.

Additional measurements were made (Fockedey, unpublished) on the variation in the fullness index of *Neomysis integer* from the subtidal of the Schelde estuary over the course of a year. The lowest indices were measured in spring (< 1) as compared to summer (1.0 – 1.2) and winter (> 1.3). The higher stomach fullness in winter is related to a higher abundance of (macrophytal and unidentifiable) detritus in the stomachs of the mysids. The lower fullness indices in spring and summer were related to a more abundant feeding on higher quality food items like mesozooplankton (*Eurytemora affinis* in spring, *Acartia* spec. in summer).

The variation of the stomach fullness index of *Neomysis integer* was determined for several 24h cycles in the turbidity maximum of the Schelde, Gironde and Elbe (Fockedey, unpublished). Although variations in the fullness index are difficult to relate to diurnal and tidal cycles, the results indicate a continuous feeding over the day (fullness index between 0.8 and 1.4 in Elbe, 1.0 and 1.5 in Schelde, and between 1.8 and 2.9 in Gironde).

The stomach fullness of *Neomysis integer* caught in the surface layers of the maximum turbidity zone of the Schelde (at night) was significantly lower in comparison to the stomach fullness of individuals caught in the bottom layers (Fockedey, unpublished). No such pattern could be demonstrated for mysids living in the maximum turbidity zone of the Gironde estuary.

Vilas and Fockedey (unpublished) used the same techniques to compare the diet of *Neomysis integer* and *Rhopalophthalmus* sp. from the Guadalquivir estuary. *N. integer* was much more omnivorous than the predator *Rhopalophthalmus* sp. and mainly consumed calanoid copepods and detritus. The diet was supplemented relatively more with zoobenthic organisms, like nematodes and harpacticoids, as compared to the Schelde, Elbe and Gironde estuary.

The seasonal variation in the diet of *Neomysis integer* from the brackish pond Galgenweel was investigated as well (Soselisa, 1994; Fockedey, unpublished). The fullness indices of the mysids living in the pond were approximately 5 times as high (5.9 – 7.4) as compared to *N. integer* living in the mesohaline of the Schelde estuary (0.8 – 1.4). High values of the fullness index in winter, summer and autumn were associated with a high abundance of calanoid copepods (*Eurytemora affinis*) in the stomachs. The significantly lower fullness index in spring coincides with a dominance of Cladocera and pollen in the stomach contents of *N. integer*.

3.2.4 Isotope fractionation in the field

Food web structure can be described studying trophic interactions based on gut analysis. The interpretations however, can be biased by the lack of couplings to the microbial food web and direct errors in the diet analysis *e.g.* caused by differences in digestion rate between food types. Natural abundances of stable carbon and nitrogen isotopes can then be used to identify the sources of organic matter, the foraging location of organisms and trophic structures in aquatic food webs. Organisms tend to become enriched in heavy isotopes as compared to their food. Isotopic fractionation data are available from the northern Baltic Proper (Hansson *et al.*, 1997) and the low-salinity zone of the Schelde estuary (De Brabandere *et al.*, 2002 and references therein). Unfortunately, these studies did not include the mysid *Neomysis integer*, albeit the species is present in both systems.

The $\delta^{13}C$ and $\delta^{15}N$ values of subadult (summer) *Neomysis integer* in the Baltic Sea (South of Stockholm) ranged from -23.1 to -21.5 ‰ and 10.2 to 12.6 ‰, respectively (Rolff, 1998; Gorokhova, 1999; Gorokhova and Hansson, 1999). No variation could be demonstrated between sexes, but $\delta^{15}N$ values increased with body size. These ontogenic changes in the isotopic composition can be caused by either decreased growth efficiency with increasing size or by a shift in diet to food from a higher trophic level (Gorokhova and Hansson, 1999). Seasonal variations in $\delta^{13}C$ values might be due to the seasonally varying energy reserves, *i.e.* lipid content.

According to the $\delta^{13}C$ and $\delta^{15}N$ values reported by Rolff (1998) for zooplankton, it is suggested that *Neomysis integer* may be feeding on the largest mesozooplankton, namely older copepodites and adults (Gorokhova and Hansson, 1999). However the cyanobacteria ($\delta^{13}C$ = -22.9 ‰ and $\delta^{15}N$ = 4.5 ‰; Rolff, 1998) and microbially degraded material ($\delta^{15}N$ = 4.5 ‰) present in the water column cannot be ruled out as possible food sources (Gorokhova and Hansson, 1999).

The fractionation of heavy isotopes is a continuous process, whose influence on the isotopic composition of different tissues depends on their growth and turnover rate (Owens, 1987). The fractionation and the speed of incorporation of food in different body tissues (muscle, exuvia) and faeces was studied for *Neomysis integer* by Gorokhova and Hansson (1999). The muscle tissue did not get in balance with the diet isotopic composition, not even after 3 months. Exuvia of *N. integer* were enriched in $\delta^{13}C$ (+1.41 ‰) and depleted in $\delta^{15}N$ (-5.59 ‰) in comparison with muscle tissue, indicating that the exoskeleton is composed of nutrients that are more directly derived from the diet. The relative abundance of carbon isotopes in the excuvia of *N. integer* is in close balance with the carbon isotopic composition of the diet during the time of exoskeleton secretion, *i.e.* the previous intermoult period. Digestion leads to increased $\delta^{13}C$ (+1.4 ‰) and $\delta^{15}N$ (+3.4 ‰) values in the faeces compared to the food. The isotopic composition of each muscle tissue, exuvia or faecal pellets may form a basis for diet reconstruction of field caught mysids (Gorokhova and Hansson, 1999): the δ13C and $\delta^{15}N$ of the faeces mirror the diet over the last few hours, exuvia δ13C values represent nutrient metabolized 2 – 3 weeks ago and muscle tissue integrates the isotopic signal over a relatively long period (weeks to months).

To perform an isotope fractionation study with *Neomysis integer* from the low-salinity, turbid reaches of estuaries would be of great interest. It can confirm earlier conceptual estuarine food webs links based on the stomach analyses of the mysid species itself (Fockedey and Mees, 1999 – Chapter 2) and the higher trophic levels consuming it (Hostens and Mees, 1999; Maes *et al.*, 2003).

3.3 Feeding rate

Feeding rates (Table 4) can be measured directly in laboratory experiments or calculated from stomach content weights combined with gut evacuation time, given the animals feed continuously on one type of food. In the laboratory the ingestion rate (DW of food ingested per time unit) and the egestion rate (DW faecal pellet produced per time unit) can be measured and the assimilation efficiency calculated. While it is well established that the feeding rates of many crustaceans are influenced by various factors including temperature, salinity, weight, gender and food density, few of these factors have been investigated for mysids and specifically for *Neomysis integer* (Roast *et al.*, 2000; Winkler and Greve, 2004).

⇨ Phytoplankton

Experimenting with *Neomysis integer* in very dense diatom cultures, Lucas (1936) measured an average consumption rate of over 1.10^6 (max 6.10^6) *Nitzschia* cells mysid^{-1} h^{-1} (Table 4). The species is feeding much in excess of their actual requirements under these circumstances (Lucas, 1936). They survived optimally at an intermediate food density of 25 – 100 cells mm^{-3}. The filtration rate of *N. integer* on *Chlorella vulgaris* suspensions yielded a mean intake of 0.5 10^6 cells ind^{-1} h^{-1}, corresponding to a specific feeding rate of 108 µgDW mysid^{-1} d^{-1} (Arndt and Jansen, 1986).

Filter feeding on phytoplankton is often measured as the clearance rate (Gauld, 1951) and expressed as the volume filtered by the animals per hour. Astthorsson (1980) performed feeding experiments with *Neomysis integer* feeding on different species of cultured phytoplankton (Table 4). Highest clearance rates were obtained on the dinoflagellate *Prorocentrum micans* (26 µm) and the coccolithophore *Cricusphaera oblongata* (13 µm), respectively 6.6 and 6.7 ml mgDW h^{-1}. Far lower filtering rates were recorded on the diatom *Chaetoceros curnectum* (13 µm) and a further unidentified small chain diatom species (10 µm): 1.7 and 2.4 ml mgDW h^{-1}. No feeding was recorded on the small flagellate *Tetraselmis* sp. (8 µm). Energetic benefit, with a higher carbon intake than respired and excreted during the course of the feeding experiments, was only possible when feeding on *C. oblongata*.

Estimations of feeding rates of *Neomysis integer* on the *in situ* phytoplankton community of the brackish lake Hickling Broad indicated that phytoplankton cells were not an important component in the diet of the species in comparison with the calanoid *Eurytemora affinis* and epiphytic algae (Irvine *et al.*, 1993; 1995). Stomach analyses of *N. integer* in a variety of habitats confirmed the minor role of algae in terms of biomass in its diet (Bremer and Vijverberg, 1982; Irvine *et al.*, 1993; Fockedey and Mees, 1999 - Chapter 2).

⇨ **Zooplankton**

Laboratory experiments and field evidence revealed that *Neomysis integer* feeds extensively on the calanoid copepod ***Eurytemora affinis*** (*e.g.* Aaser *et al.*, 1995; Irvine *et al.*, 1993; Fockedey and Mees, 1999 – Chapter 2; Winkler and Greve, 2004). Experimentally derived predation rates (Table 4) of *N. integer* on a mixture of nauplii and copepodites averaged 23 nauplii and 17 copepodites mysid^{-1} h^{-1} (Irvine *et al.*, 1993). The maximal predation rate on a similar mixture was 52 nauplii and 8 copepodites mysid^{-1} h^{-1} (Aaser *et al.*, 1995). Winkler and Greve (2004) measured a predation rate of maximally 170 copepodites mysid^{-1} d^{-1} by adult *N. integer*, significantly decreasing with decreasing mysid size and lower temperature. Fockedey *et al.* (submitted a – Chapter 5) reports a feeding rate of only 9 copepodites mysid^{-1} d^{-1}. Also ***Daphnia* sp.** is readily taken by *N. integer* (Irvine *et al.*, 1993). The feeding rates did not differ when other prey items were present or not (± 15 daphnia mysid^{-1} h^{-1}). An egg-carrying *E. affinis* female was handled for approximately 2 minutes by *N. integer* (Viitasalo *et al.*, 1998), whereas small cladocerans (like *Bosmina*) could be swallowed in its entirety.

Often ***Artemia* nauplii** are used as animal food for *Neomysis integer* under laboratory culture conditions. The maximal feeding rate of *N. integer* on *Artemia* nauplii amounts to 600 – 800 nauplii d^{-1} for adults (Astthorsson, 1980) and 200 – 300 nauplii d^{-1} for subadults (De Pauw, 1998; Fockedey, unpublished). Feeding rate is lower at a smaller body size and each time when the animals are about to moult (Astthorsson, 1980). The feeding rate increases with the prey density according to a rectilinear model (Astthorsson, 1980). The feeding rate of adult *N. integer* rapidly increases at initial prey concentrations of less than 700 nauplii l^{-1}; while higher prey densities do not longer affect the feeding rate. At prey densities below the maximum feeding rate, *N. integer* appears to search for and find all available *Artemia* nauplii (Astthorsson, 1980). On the contrary adult mysids do not attempt to hunt at low concentrations of calanoid copepod prey (Irvine *et al.*, 1993).

Filter feeding on zooplankton can also be expressed as clearance rate in volume filtered by the animals per time unit (Cooper and Goldman, 1980). It provides an estimate of the proportion of total prey removed by the predator in a given time. Clearance rate values of *Neomysis integer* when feeding on *Eurytemora affinis* are 0.34 – 0.62 l mysid^{-1} h^{-1} for naupliar prey and 0.08 – 0.15 l mysid^{-1} h^{-1} for copepodites (Irvine et el., 1993; Aaser *et al.*, 1995).

Using length-weight regressions of zooplankton (Bottrell *et al.*, 1976; Burkell and Kendall, 1982) or assigned values for the discrete life stages (Lavens, 1978; Aaser *et al.*, 1995) the feeding rates can be expressed as weight-specific feeding rate. When feeding on a mixture of nauplii and copepodites of *Eurytemora affinis*, *N. integer* specific feeding rate varies according to the predator size, the prey density and the temperature between 18 – 137 µgDW mysid^{-1} d^{-1} of 20 – 350 % body C mysid^{-1} d^{-1} (Irvine *et al.*, 1993; Winkler and Greve, 2004). When feeding on daphniid prey, the specific feeding rate varied from 67 – 149 µgDW mysid^{-1} d^{-1} (Irvine *et al.*, 1993).

Laboratory studies on the predation rates of mysids on zooplankton can have quite some artefacts. A homogeneous spread of *Neomysis integer* individuals in an experimental set-up is difficult, since the species appears to be attracted to structures and surfaces (Irvine *et al.*, 1993). Prey like *Artemia*, cladocers and calanoids have the tendency to respond photopositively and to concentrate at the side of the feeding arena where the light intensity is greatest (Astthorsson, 1980; Bergström and Englund, 2004). To make the distribution random and prevent that *N. integer* is able to collect all prey from one concentrated spot, one can work in the dark or obscure the feeding containers (Astthorsson, 1980). The attack rate of *N. integer* on cladocerans is significantly higher in small containers in comparison with large feeding arenas due to a higher encounter rate (Bergström and Englund, 2004).

Table 4: Feeding rates reported for *Neomysis integer* on different food items

Food item	Concentration	Vol (L)	Time (h)	Conditions	Size mysids	Feeding rate	Scource
Nitzschia closterium (30-400 µm)	> 2000 cells ml^{-1} 1000-2000 cells ml^{-1}	? ?	? ?	- -	? ?	1.3 10^6 cells $mysid^{-1}$ h^{-1} 0.7 10^6 cells $mysid^{-1}$ h^{-1}	Lucas, 1936
Chlorella vulgaris (4µm)		?	?	-	?	0.5 10^6 $cells.ind^{-1}.h^{-1}$ =108 µgDW.d^{-1}	Arndt and Jansen, 1986
Prorocentrum micans (26µm)	160 cells ml^{-1}	0.45	12	9°C (10 psu) – dark	4.3 – 7.2 mgDW	5.7 – 7.7 ml mgDW h^{-1} 3000-4300 cells $mysid^{-1}$ h^{-1} 3 -4 µgC $mysid^{-1}$ h^{-1}	Astthorsson, 1980
Cricusphaera oblongata (13µm)	12000 cells ml^{-1}	0.45	12	9°C (10 psu) – dark	4.3 – 7.2 mgDW	5.1-8.9 ml mgDW h^{-1} 160-190 10^3 cells $mysid^{-1}$ h^{-1} 25-30 µgC $mysid^{-1}$ h^{-1}	Astthorsson, 1980
Chaetoceros curnectum (13µm)	3000 cells ml^{-1}	0.45	12	9°C (10 psu) – dark	4.3 – 7.2 mgDW	1.6-1.8 ml mgDW h^{-1} 23-30 10^3 cells $mysid^{-1}$ h^{-1} 2-3 µgC $mysid^{-1}$ h^{-1}	Astthorsson, 1980
chain diatom (10µm)	8000 cells ml^{-1}	0.45	12	9°C (10 psu) – dark	4.3 – 7.2 mgDW	2.0-2.7 ml mgDW h^{-1} 37-70 10^3 cells $mysid^{-1}$ h^{-1} 2-3 µgC $mysid^{-1}$ h^{-1}	Astthorsson, 1980
Tetraselmis sp (8µm)	12700 cells ml^{-1}	0.45	12	9°C (10 psu) – dark	4.3 – 7.2 mgDW	0.6 ml mgDW h^{-1} 50 10^3 cells $mysid^{-1}$ h^{-1} 2 µgC $mysid^{-1}$ h^{-1}	Astthorsson, 1980
Eurytemora affinis	45 N + 39 COP l^{-1} 90 N + 78 COP l^{-1} 180 N + 156 COP l^{-1} ? ? ? ? 174N + 249 COP l^{-1}	4 4 4 6 6 6 6 4.4	1 1 2 5.5 5.5 5.5 5.5 1.2	0.5-2.6 mysids l^{-1}	8-9 mm SL 8-9 mm SL 8-9 mm SL 4 mm SL 6 mm SL 8 mm SL 10 mm SL 9 mm SL	20 N + 7 COP $mysid^{-1}$ h^{-1} 30 N + 11 COP $mysid^{-1}$ h^{-1} 34 N + 10 COP $mysid^{-1}$ h^{-1} 12 N + 11 COP $mysid^{-1}$ h^{-1} 9 N + 14 COP $mysid^{-1}$ h^{-1} 16 N + 17 COP $mysid^{-1}$ h^{-1} 55 N + 30 COP $mysid^{-1}$ h^{-1} 27 N + 44 COP $mysid^{-1}$ h^{-1}	Irvine et al., 1993
Eurytemora affinis	440 AD + COP l^{-1}	0.5 0.5 0.5 0.5 0.5	24 24 24 24 24	10°C – 20 psu – 3 mysids 10°C – 20 psu – 1 mysid 15°C – 20 psu – 5 mysids 15°C – 20 psu – 3 mysids 15°C – 20 psu – 1 mysid	Subadults 5-7 mm Adults 8-17 mm Juvenile 4-5 mm Subadult 5-7 mm Adult 8-17 mm	<5 COP $mysid^{-1}$ day^{-1} 50 COP $mysid^{-1}$ day^{-1} 20 COP $mysid^{-1}$ day^{-1} 40 COP $mysid^{-1}$ day^{-1} 170 COP $mysid^{-1}$ day^{-1}	Winkler and Greve, 2004
Eurytemora affinis	100 N + 100 COP l^{-1} 200 N + 100 COP l^{-1} 400 N + 100 COP l^{-1}	1 1 1	2 2 2	15°C mysid density 3 l^{-1}	?	15 N + 8 COP $mysid^{-1}$ h^{-1} 26 N + 5 COP $mysid^{-1}$ h^{-1} 52 N + 6 COP $mysid^{-1}$ h^{-1}	Aaser et al., 1995
Eurytemora affinis	143 COP l^{-1}	0.35	24	15°C – 5 psu – 1 mysid	Subadult 4 -8 mm SL	3-18 COP $mysid^{-1}$ day^{-1}	Fockedey et al., submitted a – Chapter 5

Table 4 (cont.)

Food item	Concentration	Vol (L)	Time (h)	Conditions	Size mysids	Feeding rate	Scource
Daphnia hyalina	60 Dh l^{-1}	3	1.75	0.5-2.6 mysids l^{-1}	Mysid 8-9 mm SL	14 Dh $mysid^{-1}$ h^{-1}	Irvine et al., 1993
Daphnia hyalina + Eurytemora affinis	60 Dh + 78 N + 86 COP l^{-1}	3	1.75	-	Mysid 8-9 mm SL	16 Dh+17N+10COP$mysid^{-1}h^{-1}$	
Daphnia magna+ Chydorus sphaericus	54 Dm + 165 CH l^{-1}	4.4	1.2	-	Mysid 9 mm SL	10 Dm+48 Ch $mysid^{-1}$ h^{-1}	
Daphnia magna+ Chydorus sphaericus Eurytemora affinis	29Dm + 88 CH + 85N + 121COP l^{-1}	4.4	1.2	-	Mysid 9 mm SL	9 Dm+ 31CH-13N+?COP $mysid^{-1}$ h^{-1}	
Artemia nauplii	50 N l^{-1}	2	3	9-16°C - ?psu (Finnish Baltic water)	18.2 mm TL =5.82mg DW	11.62 - 16.26 µg C h^{-1}	Lindén et al., 2003
Artemia nauplii	50 – 2400 N l^{-1}	0.5	24	9°C (10psu)	Adult	Max at 300-450 N $mysid^{-1}$ day^{-1}	Astthorsson, 1980
Artemia nauplii	2000 N l^{-1}	0.5	24	9°C (10psu) 16°C (10 psu)	1.5 - 7.4 mg DW 0.7 - 10.2 mg WD	90 – 480 N $mysid^{-1}$ day^{-1} 70 – 450 N $mysid^{-1}$ day^{-1}	Astthorsson, 1980
Artemia nauplii	2000 N l^{-1} 1000 N l^{-1} 500 N l^{-1}	0.5 1 2	24	9°C (10 psu)	1.5 - 7.4 mg DW 1.5 - 7.4 mg DW 1.5 - 7.4 mg DW	90 – 480 N $mysid^{-1}$ day^{-1} 40 – 380 N $mysid^{-1}$ day^{-1} 20 – 360 N $mysid^{-1}$ day^{-1}	Astthorsson, 1980
Artemia nauplii	5 N l^{-1} 13 N l^{-1} 25 N l^{-1} 50 N l^{-1} 100 N l^{-1} 150 N l^{-1} 200 N l^{-1} 400 N l^{-1}	5	6	9°C (10 psu)	4.5 mg DW	3.8 N $mysid^{-1}$ h^{-1} 10.2 N $mysid^{-1}$ h^{-1} 15.7 N $mysid^{-1}$ h^{-1} 11.5 N $mysid^{-1}$ h^{-1} 16.0 N $mysid^{-1}$ h^{-1} 22.3 N $mysid^{-1}$ h^{-1} 20.8 N $mysid^{-1}$ h^{-1} 17.7 N $mysid^{-1}$ h^{-1}	Astthorsson, 1980
Organic poor sediment	?	?	16	5°C – 10 psu – males 15°C – 10 psu – males 1 psu – 10°C – males 30 psu – 10°C – males	?	0.057 mg faeces mg^{-1} mysid DW h^{-1} 0.132 mg faeces mg^{-1} mysid DW h^{-1} 0.084 mg faeces mg^{-1} mysid DW h^{-1} 0.096 mg faeces mg^{-1} mysid DW h^{-1}	Roast et al., 2000
Estuarine flocs		0.85	24	5 subadults	Mysid 7 – 10 mm SL	38 flocs $mysid^{-1}$ h^{-1}	Fockedey et al., submitted c – Chapter 4
		0.85	24	8-10 small subadults 2-3 large subadults	Mysid 4 – 6 mm SL Mysid 9 – 11 mm SL	0.039 mgDW faecesmg^{-1} mysid DW h^{-1} 0.021 mgDW faeces mg^{-1} mysid DW h^{-1}	Fockedey et al., submitted d – Addendum 2

Ch : *Chydorus sphericus* ; **Dm**: *Daphnia magna*; **Dh** : *Daphnia hyalina* ; **N** : nauplii ; **COP** : copepodites and adults

Astthorsson (1980) though, report the container size not to have a significant impact on the maximal feeding rates of *N. integer* on *Artemia* nauplii. Gorokhova and Hansson (1997) report the effects of other experimental conditions like light regime, duration of the experiment and extent of starvation on the feeding rate estimate of mysids (*Mysis mixta*). Laboratory derived feeding rates must be considered as overestimates (Aaser *et al.*, 1995) due to the relative high prey density in comparison to the field, an aberrant prey and predator behaviour and due to the fact that *N. integer* in the field does not feed exclusively on zooplankton, but has an omnivorous diet.

⇨ **Phyto- and zoobenthos**

Neomysis integer is known to feed in some locations on phyto- and zoobenthos like benthic diatoms, meiofaunal nematodes, harpacticoids and ostracods, amphipods, chironomids, and oligochaets (Astthorsson, 1980; Bremer and Vijverberg, 1982; Haesloop, 1990; Speirs *et al.*, 2002; Vilas and Fockedey, unpublished). Although it can survive on harpacticoid copepods (Mauchline, 1971) or oligochaets (Haesloop, 1990) in aquaria, no further data are available on the feeding rates on these food itmes. Recently, Albertsson (2004) hypothesised a predator-interaction of *N. integer* on juveniles of the amphipod *Monoporeia affinis* but could not confirm this in mesocosm experiments. The mesocosm experiments however, could demonstrate a significant predation of *N. integer* on near-bottom zooplankton (mainly cyclopoids) in the Baltic (Albertsson, 2004).

⇨ **Detritus and sediments**

Qualitative stomach content analyses of *Neomysis integer* described the species to feed on fragments of leaves of higher plants and macroalgae, and on amorph suspended detritus. Ingestion rates of macrophytal detritus can be measured directly by weight difference of the food eaten over a certain time period (*e.g.* Nilsson, 1974). However, a significant decrease in food weight is difficult to measure and leads to a very variable feeding rate (Marchant and Hynes, 1981). The duration of the experiment have to be long enough and/or should contain many individuals. However, no experiments to determine ingestion, egestion and gut evacuation rates on macrophytal detritus or suspended particulate matter have been performed with *N. integer*, except for Fockedey *et al.* (submitted c – Chapter 4) and Fockedey *et al.* (submitted d – Addendum 2).

Neomysis integer also feeds on the sediment surface. It feeds raptorially on the whirled up particles (Parker and West, 1979) or directly ingests aggregations of surface sediment (Roast *et al.*, 2000). The egestion rate of *N. integer* on sieved, organically poor sediments was determined as a measure for the ingestion rate (Roast *et al.*, 2000). Egestion rate increased with increasing salinity and temperature.

3.4 Selectivity experiments

Selectivity of *Neomysis integer* for specific prey types or prey sizes can be determined in two ways: (1) via feeding experiments in artificial laboratory conditions, or (2) via the analysis of ingested food items. In laboratory experiments, nauplii and the smallest copepodites of *Eurytemora affinis* are most strongly selected (Irvine *et al.*, 1993; Aaser *et al.*, 1995). *N. integer* also readily feeds on *Daphnia hyalina* and again smaller prey individuals are preferred. Selectivity coefficients are significantly greater for *Daphnia* sp. than for copepodites of *E. affinis* (Irvine *et al.*, 1993). When administering a mixture of natural zooplankton, *N. integer* seemed to be largely missing the older *Eurytemora* copepodites as these are capable of more vigorous flight reactions (Arndt and Jansen, 1986). In the Elbe, *N. integer* was found to feed on elder developmental stages of *E. affinis* (Bernát *et al.*, 1994). Juvenile mysids preferred small rotifers and copepod nauplii, while larger *N. integer* favoured larger prey like Cladocera and calanoid copepodites over Rotifera (Arndt and Jansen, 1986). Larger *N. integer* individuals consumed a larger size of *E. affinis* (Fockedey and Mees, 1999 – Chapter 2).

In a Frisian brackish lake *N.integer* showed a strong negative selection for the filamentous blue-green alga *Oscillatoria* and a rejection of the filamentous green alga *Planctonema*, while it was preferably feeding on *Bosmina* sp., cyclopoids and detritus (Bremer and Vijverberg, 1982).

3.5 Structuring of zooplankton and phytoplankton populations

It is well known from fresh- and brackish water lakes, that high mysid densities may affect phytoplankton and zooplankton composition and abundance, especially in periods of low vertebrate predator abundance (Moss and Leah, 1982; Hanazato, 1990; Jeppesen *et al.*, 1994; Aaser *et al.*, 1995). This phenomenon has also been suggested for brackish coastal areas, e.g. the Baltic (Rudstam *et al.*, 1986; Hansson *et al.*, 1990). Information on the structuring impact of *N. integer* on the mesozooplankton (and phytoplankton) communities in dynamic estuarine systems is still lacking.

The high abundance of *Neomysis integer* in **brackish water ponds and lakes** is typically associated with a low abundance of pelagic Cladocera and copepods (Espeel, 1982; Van De Vijver, 1983; Aaser *et al.*, 1995), indicating the governing role of mysids in the structuring of zooplankton communities. In a Danish lake, Aaser *et al.* (1995) could demonstrate the negative impact of *N. integer* on *Eurytemora affinis*. By its heavy predation on the zooplankton community *N. integer* reduces the grazing pressure on the phytoplankton and enhances the eutrophication in nutrient-rich brackish lakes (Aaser *et al.*, 1995; Samuels and Mason, 1998). Moreover, *N. integer* also directly stimulates the phytoplankton growth (Aaser *et al.*, 1995), perhaps because nutrients consumed when feeding on the sediment surface are subsequently excreted to the water column and become available to the phytoplankton.

In laboratory experiments, *Neomysis integer* extensively feeds on nauplii and copepodites of *Eurytemora affinis* and Cladocera and thus has the potential to dramatically affect the population structure and density of its prey (Irvine *et al.*, 1993). However, in the field (Hickling Broad) no evidence was found of a link between the population dynamics of *N. integer* and *E. affinis* (Irvine *et al.*, 1995), except for a slight reduction in the total biomass and size-at-maturity of *E. affinis* in periods when larger mysids are relatively more abundant (cfr. these feeding more effectively on larger prey). The copepod reproduces so rapidly that its population is unlikely to be controlled by the mysid predation (Irvine *et al.*, 1993). Vice versa there was no indication that *Neomysis integer* was affected by (interannual) changes in the *Eurytemora affinis* population dynamics. The potential for omnivorous feeding in mysids implies that they may modify their diets in response to changes in the food quality and abundance. In periods of low zooplankton densities, the omnivorous *N. integer* can switch its diet from zooplankton to other food items, like epiphytic algae, (macrophyte) detritus and even organic matter in sediments. In this way, *N. integer* can keep its densities high and maintain a potentially high predation pressure on the remaining zooplankton (Irvine *et al.*, 1995).

Neomysis integer is an important regulator of zooplankton abundance and species composition in the **Baltic** as well (Jansen *et al.*, 1983; Jansen and Heerklos, 1983; Hansson *et al.*, 1990), except for the northern part of the Baltic Sea where the species contributes only 3 % of the total mysid biomass (Rudstam *et al.*, 1992), while another mysid species (*Mysis mixta*) and clupeid young-of-the-year larvae are the most dominantly zooplanktivores (Rudstam *et al.*, 1992). In coastal waters of the southern Baltic, *N. integer* consumption was estimated to amount to 2.7 – 20.1 % of the total annual zooplankton production in the Darss-Zingst estuary (Jansen, 1985b; Thiel, 1992). *N. integer* has a minor impact on the phytoplankton in the Baltic region (Jansen *et al.*, 1983; Jansen and Heerklos, 1983). Jansen (1985b) found zooplankton to constitute up to 37 % of the stomach content of *N. integer* in a bay of the southern Baltic Sea.

During periods when juveniles dominated the *N. integer* population, small Rotifera and copepod nauplii played a greater role in the food spectrum, while larger mysids selectively preferred larger prey like Cladocera and calanoid copepods (Arndt and Jansen, 1986). Only 8 % of the total annual rotifer production is consumed by *N. integer* in the southern Baltic. Still, *N. integer* juveniles are the main predators and select the larger rotifer species (like *Brachionus plicatilis*), the larger size classes and egg-bearing females (as demonstrated by feeding experiments by Arndt (1988).

A long-term dataset on the seasonal variation of *Neomysis integer* density in the Gironde **estuary** revealed a significantly positive correlation with copepod densities (*Eurytemora affinis* and *Acartia* spp.) and suggested predation by *N. integer* on copepods in the turbid reaches of the estuary with a possible food limitation (David *et al.*, 2005). No correlation between *N. integer* and *E. affinis* or chlorophyll *a* could be statistically demonstrated in the brackish regions of the Elbe estuary (Köpcke and Kausch, 1996).

3.6 Diet overlap with coexisting species

Larvae and young of zooplanktivorous estuarine fish (like herring and smelt) can heavily predate on zooplankton in some periods of the year, especially in years of high recruitment (Thiel, 1996), and then show a high degree of diet overlap with *Neomysis integer* (Kinne, 1955, Sanina, 1961, Maciejewska, 1992). The zooplanktivorous fish select their prey visually and prefer larger prey like larger cladocerans, calanoid copepods, and *N. integer* itself (Thiel, 1996). The mysid exhibits a more tactile behaviour (next to visual cues) in their prey selection and is able to prey on smaller organisms like larger rotifers and nauplii of copepods and cladocerans (Jansen, 1985b). *N. integer* and planktivorous fish respectively consume 20.1 % and 25.4 % of the total annual zooplankton production in the Baltic (Thiel, 1992). *N. integer* competes for food with the early fish developmental stages, but is at the same time a food component of the older stages of *e.g.* herring and sprat (Maciejewska and Opalinski, 2002).

Neomysis integer and *Praunus flexuosus* compete for the same food resource *Eurytemora affinis* (Winkler and Greve, 2004). In situations where not a lot of copepods are available, *Praunus flexuosus* will feed on the younger life stages of *N. integer* (Winkler and Greve, 2004), while *N. integer* will shift to a more detrital feeding mode under limited prey circumstances (*e.g.* Arndt and Jansen, 1986).

Remerie (1999) compared the stomach contents of *Neomysis integer* of the Schelde with other estuarine mysid species like *Gastrosaccus spinifer*, *Praunus flexuosus*, *Schistomysis kervillei* and *S. spiritus N. integer* was the only species feeding during day ánd night, while the others were mainly night feeders. For all of the species, stomachs contained large amounts of unidentifiable detritus, originating from estuarine micro-flocs typically formed in the estuary by flocculation of sediment, particular suspended and dissolved organic matter (Eisma, 1986).

3.7 Feeding appendages

The feeding appendages of mysids consist, in anterior to posterior order, of an unpaired labrum, and paired mandibles, paragnaths (labia), maxillules and maxillae (Mauchline, 1980). The mouth is situated ventrally and is enclosed by a chamber formed by the labrum, mandibles and paragnaths. The mandible has cutting, grinding and macerating regions and a forwardly directed mandibular palp. The morphology of all these mandibular features vary between species according to their feeding habits (Mauchline, 1980). The endopods of the thoracic legs function in filter feeding. The anterior thoracic endopods, together with the mouthparts form a “food basket” in which organic matter collected from the sediment surface is collected, mainly by the mandibular palp, and held in the basket prior to maceration by the mouthparts (Mauchline, 1980; Roast *et al.*, 2004).

Remerie (1999) and Maciejewska (1992) studied the morphology of the mandibles and thoracopods of *Neomysis integer*, since it can give information on their diet. The length and the distance between setae of the thoracopod endopods, identifying the surface and mesh size of the sieving device (Jerling and Wooldridge, 1994), was small in *N. integer* and indicate that filter feeding is of minor importance to the species. The structure of the mandibles, like the surface of the *pars molaris* (pm) and the length of the *pars incisivia* (pi), makes it possible to hypothesise on the degree of herbivory or carnivory of a species. For *N. integer* the pm/pi-ratio is low in comparison to other estuarine species and the presence of large, sharp incisive teeth on the *pars molaris* indicates a carnivorous or detritivorous feeding. When mysids are filter feeding they use the setae on the proximal endite of the maxilla for food collection (Cannon and Manton, 1927). Maxilla have feather-like setae with 2 rows of setules and a second type of more robust setae with short irregular setules overlaying the heather-like ones. The distance between setae and between setules on the maxilla of *N. integer* are respectively 4 – 5 and 2 – 3 µm apart (Astthorsson, 1980) and should be able to retain particles as small as 2 – 3 µm.

3.8 Gut morphology, chitinases and cellulases

The alimentary canal of crustaceans is typically devisable in three regions (Molloy, 1958; Brunet *et al.*, 1994): foregut, midgut and hindgut. In Mysidacea the foregut is more or less distinctly divided into four regions (Kobusch, 1998): the oesophagus, the cardiac and pyloric chambers of the stomach and the funnel. The midgut consists of a comparatively long straight intestine bearing a number of blind-ending caeca at its junction with the foregut.

Gelderd (1909), Molloy (1958), Haffer (1965), Mauchline (1980) and Kobusch (1998) all described the histological and morphologic structure of the gut of *Neomysis integer* (Figure 4a, b). Its oesophagus is short and muscular, lined with chitin and has spines that tend to point upwards towards the stomach. The stomach is divided into a large anterior 'cardiac' region and a smaller posterior 'pyloric' region. Both are armed internally with strong spines and setae and posses folds to assist the passage of food through the stomach. In general, the omnivorous *N. integer* retains a large mass of food in the cardiac chamber of the stomach, where it is continuously being worked up by the various cardiac folds, spines and teeth (Molloy, 1958).

Neomysis integer has a single, large dorsal diverticulum (Figure 4b) that arises as an extension of the midgut in the posterior dorsal area of the pyloric region of the stomach. It continuously secretes the peritrophic membranes into the intestine, within which the faecal material is bound (Molloy, 1958). The digestive glands (or hepatopancreas), consisting of two groups of five blind-ending caeca, open with a common duct into the posterior ventral area of the pyloric region of the stomach (Figure 4c, d). Part of the food passes from the stomach into the lumina of the digestive glands. The walls of the digestive glands posses circular muscles that power the movement of food and digestive enzymes within the lumina. The finely particulate food is digested and absorbed there. The caeca can reach up to the abdomen and is coloured yellowish green to brown in freshly caught specimens (Molloy, 1958). The intestine emerges from the stomach in the 3rd or 4th thoracic segment and extends posteriorly (as midgut) to the posterior end of the fifth abdominal segment where it becomes the hind gut, wider, lined with chitin and more muscular. Studies of a number of crustacean species revealed that cells of the digestive epithelium are cyclically shed (Brunet *et al.*, 1994) and replaced as is supposed to happen in *N. integer* as well (Bradshaw *et al.*, 1989). The hindgut is short, extending only from the 6th abdominal segment to the anus, which is situated ventrally at the base of the telson. The volume of the gut of *N. integer* is approximately 7.5 mm^3 for a 10 mm long (SL) mysid (Irvine *et al.*, 1993).

Cellulases and chitinases have been identified in whole specimen extracts of *Neomysis integer*, probably present in the alimentary canal (Molloy, 1958). So it can be assumed the species is capable of digesting exoskeleton remains of ingested zooplankton, their own moults and faeces (with chitinous peritrophic membrane) and the (refractile) macrophyte detritus. Also it is assumed that some kind of inhibitor must be present as well to prevent digestion of the chitinous lining of the hindgut and the chitinous peritrophic membrane surrounding the faeces (Molloy, 1958).

In other detritivore crustaceans, cellulolytic bacteria are described to mobilize previously unavailable material in the faeces (Hargrave, 1976). Starved *Neomysis integer* individuals are known to re-ingest their faeces and may increase the efficiency of nutrient extraction due to both processes (enzymes and bacterial breakdown). Its own digestive system can be complemented by the 'external rumen' of bacterial action through coprophagy (Parker and West, 1979). The cellulolytic bacteria are not yet specified in the mysid *N. integer* though, although Armitage *et al.* (1981) mention the presence of general gut micro-organisms in the species. Other authors (*e.g.* Hargrave, 1970) suggest that the main energy value of the macrophyte detritus for crustaceans lies in the associated bacteria, fungi and protozoans present on the detritus, while the detritus itself is egested unchanged.

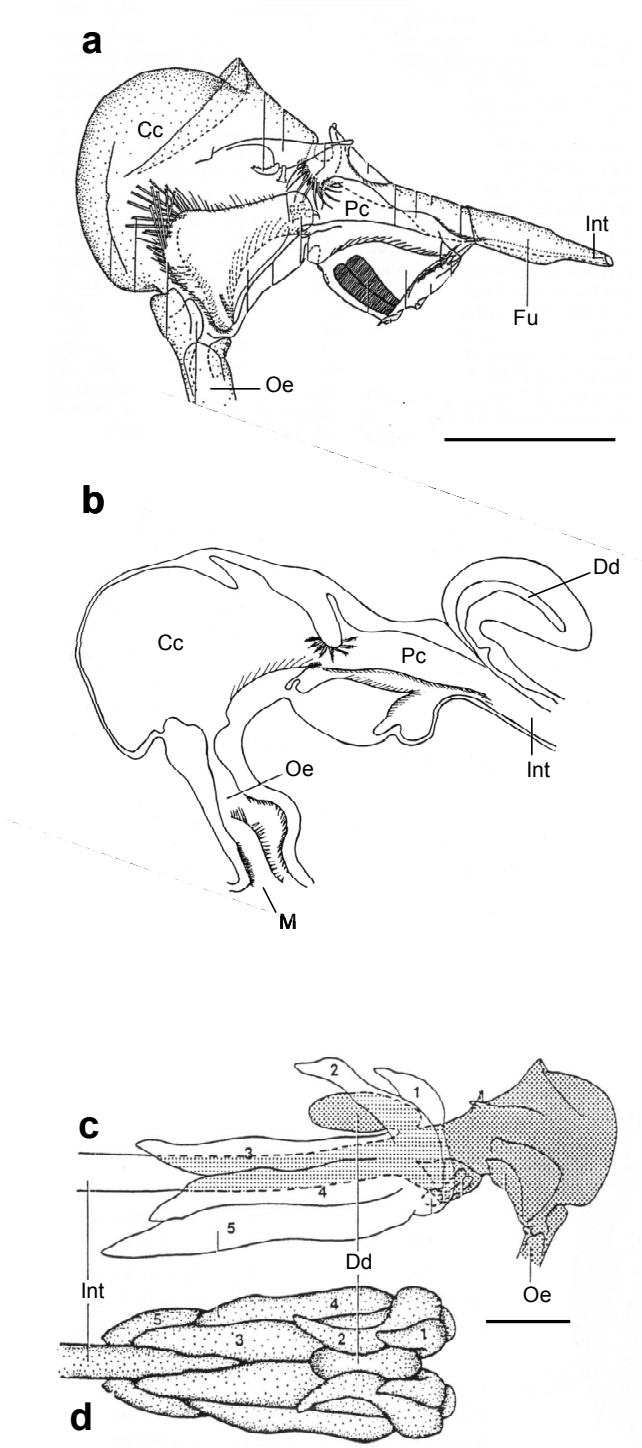


Figure 4: (a) Foregut of *Neomysis integer* in lateral view, with dorsal diverticulum omitted (Kobusch, 1998). (b) Schematic view of a longitudinal section through the foregut (Molloy, 1958; Mauchline, 1980). (c) Midgut glands in relation to the foregut in lateral view (Kobusch, 1998) and (d) in dorsal view with the foregut removed usch, 1998). Cc: Cardiac chamber (foregut); Dd: Dorsal diverticulum (midgut); Fu: Funnel (foregut); Int: Intestine (midgut); M: mouth; OE: oesophagus (foregut); Pc: Pyloric chamber (foregut); 1-5: five tubes of the digestive glands on each side. Scale bar: 500µm

3.9 Gut passage time

Molloy (1958) noted that carmine particles require 30 – 40 minutes, occasionally as much as 90 minutes, passing along the complete length of the alimentary track of *Neomysis integer*. The food stays in the stomach and anterior part of the midgut for most of the time. The intestine of *N. integer* starts anti-peristaltic movements when faecal material passes into the abdominal part of the intestine (Molloy, 1958). The rhythmic pumping of the hindgut muscles is associated with gulping in of water through the anus, and subsequent defecation. These gulping movements appear to initiate a forward wave of contractions along the intestine (anti-peristalsis).

Direct observations of the passage of food through the gut of *Neomysis integer* were performed by Ferguson (1973). Animal food (crab hepatopancreas) had a considerably longer time in the gut than the (natural and laboratory-made) detrital food sources; the first faecal pellets were produced after respectively 177 – 188 and 35 – 56 minutes and gut clearance took 4 to 6 times as long as on natural detritus. There was little difference in the digestion rate between juvenile and adults feeding on the same food source. *N. integer* produced more faecal pellets on the detrital diet as compared to the animal diet, although the time allowed for ingestion was similar (Ferguson, 1973). The higher the assimilation efficiency of a certain food source, the longer the gut passage time (Ferguson, 1973). The higher the ash content of the food, the shorter the gut passage time (Ferguson, 1973). Fockedey *et al.* (submitted d – Addendum 2) determined the gut passage time on environmentally relevant food sources for estuarine *N. integer* to be between 0.5h (estuarine aggregates) and 2.6h (*Eurytemora affinis*).

3.10 Faecal pellets and coprophagy

Neomysis integer produces faecal material surrounded by a chitinous peritrophic membrane. The pellets break apart into smaller pieces after egestion. One fifth of the produced faecal pellet weight disintegrates and disperses into the surrounding water in which the animal is living (Bradshaw *et al.*, 1989; Maciejewska and Opalinski, 2002).

Neomysis integer feeds on its own faeces when there is a shortage of food (Molloy, 1958; Parker and West, 1979; Weisse and Rudstam, 1989; Roast *et al.*, 2000). The faecal pellets of *N. integer* are potential sources of energy; especially when derived from organically rich food sources, the faecal pellets have a high carbon content (40 – 60 %; Ferguson, 1973). A more efficient assimilation of a specific food item does not automatically implicate organically poorer faecal pellets (Ferguson, 1973). An assimilation efficiency of more than 75 % resulted mostly in faeces containing > 35 – 66 % organic matter. When *N. integer* is offered its own faecal pellets as food, the assimilation efficiency is 10 – 25 %. Although this is not particularly high, it indicates that some nourishment can be derived from the faecal pellets. The faecal pellets produced by *N. integer* on a variety of food environmentally relevant sources are studied in detail (scanning electron micrographs and C:N analysis) by Fockedey *et al.* (submitted d – Addendum 2).

3.11 Starvation

Juvenile and subadult *Neomysis integer* survived no longer than 7 weeks when starved at 9 °C (Gorokhova and Hanssen, 1999). Morris *et al.* (1977) and Armitage *et al.* (1978) starved *N. integer* by feeding it with kaolin clay and obtained a mortality of 60 % after 6 to 8 days. Survival to starvation is dependent on salinity and temperature conditions and size of the mysid (Vlasblom and Elgershuizen, 1977; Winkler, 2000).

Starvation of *Neomysis integer* during 5 weeks resulted in a 36 % mortality, a dry weight decrease of 18.6 % and 7.6 % reduction of body carbon (Gorokhova and Hanssen, 1999; Gorokhova, 2002). Starvation reduces the protein content of *N. integer* (-41 %) and thus reduces the dry weight (Armitage *et al.*, 1977; 1978). Wet weight does not alter much during starvation, because of the increase in water content (Armitage *et al.*, 1978). The level of total free amino acids was reduced (28 – 29 %) in starved animals (Armitage *et al.*, 1977; 1978). Starvation did not change the isotopic composition of *N. integer*, as might be expected since progressively lighter isotopes are expected to be catabolized first (Gorokhova and Hanssen, 1999).

A prolongation of the starvation period from 6 to 30 hours significantly reduced the ammonia excretion rate of *Neomysis integer* (Weisse and Rudstam, 1989), but did not affect the oxygen consumption or dissolved inorganic phosphorus excretion rate. Starvation reduces the carbohydrate reserves of *N. integer* (Raymont and Conover, 1961), but does not reduce significantly the total lipid content (Linford, 1965). More recently, starvation was demonstrated to cause an increased atomic O:N ratio, indicator for the reserve substrate being catabolized (Weisse and Rudstam, 1989). The actual amount of glycogen is small, and allows the mysid to live for only a few hours (Raymont *et al.*, 1966; 1968). The (low) amount of lipid reserves of *N. integer* (12 – 15 % of DW) is enough to maintain respiration rates and activity levels for at least 48 h (Weisse and Rudstam, 1989). When starved for a longer period, the species can deaminate body protein (Raymont *et al.*, 1964; 1967; 1968; Verslycke and Janssen, 2002).

When starved, mysids are known to increase the retention time of the food present in their stomach (Murtaugh, 1984). Molloy (1958) starved *Neomysis integer* in order to clear the gut, but 5 – 7 days after being deprived of food, the alimentary track still contained food items. When food is limited, *N. integer* is feeding coprophagously on its own faeces (Weisse and Rudstam, 1989; Roast *et al.*, 2000). They flex their body and bring the faecal thread close to the mouthparts where it is seized, drawn out and eaten (Parker and West, 1979). They also feed on dead *N. integer* individuals, though living ones, other than lost larvae and just released juveniles, are not attacked when there is shortage of food (Raymont and Krishnaswamy, 1960; Parker and West, 1979; Fockedey, unpublished). Usually only the thoracic region of the dead *N. integer* is eaten. It is thus difficult to ensure complete starvation conditions experimentally for *N. integer*. Armitage *et al.* (1977, 1978) solve this by administering kaolin clay, since the mysids keep on feeding and hence do not retrieve the remaining food in the stomach.

3.12 Feeding ecology and changing temperature and salinity

Generally, the ingestion rate increases with increasing temperature, as anticipated from the general effect of temperature on most rates of physiological processes including the feeding responses of aquatic invertebrates. Increased temperature increases the predation rate of *Neomysis integer* (Astthorsson, 1980; Winkler and Greve, 2004) and the egestion rate on organically poor sediments (Roast *et al.*, 2000). Temperature has a strong effect on the excretion rates (ammonia and DIP) of *N. integer* (Weisse and Rudstam, 1989). The feeding rate of *N. integer* feeding on organically poor sediments increased also with increasing salinity (Roast *et al.*, 2000), probably because more energy is spent in osmoregulation.

Roast *et al.* (2000) used the response of the egestion rate (as a measure of the ingestion rate) to changes in salinity and temperature under laboratory conditions, to calculate the tidal and seasonal changes in the feeding rate of *Neomysis integer* in the East Looe River estuary (with extreme tidal fluctuations in the salinity and temperature). They concluded that the feeding rates of *N. integer* are generally low during the tidal cycle, except for a short period of 2 hours around high tide. Seasonal temperature changes cause seasonal changes in the feeding rate of *N. integer*, with increased rates in the warmer summer months, *i.e.* the main reproductive period (Roast *et al.*, 2000).

Two other aspects of the feeding ecology affected by the prevailing temperature and salinity are: (1) the survival to starvation (see above; Vlasblom and Elgershuizen, 1977) and (2) the assimilation efficiency of *Neomysis integer* increases with increasing temperature when feeding on animal food (Ferguson, 1973), though not when feeding on organically poor sediments (Roast *et al.*, 2000). Salinity has little or no impact on the assimilation efficiency of *N. integer* feeding on animal food or sediments (Ferguson, 1973; Roast *et al.*, 2000).

3.13 Survival, growth and reproduction on different diets

Survival, growth, development and reproduction rates can be used as indicators of food quantity and food quality. Feeding rate alone cannot explain the differences observed in growth, development, egg production or mortality (Koski *et al.*, 1998) and thus experiments are needed to elucidate the degree to which specific food items are ingested, digested and – especially – assimilated. Somatic tissue and eggs have a different chemical composition, which demand a different nutritional composition of the food. Probably specific lipids and fatty acids are more critical for gonad development and egg production, while proteins are more important for somatic growth (Kiørboe *et al.*, 1985).

Until now, few studies have examined the survival and growth rates of mysids in relation to food quality (Lehtiniemi *et al.*, 2002) and little information is available on the impact of food quality on their reproduction (Domingues *et al.*, 2002). Some studies are available on the impact of food quality on the feeding activity, ingestion and assimilation efficiency (Ferguson, 1973; Astthorsson, 1980). Filter feeding experiments with *Neomysis integer* on 5 species of cultured algae (Astthorsson, 1980) suggested that only when feeding on one species (*Cricussphaera oblongata*), the mysid was able to meet all its metabolic requirements. On the other phytoplankton *N. integer* experienced some kind of shortage.

For *Neomysis integer*, only Ferguson (1973) performed experiments for comparing growth efficiencies of selected size classes of mysids feeding them an animal diet (crab hepatopancreas) and two detrital diets (artificial detritus of aged algal culture and natural detritus). The smallest animals exhibited the highest growth efficiencies. When feeding artificial detritus, the growth efficiency was significantly smaller than on the animal food. On natural detritus, collected from the surface of the marsh creek beds, the animals lost weight due to the poor quality of the natural detritus sample. Fockedey *et al.* (submitted a – Chapter 5) evaluated survival, growth and moulting of subadult *Neomysis integer* when fed *Eurytemora affinis*, estuarine aggregates and macrophytal detritus in order to evaluate the nutritive value of these environmentally relevant food sources.

4 LIFE HISTORY

Reliable estimates of secondary production and well documented life history data are necessary for key species in order to understand the functioning of estuarine ecosystems. As life history characteristics can vary considerably from one habitat to another, local knowledge on the species' biology is essential for further use in ecosystem modelling, energy flow studies, experimental and toxicological work. For *Neomysis integer*, quite some data are available on its life history over a wide geographical and habitat range (Table 5), and quite some variations exists between populations. Life history of southern populations < 51°N are poorly known, with the exception of the Gironde population (Sorbe, 1980). Studies on the Guadalquivir population, at the southern most border of the species distribution area are ongoing and not published yet (Vilas, personal communication).

4.1 Seasonal dynamics of *Neomysis integer* populations in the estuary

Most studies on the population dynamics of *Neomysis integer* are exclusively based on field data (*e.g.* Mees *et al.*, 1994 and the references herein). Generally, length frequency distributions are obtained through regular sampling (once or twice per month) of the population for at least one year. As a result of the asynchronous moulting between individual mysids, the lengths within a cohort are presumed to be normally distributed. Cohorts can then be segregated by modal progression analysis, but this is often complicated due to the occurrence of overlapping generations and prolonged reproductive periods (*e.g.* Astthorsson and Ralph, 1984; Mauchline, 1985; Irvine *et al.*, 1995). In order to detect and separate cohorts in a more objective way, length frequency distributions can be analyzed with the Bhattacharya method (Bhattacharya, 1967 implemented in Pauly and Caddy, 1985). It splits composite length-frequency distributions into separate normal distributions. The means of the normal distribution for all sampling dates are then plotted over time to trace the modal length progression (growth curve) of the cohorts. This technique was used for *N. integer* populations in the Schelde, Galgenweel, Gironde, Tamar and Guadalquivir (Mees *et al.*, 1994; Fockedey, unpublished; Mees *et al.*, unpublished; Villas, personal communication; Moffat, 1996). For each of the cohorts identified, density, biomass and production can be estimated, and growth curves can be fitted. The growth rate (mm d^{-1}) of each cohort can then be calculated as the increase in the mean length during each sampling interval (Omori and Ikeda, 1984).

Based on the development of the secondary sexual characteristics, the mysid individuals within the population can easily be staged and sexed (Mauchline, 1971) into the following classes: (1) juveniles, (2) immature males, (3) mature males, (4) immature females, (5) adult females and (6) gravid females. Adult males are distinguished by their well developed 4th pleopods which reach beyond the posterior edge of the last abdominal segment. They are further characterised by a well-developed and setose lobus masculinus between the flagellae of the antennal peduncle. Adult females all have a well developed marsupium between the thoracic legs. Juveniles lack secondary sexual characteristics. A further distinction between adult and subadult (immature) males and females is often more subjective. For subadult males the following criteria were used by Mees *et al.* (1994), Mees *et al.* (unpublished) and Fockedey (unpublished): the 4th pleopod stop short of reaching the end of the last abdominal segment and/or the lobus masculinus is present but it is much smaller than in adult males and it is not yet setose. The latter criterion seemed to be the most reliable when distinguishing immature males from juveniles. Females were categorised as adults when their marsupial were large enough to be seen from the lateral side. In contrast, the developing Oostegites in subadult females are only visible between the thoracopods when the ventral side of the animal is carefully examined. Adult females are further divided into females without embryos or larvae (fully developed but empty marsupia) and 'gravid' or ovigerous females (embryos or larvae present in the marsupium). When gravid females are present one can make larval counts of females with complete broods.

Information on the population structure at subsequent moments within the year, like the relative number of adults and gravid females or the appearance of high amounts of small juveniles, helps to identify the breeding season and distinguish the subsequent cohorts within the length-frequency distributions.

Some authors distinguish juveniles from subadult stages at a fixed length: 6 mm TL (Platenkamp, 1983), 6 mm TL (Borghouts, 1978), 8 mm TL (Kinne, 1955) and 9 – 10 mm TL (Beattie and de Kruijf, 1978; Bremer and Vijverberg, 1982). However, this is an inadmissible simplification since the transition from juvenile to subadult occurs at a different size, dependent on the season, sex of the animal and the latitude it is living at (Mauchline, 1971; Schuchardt *et al.*, 1989; Mees *et al.*, unpublished).

4.1.1 Annual production

Annual production can be estimated from the length-frequency data and a length-weight regression (Table 2). Three commonly used methods, each with their own strengths and weaknesses are: (1) the growth summation method (Winberg, 1971; Crisp, 1984), (2) the removal summation method (Crisp, 1984) and (3) the size frequency method (Hynes and Coleman, 1968; Menzie, 1980). Furthermore, production of mysids can independently be estimated using the estimated mortality rate. This low effort method only requires the length-frequency distributions and an estimate of the mean annual biomass (Brey, 1986). The total mortality of a population equals the P/B ration, if the individual growth can be described by a von Bertalanffy function (Allen, 1971). The first method is applied most in production estimates of *Neomysis integer* (Bremer and Vijverberg, 1982; Arndt and Jansen, 1986; Mees *et al.*, 1994; Irvine *et al.*, 1995). The different methods were compared with each other in a study of the population dynamics of *N. integer* in the Schelde estuary (Mees *et al.*, 1994). The growth summation and removal summation method yielded comparable production estimates. The size-frequency method only gave similar results when applied to the 3 cohorts and to both sexes separately. Although the identification of cohorts is not a prerequisite to obtain a production value with this method, it is advisable in order to avoid an overestimation (up to 40 %). The production estimate based on the mortality rate of the different cohorts resulted in values comparable for the overwintering generation, but overestimated the spring and summer cohort production with 24 %.

The annual production of *Neomysis integer* in the Schelde **estuary** was 322 – 449 mgADW $m^{-2} y^{-1}$ (Mees *et al.*, 1994). Despite the long life span of the winter generation it generated only a quarter of the annual production, while the spring generation accounted for almost half of it.

Several annual production estimates of *Neomysis integer* are available for the **Baltic** region. In the southern Baltic (Darss-Zingst estuary and adjacent bays), the annual production was estimated as 3.0 – 4.7 gWW $m^{-2} y^{-1}$ (Arndt, 1985) or 437 – 876 mgDW $m^{-2} y^{-1}$ (Arndt and Jansen, 1986); but Thiel (1992) obtained a higher production of 9 gWW $m^{-2} y^{-1}$ for the same region. The annual production in the shallow littoral water (< 1.5 m) is one order of magnitude higher as compared to deeper water of the Darss-Zingst Bodden: 400 – 800 vs 30 – 60 mgDW $m^{-2} y^{-1}$ (Arndt and Jansen, 1986).

The annual production of *Neomysis integer* in **brackish lakes** is variable. For Lake Ferring (Denmark) it amounted to 2.2 gDW $m^{-2} y^{-1}$ (Aaser *et al.*, 1995), and daily production peaked in July and August when respectively 35 and 29 mgDW $m^{-2} d^{-1}$ were recorded. In Hickling Broad (England) the daily production ranged from 2 to 73 mgDW $m^{-2} d^{-1}$ (Irvin *et al.*, 1995), yielding a total annual production (including intra-marsupial production) of 5.8 gDW $m^{-2} y^{-1}$. Soselisa (1994) reports an annual production of 5.6 gADW $m^{-2} y^{-1}$ in the Belgian brackish pond Galgenweel. Bremer and Vijverberg (1982) and Bremer (1980) calculated a far lower production of *N. integer* in the Dutch lakes Slotermeer and Tjeukemeer as 10 mgDW $m^{-2} y^{-1}$ and 0.03 mgDW $m^{-2} y^{-1}$, respectively.

Most estimates of the production of *Neomysis integer* must be considered to be underestimates, since net efficiency, mesh selection or weight-loss due to formalin conservation are generally not taken into account. In none of the former studies the loss through moulting or the intra-marsupial production were considered. One exception on the latter is Irvine *et al.* (1995), who calculated the intra-marsupial production rate using the growth increment summation method as being always lower than 10 % of the total production.

Table 5: Available life history studies on *Neomysis integer*

Lat	Long	Name location	#cohorts	Longelivity cohorts	Breeding season	**Summer (Aug-Sept)** TL gravid females (in mm)	Brood size (# embryo ind^{-1})	Source
58°N	17°E	Baltic – Himmerfjärden (S)	2	no information	no information	12-13	no information	Rudstam et al., 1986
57° N	2° W	Estuary – Ythan (Scot)	2	S: May to Aug/Sept W: Jul/Sept to May+	Mar-Sept + winterstop	13-17 (16°C/ ? psu)	15-32	Astthorsson, 1980; Astthorsson and Ralph, 1984
56°N	5°W	Estuary/Loch – Etive (Scot)	3†	Sp: Mar/May to Jul S: Jun/Jul to Oct/… W: Sept/… to Jun/Jul+	All year round Low in winter	9-15	14-32	Mauchline, 1971
56°N	8°E	Lake – Lake Ferring (D)	2	S: May/Jun to Aug/Sept W: Jul/Aug to May+	May-Oct + winterstop	no information (3-6 psu)	no information	Aaser et al., 1995
54°N	18-19°E	Baltic – Gdansk Bay, Vislinkiy Bay (P)	2	S: 5-6 months W: 11 months	May-Nov	13	17	Wiktor, 1961; Tehn, 1992
54°N	9-10°E	Kiel Canal, at entrance Eider-Ring Canal (G)	2/3	Sp: May-Jun to Jul/Aug S: Jul to Sep or Jun+ W: Sep to June+	Apr-Sept + winterstop	10-13 (16°C / 7-14 psu)	9-22	Kinne, 1955
54°N	12-13°E	Baltic – Darss-Zingster Bodden (G)	2	S: May/Jun to Aug/Sept W: Aug/Sept to May/Jun+	May-Nov + winterstop	10-17 (15-18°C/ 0.5-15psu)	8 – 30	Jansen et al., 1980; Arndt and Janssen, 1986; Jansen, 1986
53°N	9°W	Estuary/Loch – Furnace (IR)	3†	Sp: Apr/May to Aug S: ? to … W: Sept/… to May+	All year round Low in winter	10-14 (0-2psu)	10	Parker and West, 1979
53°N	6°E	Lake – Bergumermeer (NL)	2	Sp: May/Jun to Sept W: Sept to May+	May-Sept + winterstop	no information	no information	Beattie and de Kruijf, 1978; de Kruijff, 1977
53°N	8°E	Estuary – Weser (G)	3	Sp: May/Jun to Jul/Aug S: Jul/Aug to Nov W: Sept/Oct to May+	Apr-Oct + winterstop	10-15 (10°C)	18-20	Schuchardt et al., 1989; Haesloop, 1990
52°N	1°E	Lake – Hickling Broad (Eng)	2	S: Apr/May to Jul (or Jul+?) W: Jul to May+	Feb/Mar-Oct + winterstop	7-8 (?°C/?psu)	no information	Irvine et al., 1993 Irvine et al., 1995
52°N	4°E	Lake - Rowing course (NL)	---	Sp: Jul – die in August! W: imigration in Jun/Jul	No survival	Died! (>21°C / 0.7psu)	No offspring	Vorstman, 1951
52°N	5°E	Lake – Slotermeer (NL)	3	Sp: Jun to Jul S: Jul to Sept W: Aug/Oct to Jul+	May-Oct + winterstop	10-13 (20°C / 0.4psu)	13-22	Bremer, 1980; Bremer and Vijverberg, 1982

Table 5 (cont.)

Lat	Long	Name location	#cohorts	Longelivity cohorts	Breeding season	**Summer (Aug-Sept)** TL gravid females (in mm)	Brood size (# embryo ind^{-1})	Source
52°N	5°E	Lake -Tjeukemeer (NL)	3	Cfr. Slotermeer, but with 1-2 weeks delay	no information	No information (0.1-0.3psu)	No information	Bremer, 1980
52°N	5°E	Lake – Barnegat (NL)	3	Sp: Apr/May to Aug S: Jul to Aug W: Aug to Jul+	Mar-Sept + winterstop	7-13 (?°C / 2.5psu)	± 6	Vorstman, 1951
51°N	3°E	Lake – Den Inkel (NL)	3	Sp: May to Jun/Jul S: Jun to Aug/Sept W: Aug to May+	May-Aug + winterstop	7-9 (17°C / 16psu)	± 5*	Borghouts, 1978
51°N	3°E	Lake –Veerse meer (NL)	3	Sp: May to Jun/Jul S: Jun to Sept W: Sept to May+	Apr-Sept + winterstop	10-15 (17°C / 13-23psu)	8-42*	Borghouts, 1978
51°N	3-4°E	Grevelingen (NL)	3	Sp: May to Jun S: Jun/Jul to ? W: ? to May/Jun+	Apr-? + winterstop	no information (13psu)	no information	Platenkamp, 1983
51°N	4°E	Estuary – Schelde (NL/B)	3	Sp: Apr/May to Sept S: Jun to Nov W: Aug/Sept to Jun+	Apr-Oct + winterstop	10-13 (19°C/23psu)	14-22*	Mees et al., 1994
51°N	4°E	Galgenweel (B)	3	Sp: Mar to Jul S: June to Sept W: Aug to May+	Mar-Sept	7-12 (18°C/4psu)	5-25*	Soselisa, 1994; Fockedey, unpublished
51°N	2°E	Lake - Stuivekenskerke (B)	2/3?	Sp: May to Jul S: Jul to ? W: ? to May+	Apr-Sept + winterstop	no information	no information	Espeel, 1979; 1982
51°N	1°W	River Test (UK)	---	Sp: March to ? no further information	All year round Low in winter	no information (15-21°C/2-27psu)	no information	Raymont et al., 1966
45°N	0°W	Estuary – Gironde (F)	>3†	Sp: Feb to May S†: May to Aug/Dec W: Aug to May+	Feb-Nov + winterstop	7-8 (?°C / ? psu)	no information	Sorbe, 1980; Mees et al., unpublished

TL: Total length; **Sp**: Spring generation; **S**: summer generation; **W**: winter generation; **+**: following year; **?**: no information on salinity and/or temperature conditions; ***** derived from fecundity-size regression given in the paper; † no distinct generation, but rather modal age groups due to intensive breeding in certain periods of the year against a backgroup of continous breeding; **…**: juveniles appear through winter alt a very low rate

4.1.2 P/B ratio: biomass-specific production

The P/B coefficient can be of more general significance than the production value itself (Greze, 1978). The P/B decreases with size and body mass within and between populations. Within a population the young animals show low body mass and relatively high growth (*i.e.* production) and have a comparatively high P/B, whereas the large and older animals have a reduced growth and a high biomass and resulting in a comparatively low P/B ratio. P/B ratio decreases with each trophic level by one order of magnitude, as the transfer efficiency among trophic levels amounts to 10%. P/B is mostly measured on an annual scale or daily scales.

The **estuarine** *Neomysis integer* population from the Schelde has an annual P/B ratio of 6, while the average cohort P/B was 3 (Mees *et al.*, 1994). The daily P/B coefficients of *N. integer* in the southern **Baltic** are 0.011 to 0.013 (Arndt and Jansen, 1986). In **brackish lakes**, the daily P/B ratio for *N. integer* varies between 0.001 and 0.050 in Frisian lakes (Bremer and Vijverberg, 1982), while in a lake in Jutland values between 0.001 and 1.0 were recorded (Aaser *et al.*, 1995). Peak values of the daily P/B coefficient coincide with periods when the recruitment of juveniles into the population is high (Bremer and Vijverberg, 1982). In brackish lakes, the annual P/B ratio is 3.3 to 14.8 (Bremer and Vijverberg, 1982; Irvine *et al.*, 1995; Soselisa, 1994; Fockedey, unpublished). The lower and upper limits of the daily P/B coefficients of *N. integer* based of **laboratory experiments** are 0.009 to 0.051 (Kuhlmann, 1982) and are comparable to the daily P/B ratios measured in the field.

4.2 Number of cohorts or generations per year

In the most northern populations (> 53°N) generally 2 generations per year are reported, while in the more southern studies (< 53°N) 3 generations or more are described per year. In the Baltic region of Darss-Zingst (Arndt and Jansen, 1986), the Swedish coast (Rudstam *et al.*, 1986), Gdansk bay (Wiktor, 1961) and the Kiel Canal (Kinne, 1955), only 2 generations are reported. In some brackish lakes, like Lake Ferring (Aaser *et al.*, 1992), Bergumermeer (Beattie and de Kruijf, 1978), Hickling Broad (Irvine *et al.*, 1995) the spring or summer generation is not developed or it is difficult to distinguish them from each other (Borghouts, 1978; Parker and West, 1979). In the Ythan estuary (Astthorsson, 1980; Astthorsson and Ralph, 1984) only 2 generations are described. Sorbe (1980) originally categorized *N. integer* in the Gironde estuary as a bivoltine species as well, although the author expected an additional spring generation to be present between February and May. A later study of Mees *et al.* (unpublished) concluded that even more than 3, highly overlapping generations are present in the Gironde estuary.

The creation and maturation of the specific cohorts differs between the different populations (Table 5). Along the west coast of Ireland and Scotland, in lakes Hickling Broad, Barnegat, Galgenweel and in the estuaries of the Schelde and Gironde, the **spring generation appears** in the population in April –May. In other locations the juveniles of the spring generation are released in May and/or June (Baltic populations, east coast of Scotland; lake Ferring, Dutch lakes Grevelingen, Bergumermeer, Slotermeer, Tjeukemeer, lake Veere, Den Inkel, the clay pits of Stuyvekenskerke and the Weser estuary).

The moment when this **spring generation reaches maturity and releases brood** is not linked to the moment they appear in the population but probably to environmental variables (like temperature, salinity, food conditions, …). In Slotermeer and Tjeukemeer e.g., the spring generation only appears in the course of June but rapidly reaches maturity to release a **summer generation** in the course of July (Bremer and Vijverberg, 1980; Bremer, 1980). This phenomenon is also observed in the other Dutch lakes (Borghouts, 1978; Platenkamp, 1983), with the exception of the oligohaline Barnegat (Vorstman, 1951). Here the summer generation is considered as the latest hatching product of the overwintering generation before they die. In other populations with a 'late' spring generation, like for example in Lake Ferring (Aaser *et al.*, 1995) or the Barther Bodden (Arndt and Jansen, 1986), the **summer generation** is completely **lacking** due to the delayed maturation of the spring generation in late summer (August/September). Those populations with an early spring generation all produce a summer generation, with the exception of Hickling Broad (Irvine *et al.*, 1993; 1995).

The **appearance** of the individuals that will **overwinter** as large juveniles or subadults generally occurs in late summer (August/September) in most populations with 3 annual generations per year. In the populations of the Weser and Slotermeer this period is prolonged up to October. In loch-like estuaries along the Irish and Scottish west coast breeding continues in winter, although at a very low rate.

In populations with 2 generations a year, the juveniles of the overwintering generation generally appears in July. In the Darss-Zingster Bodden and the Bergumermeer, overwintering juveniles appear in late August/September. The **overwintering generation disappears** from the population generally within the same month the spring generation appears or 1 month later at the most. However in loch Etive, Barnegat, Schelde and Gironde, the overwintering adults only die 3 to 5 months later.

4.3 Maximal longevity / life span

Most epipelagic species of the littoral zone have relatively short lives of 2 – 9 months (Mauchline, 1972). *Neomysis integer* is estimated to be tri- or bivoltine (see Table 5). The winter generation has a longer life span than the spring and summer generations. The latter reach maturity within 1 – 2 months after having left the brood pouch and probably live for maximally 4 months (Mauchline, 1971). The winter generation has a retarded growth and maturation due to the low winter temperature, and starts reproduction only in spring of the following year. They are generally present for 9 – 11 months in the population (Table 5). Mauchline (1971b) reports for the Clyde Sea that remnants of the spring generation (born in June/July) contribute to the winter generation that reproduces in March/May and their longevity is thus maximally 12 – 13 months. Some survivors of the summer generation of the previous year probably are still present in the population of Hickling Broad the next summer (Irvine *et al.*, 1995) and longevity is estimated to be one year. Tattersall and Tattersall (1951) estimate a maximal longevity of 18 months.

Along the west coast of Scotland and Ireland, females of the overwintering generation die first, the males later (Mauchline, 1971; Parker and West, 1979), while in the Grevelingenmeer, Lake Veere, pond Den Inkel and the Schelde estuary females outlive the males (Borghouts, 1978; Platenkamp, 1983; Mees *et al.*, 1994). In the Bergumermeer the males and females died simultaneously (Beattie and de Kruijf, 1978). No difference in the mortality between the sexes is observed for spring and summer cohorts (Mees *et al.*, 1994).

4.4 Size-at-maturity

The animals from the spring and summer generations reach a smaller length at maturity in comparison with the overwintering generation (*e.g.* Mees *et al.*, 1994). In Frisian lakes for example, animals of the summer generation reach at most 15 mm TL, while adults of the overwintering generation reach a maximum length of 19 mm TL (Bremer and Vijverberg, 1982).

Marked differences are apparent in the growth patterns of the 2 sexes within each cohort. Adult females generally have a larger length than males. Adult females of (late summer) *Neomysis integer* (Baltic proper) are approximately 30 % larger than males (Weisse and Rudstam, 1989). Dry weight of adult males from the Baltic ranged from 2.7 to 3.2 mg (overall mean 2.9 mg) and for females between 4.0 and 4.8 mg (overall mean 4.2 mg) (Weisse and Rudstam, 1989). Mees *et al.* (1994) found adult males and females of the overwintering generation – respectively 10 and 14 mm SL (*i.e.* 12 and 16 mm TL) – to be larger than the spring/summer generation at respectively 9.5 and 10 mm SL (*i.e.* 11 and 12 mm TL).

Comparing the population dynamics of *Neomysis integer* in 2 lakes in SW Netherlands, Borghouts (1978) found the size at maturity to be significantly smaller in the more densely populated lake (Den Inkel). Size at maturity of the spring generation was respectively 15 – 19 mm TL and 10 – 13 mm TL in Lake Veere and Den Inkel; in summer respectively 10 – 15 mm TL and 7 – 9 mm TL.

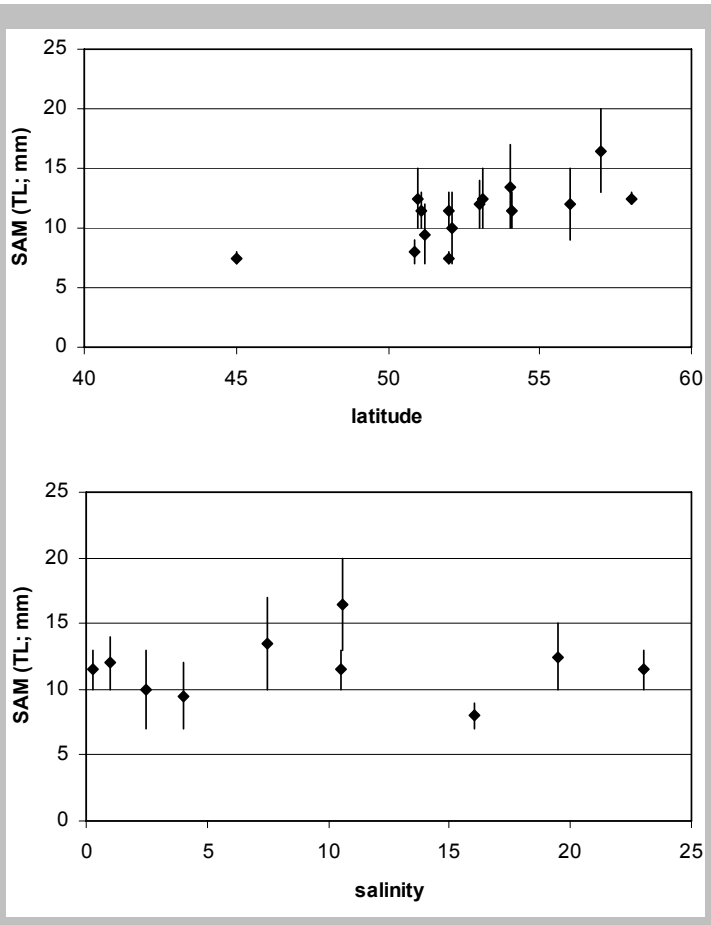


Figure 5: Effect of latitude and salinity on the size-at-maturity (SAM) of all available information in literature

Parker and West (1979) report the *Neomysis integer* of Loch Furnace to be smaller (10 – 14 mm TL) than elsewhere in Europe. Comparing all studies available up till 2005, this postulation no longer holds. The reported size-at-maturity in August/September is smallest (<10 mm TL) in the lakes Hickling broad, Den Inkel and the Gironde estuary. Largest size at maturity (>15 mm TL) are observed in the Ythan and the Darss-Zingster estuaries. Late summer size-at-maturity (August-September) is significantly related to latitude (Spearman rank = 0.66, p = 0.01), but no effect of salinity could be demonstrated (Figure 5).

The comparison of the published data resulted to difficult, mainly because of differences in the measuring and staging techniques used by the different authors. In order to overcome this problem, Mees *et al.* (unpublished) measured and staged *N. integer* collected in spring and summer from populations of the estuaries Guadalquivir, Gironde, Adour, Schelde, Eems, Elbe, Shannon and Lay (Figure 6). A clear logitudinal effect could be observed in the size-at-maturity of *N. integer*.

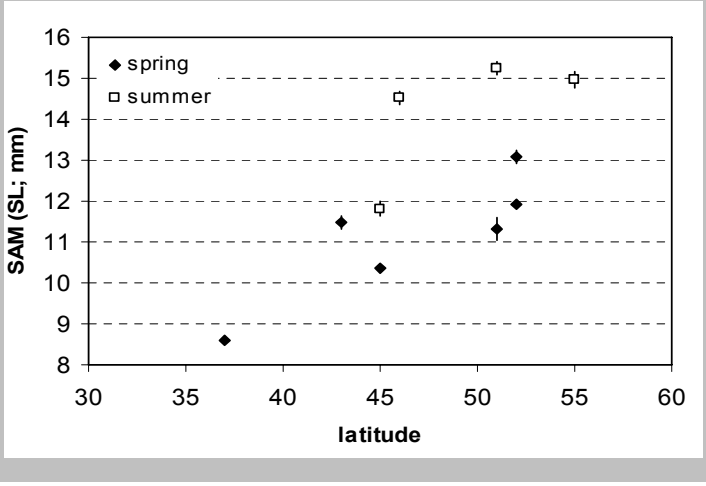


Figure 6: Effect of latitude on the size-at-maturity (SAM) of *Neomysis integer* from Guadalquivir, Gironde, Adour, Schelde, Eems, Elbe, Shannon and Lay (according to Mees *et al.*, unpublished).

4.5 Fecundity

The fecundity of a *Neomysis integer* population, *i.e.* the number of young recruiting to the population, is determined by (1) the prevailing temperatures which governs the breeding season, (2) size-at-maturity and associated brood size, (3) the number of successive broods, (4) intra-marsupial development rate and (5) intra-marsupial mortally. Also, (7) the size of the pool of large mysids that successfully reaches maturity, especially after the winter, and the time to reach maturity also have an important role in the population's fecundity (Irvine et al, 1995).

4.5.1 Breeding season

In the most western populations of *Neomysis integer* of the Scottish and Irish Lochs and the estuaries Severn, Tamar, Test and Conwy breeding is continuous over the year (Raymont *et al.*, 1966; Mauchline, 1971; Parker and West, 1979; Moore *et al.*, 1979; Hough and Naylor 1992; Moffat, 1996). However, periods of intensive breeding result in the production of distinct spring (March-May), summer (June-July) and overwintering (August-September) generations (Mauchline, 1971; Parker and West, 1979). There is always a proportion of the population breeding, but the intensity of breeding in winter (October-February) is low with gravid females representing less than 1 – 2 % of the population (Mauchline, 1971; Moore *et al.*, 1979). Moffat (1996) also mentions continuous breeding in the Tamar estuary, since juveniles are present all year round in the samples.

Other authors (see Table 5) report no reproductive activity during the cold winter period when no gravid females are found, but the breeding season varies substantially between the different populations. The species is described to breed for 5 – 7 months between April/May and September/October in most of the populations. *E.g. Neomysis integer* breeds for 7 months, respectively between April and October in the Schelde estuary (Mees et al., 1994) and between March and September in the pond Galgenweel (Soselisa, 1994; Fockedey, unpublished). The breeding season starts earlier in February/March in the *Neomysis integer* populations of Hickling Broad, Barnegat and Gironde and gets on to November in the populations of Darss-Zingster Bodden and Gironde. An extremely short breeding season of 4 months is recorded in Den Inkel, while extreme long (but intensive) breeding is observed in Hickling Broad (9 months) and the Gironde (10 months).

During the period of most intensive breeding (spring), the relative abundance of gravid females into the population can increase to 17 – 30 % of the total population or more than 80 % of the total number of adults females (Kinne, 1955; Mauchline, 1971; Moore *et al.*, 1979). In the Weser (Schuchardt *et al.*, 1989) and Bergumermeer (Beattie and de Kruijf, 1978) only 40 – 50% of the adult females were gravid. Schuchardt *et al.* (1989) ascribe this relative low value of the proportion of gravid females in the breeding season to (1) an inaccurate separation of the subadult and adult females during the analysis while distinguishing stages; or (2) to high relative numbers of females with the brood recently hatched, or (3) to a relative long period of sexual inactivity in between subsequent broods, although a bad conservation can also be the cause of this low number (Mees, personal communication).

The first breeding in spring is quite synchronous. Given the multiple broods of one female, the synchronicity diminishes over the course of summer and it becomes more and more difficult to distinguish the breeding efforts in subsequent cohorts (Schuchardt *et al.*, 1989). Some authors give the advice to consider the whole period of development of the population as one period of continuous reproduction with 2 or 3 periods of intensive breeding which can be followed for some time as pulses in the length frequency distribution of the population (Mauchline, 1971; Beattie and de Kruijf, 1978; Bremer and Vijverberg, 1982; Schuchardt *et al.*, 1989).

Table 6: Length-specific brood size regressions

Location	Lat	Salinity (psu)	Relation brood size (F) and length		Time period	Source
Estuary – Ythan (Scot, UK)	57°N	10.5	$F_I = 6.0209\ TL - 45.0079$	n=198; r=0.61	Stage I, winter generation	Astthorsson, 1980
			$F_{III} = 5.2774\ TL - 42.1283$	n=86, r=0.36	Stage III, winter generation	
			$F_I = 1.2470\ TL + 12.4118$	n=251; r=0.36	Stage I, summer generation	
			$F_{III} = 2.6434\ TL - 1.2122$	n=297, r=0.38	Stage III, summer generation	
Fjord – Loch Etive (Scot, UK)	56°N	>18	$\log F = 1.0385 \log (TL^3) - 2.0887$	N=750; r=0.739; p<0.01	All year	Mauchline, 1973
Estuary – Kiel Canal (G)	54°N	18-33	$F = 0.0082\ TL^{3.19}$	No information	All year	Kinne, 1955
Baltic – Darss-Zingst (G)	54°N	0.5-15	$F=TL^{1.397298}$	$R^2 = 0.95$	Winter	Arndt and Jansen, 1986
			$F=0.056998\ TL^{2.26274}$	$R^2=0.92$	Summer	
Lake – Bergumermeer (NL)	53°N	0.2-0.4	$F = 0.328\ TL^{1.62}$	No information	All year	de Kruijf (1977)
Lake – Hickling Broad (Eng, UK)	52°N	2.7-3.6	$\ln F = -2.41 + 2.28\ \ln SL$	n=10; r^2=0.96; p<0.001	1988	Irvine et al., 1995
			$\ln F = -4.11 + 2.75\ \ln SL$	n=9; r^2=0.99; p<0.001	1989	
Lake – Slotermeer (NL)	52°N	0.2-0.4	$F = 0.0522\ TL^{2.34}$	n=260, r=0.77	All year	Bremer and Vijverberg, 1982
Lake – Tjeukemeer (NL)	52°N	0.2-0.4	$F = 0.00706\ TL^{3.25}$	No information	All year	Vijverberg, unpublished*
Lake – Den Inkel (NL)	51°N	15-16	$F = 0.957(TL-7)^{1.7512}+3.3$	No information	All year	Borghouts, 1978
Lake – Veerse meer (NL)	51°N	11-24	$F = 0.957(TL-7)^{1.7512}+3.3$	No information	All year	Borghouts, 1978
Estuary – Schelde (NL/B)	51°N	15	$F = 0.0365\ SL^{2.656}$	n=420, r=0.866; p<0.001	All year	Mees et al., 1994
		15	$\ln F=-3.720+2.828\ \ln SL$	n=167, r=0.655; p<0.01	Winter	
		16	$\ln F=-2.307+2.223\ \ln SL$	n=149, r=0.562; p<0.01	Spring	
		16	$\ln F=-0.974+1.673\ \ln SL$	n=104, r=0.615; p<0.01	Summer	
Lake – Galgenweel (B)	51°N	4	$F = 0.008\ SL^{3.242}$	N=1070; r=0.852; p<0.001	All year	Soselisa, 1994; Fockedey, unpublished

*Cited in Bremer and Vijverberg, 1982; **F**: Brood size (in number of embryo per marsupium); **TL**: Total length of the female (in mm), as distance between the base of the eyestalk and the posterior end of the uropods excluding the setae (Mauchline, 1971) = distance between the front of the eye till the end of the telson (Kinne, 1955) = 1.05x (distance between the front edge of the eye and the end of the uropods excluding the setae (Vorstman, 1951)); **SL**: Standard length of the female (in mm); **B**: Belgium; **Eng, UK**: England; **G**: Germany; **NL**: The Netherlands; **Scot, UK**: Scotland

4.5.2 Brood size

The number of embryos/larvae in the marsupium depends on body size, the size of the individual eggs, and the season of the year. Brood size also differs between populations living at different latitudes (Mauchline, 1980; Mees et al., unpublished). The maximum brood size reported for *Neomysis integer* is 98 embryos per female in the Ythan estuary (Astthorsson, 1980) and in the Schelde estuary (Mees *et al.*, 1994).

For *Neomysis integer* brood size is demonstrated to be highly depended on female **body size** (Table 6). Bremer and Vijverberg (1982) report a little variation of this relationship over the course of the year, but other authors (Astthorsson, 1980; Arndt and Jansen, 1986; Mees *et al.*, 1994) observed a significantly different size-fecundity relationship between the overwintering generation and the spring- and summer generations.

Seasonal variation in size at maturity, and consequently in fecundity, between different cohorts has been reported. The late summer and autumn breeding animals usually have a smaller size at maturity and related fecundity as compared to those breeding in spring and early summer (Vorstman, 1951; Kinne, 1955; Borghouts, 1978; Parker and West, 1979; Astthorsson, 1980; Bremer and Vijverberg, 1982; Arndt and Jansen, 1986; Mees *et al.*, 1994). Females of the winter generation generally produce more eggs than the spring and/or summer females of the same body size (Mauchline, 1971; Arndt and Jansen, 1986; Mees *et al.*, 1994). For example, the brood size of *Neomysis integer* from the overwintering generation is 50 (40 – 65 ind^{-1}) eggs per female in the Darss-Zingst estuary of the southern Baltic (Arndt and Jansen, 1986); females of the summer generation generally produce far less eggs (9 – 28 ind^{-1}). In Loch Etive breeding continues during winter at a rate of 12 – 27 ind^{-1}, while brood size in spring, early summer and late summer was 29 – 46, 14 – 57 and 14 – 32 ind^{-1}, respectively (Mauchline, 1971). Also, size-specific brood size can vary between successive years (Irvine *et al.*, 1995).

Bremer and Vijverberg (1982) and Schuchardt *et al.* (1989) demonstrated a lower brood size in almost freshwater populations (0.2 psu) in comparison to populations living in more saline water (10 – 18 psu).

Comparing the size-specific brood size of *Neomysis integer* living in the Schelde estuary (15 psu) and a population living in a nearby brackish pond (5 psu), Fockedey and Mees (unpublished) can make a similar conclusion (Figure 7).

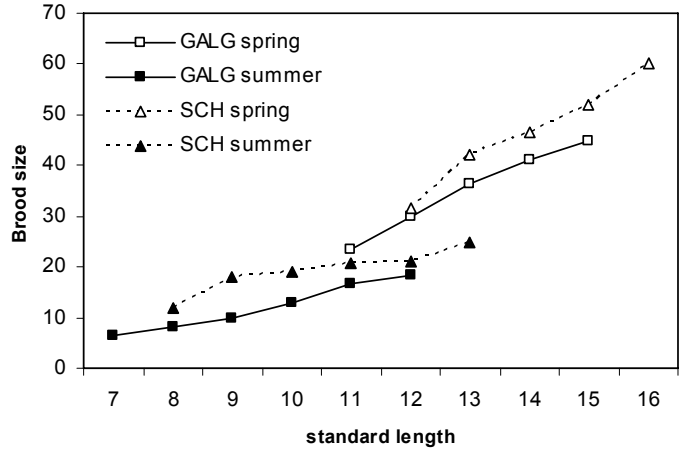


Figure 7: Size-specific brood size of *Neomysis integer* in Galgenweel (GALG) and Schelde (SCH) in the spring and summer generation.

Mees *et al.* (unpublished) report the Schelde population of *Neomysis integer*, living at a higher **salinity** (15 psu) than other estuarine populations (< 5 psu), to be characterised by the largest brood size.

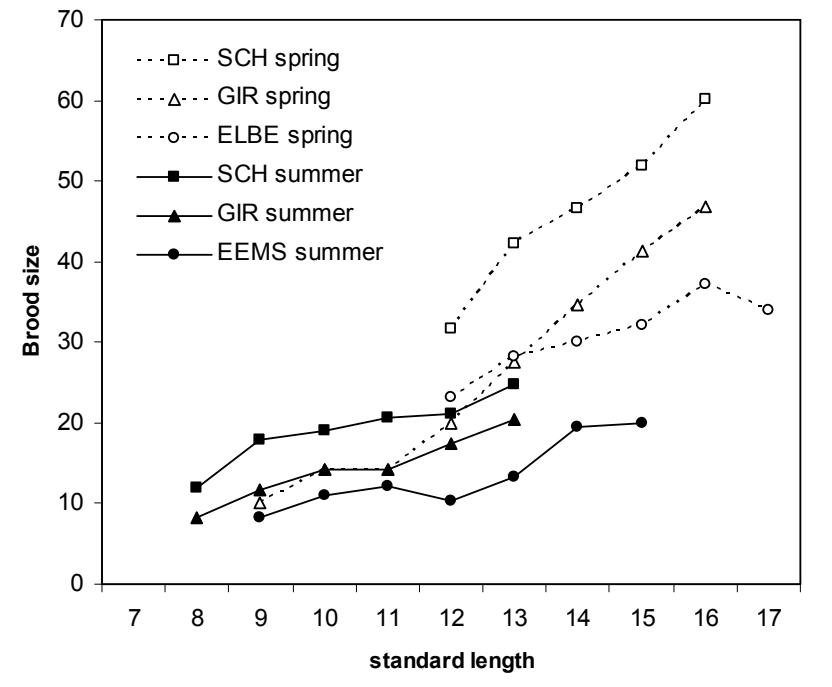


Figure 8: Effect of latitude on the brood size of the *spring and summer generation* in the Elbe (ELBE), Eems (EEMS), Schelde (SCH) and Gironde (GIR) estuaries.

It remains unclear why most estuarine populations live at a low salinity that finally results in a relatively smaller brood size. Possible explanations may include a trade-off for suboptimal brood sizes with competitive advantages of living in low-salinity waters which in estuaries coincide with higher turbidity, lower predation pressure, a higher food availability, less competition with other mysids or benthic filter feeders (Mees *et al.*, 1994).

4.5.3 Number of subsequent broods per cohort

Whether a higher brood size also results in a higher fecundity is difficult to say based on field data. Smaller brood sizes may be compensated by the production of several subsequent broods per female in the spring and summer generations. However, without laboratory observations, it is difficult to decide whether females breed more than once (Vorstman, 1951). Tattersall and Tattersall (1951) coin the possibility of 3 or 4 subsequent broods in the spring individuals. Astthorsson (1980) assumes that *Neomysis integer* in the Ythan produces 2 – 3 subsequent broods. Extrapolating laboratory derived development times to the field observations, Kinne (1955) concludes that the winter generation of *N. integer* in the Kiel Canal produces 3 broods and the summer generation 4 – 6 broods. Mees *et al.* (1994) report unpublished culture experiments (Janssen, unpublished) where *N. integer* produce 5 consecutive broods at 20 °C.

In the laboratory (Fockedey, unpublished; Table 7) *Neomysis integer* produced 4 successive broods at 15 °C, independent of salinity (5 or 15 psu). At 20 °C, up to 5 broods were produced per female. The time between successive brood is 0 – 4 days and 0 – 7 days at 15 and 20 °C.

Table 7: Unpublished laboratory experiments on the *in vivo* intra-marsupial development of *Neomysis integer.*

		15°C – 5 psu		15°C – 15 psu		20°C – 5 psu	
length experiment (days)		61		61		55	
# females brought into experiment		38		32		43	
50% mortality (days)		16		33		21	
Mauchline (1980)	Wittmann (1981)	days	%	days	%	days	%
Egg	Embryonic phase	5.3	32	5.1	32	3.2	29
Larva	Nauplioid phase	6.5	40	6.7	42	4.2	38
Eyed larva	Post-nauplioid phase	4.6	28	4.3	26	3.7	34
Incubation time (days)		16.5		16.1		11.1	
# successive broods		max. 4		max. 4		max. 5	
time between successive broods (days)		0 – 2		0 - 4		0 – 7	
# juveniles liberated per brood		24 / 13 / 6 / ?		22 / 11 / 7 / ?		7 / 7 / 6 / ? / ?	

4.5.4 Mortality during intra-marsupial development / hatching success

The number of early embryos in the marsupium always outnumbers the number of later larval stages (Astthorsson, 1980; Mauchline, 1980). Generally, 10 % of the young are lost in a premature condition (Mauchline, 1973; Wittmann, 1981). Mortality or loss of eggs initially laid in the marsupium was estimated to be 27 % for the winter generation; for the summer generation the marsupial mortality was dependent on the body size of the female and was 25, 17 and 3 % for gravid females with a total length of 12, 14 and 16 mm, respectively (Astthorsson, 1980). By comparing the abundance of embryos/larvae in brood carrying females and the subsequent abundance of neonates (< 3 mm) in the field, Irvine *et al.* (1995) suggest a high mortality (> 50 %), especially in the early embryo stages.

Little data were available on the hatching success of embryos of *Neomysis integer*. Vlasblom and Elgershuizen (1977) tested survival of embryos at a relative narrow range of salinities at 15 °C. **Hatching success** was optimal at a salinity between 11 and 18 psu. The optimal salinity for hatching is strongly related to the salinity the animals are adapted to and hatching percentage amounted to 60 – 80 % for animals adapted to low salinity (7 psu) and 40 – 60 % for animals adapted to higher salinity (23 psu). The early embryos had a smaller salinity tolerance than the later larvae (Vlasblom and Elgershuizen, 1977).

More in-depth information on the intra-marsupial development of *Neomysis integer* and the impact of environmental variables on mortality, hatching success, and the duration of the developmental stages is available in Fockedey *et al.*, submitted b – Chapter 6). Information on the impact of biotic factors (size female, brood size, egg size) is still lacking.

4.5.5 Morphology of the developing embryos

Mauchline (1980) divides the intra-marsupial development into three easily distinguishable stages. The early embryo, at first egg-like but later with rudiments of antennae and abdomen developing, are named ‘stage I’ or ‘eggs’. The latter name however is a confusing term, since eggs are immediately fertilized after being deposited from the oviduct into the marsupium. Better is to use the term egg-shaped embryo or (sub)-spherical embryo. The stage I embryos are still surrounded by the egg membrane. Stage II larvae or ‘eyeless larvae’ are hatched from the egg membrane and develop the antennae and the thoracic appendages, while the eyes become pigmented. Stage II terminates in a moult. Stage III or ‘eyed larvae’ have stalked eyes and moult to a free living juvenile when released from the marsupium. Most authors follow this division (*e.g.* Wittmann, 1984).

Before, de Kruijf (1977) described 6 distinct developmental stages of the embryo in the brood chamber of *Neomysis integer* and can be distinguished as follows: Stage I is a simple egg-like structure, spherical in shape. The next stage (II) contained a rudimentary abdomen with a clear distinction between the rounded anterior and the pointed posterior of the larva. Development into stage III comprised a further extension of the abdomen, a rudimentary telson and two thoracic appendages. In stage IV the body was further extended and had the clear beginning of abdominal segmentation. In stage V there was a first projection of the head with development of the eyes, further segmentation of the abdomen, and first development of pleopods. Stage VI had distinct eye projections and development of the pleopods and uropods. The body contained an obvious carapax and elongated abdomen. The morphological stages described by de Kruijf (1977) were used by Irvine et al. (1995) in the intra-marsupial staging of *N. integer*, but Fockedey *et al.* (submitted b – Chapter 6) considered them to be impractical and based on subjective criteria. Wittmann (1981) even used a third set of criteria to stage the embryos and larvae of mysids in general and Fockedey *et al.* (submitted b – Chapter 6) compares the different terminologies used.

Detailed descriptions of the histology of successive larval stages of *Neomysis integer* are given by Wagner (1896) and Needham (1937). External morphological descriptions of the intra-marsupial development are available by Kinne (1955) and de Kruijf (1977). A description of the embryonic and larval stages of *N. integer*, together with pictures illustrating the development, is given in Fockedey *et al* (submitted b – Chapter 6).

4.5.6 Duration of the intra-marsupial development

Neomysis integer, like all other mysid species, carries its embryos in a marsupium within which the entire larval development takes place from oviposition to the release of free swimming juveniles (Wittmann, 1984). No correlation could be found between the duration of the intra-marsupial development and the prevailing salinities (0.4 – 16 psu) at 15 °C (Vlasblom and Elgershuizen, 1977). Individuals adapted to a higher salinity of 23 psu are able to develop their embryos, but over a longer time span (*i.e.* 17 – 22 days) than the population adapted to lower salinity of 7 psu (15 – 18 days). Irvine *et al.* (1995) report an intra-marsupial development time of 42 days at 6 °C and 5.8 days at 20 °C measured *in vivo* in laboratory experiments. Indirectly estimated development times are obtained from field observation in Hickling Broad (Irvine *et al.*, 1995): 56 days at 7 – 16.5 °C, 29 days at 16.5 – 18.0 °C and 13 – 14 days at 19.5 – 20 °C.

Generally, most breeding females are found with eyeless larvae in their marsupium, indicating that this is the longest larval stage in mysids intra-marsupial development (Mauchline, 1973; 1980; Parker and West, 1979). Astthorsson (1980) found on average almost equal proportions of gravid females with spherical larvae, eyeless larvae and eyed larvae in a 2 year study of the *Neomysis integer* population from the Ythan.

Following the intra-marsupial development in detail *in vivo*, *i.e.* through the semi-transparent oostegites, is difficult (Fockedey, unpublished; see table 7) or needs anaesthetization (Irvine *et al.*, 1995). Information on the dependence of the intra-marsupial development time with temperature or/and salinity is reported in Fockedey *et al.* (submitted b – Chapter 6).

4.5.7 Size, growth and intra-marsupial production of the embryos

Embryo size of *Neomysis integer* from Hickling Broad generally falls within the range of 0.48 – 2.1 mm (Irvine *et al.*, 1995). The diameter of the egg-shaped embryo of *N. integer* from Loch Etive equals 0.5 – 0.6 mm (Mauchline, 1972). The length of the eyeless larvae is 1.3 – 1.5 mm (Mauchline, 1972). The length of the eyed larvae is 1.9 – 2.1 mm (Mauchline, 1972) and the total length of freshly emerged juvenile is ± 2.0 mm, *i.e.* 1.6 – 2.4 mm (Vorstman, 1951; Kinne, 1955; Mauchline, 1971; 1972; Astthorsson, 1980; Aaser *et al.*, 1995; Moffat, 1996).

The biomass of embryos of *Neomysis integer* was estimated from their volumes as 11.3 µg DW for the early spherical embryos, 16.0 µg DW for ellipsoid embryos and 13 – 14.4 µg for the later larval stages (Irvine *et al.*, 1995). The size of the (earliest) embryos in *Neomysis integer* can vary seasonally (Mauchline, 1973; Irvine *et al.*, 1995), with winter embryos being larger than in spring or summer. The smaller embryo appeared to contain fewer and smaller oil globules (Mauchline, 1973). Although no more details are given, Irvine *et al.* (1995) estimated the intra-marsupial production rate of *Neomysis integer* at all times to be less than 10 % of the total production.

4.5.8 Instantaneous birth rate

The instantaneous birth rate b' of *Neomysis integer* can be estimated from the equation:

$$b' = \ln((E/N) + 1)/D$$

with E the egg density, N the total density of all life stages and D the development time at the appropriate temperature (Paloheimo, 1974). Since the mortality during the first embryonic stages is high (> 50 %) instantaneous birth rate b' was calculated by Irvine *et al.* (1995) based on the egg ratio E and development time of the latest larval stages only. In the reproductive periods (June to October) the instantaneous birth rate of *N. integer* in a brackish lake (Hickling broad) was measured as 0.05 – 0.15, *i.e.* between 5 and 15 births per 100 individuals (Irvine *et al.*, 1995). Generally, mysids have a low instantaneous birth rate and thus a low intrinsic rate of natural increase (Fager and Clutter, 1968).

4.5.9 Instantaneous rate of population change

Instantaneous rate of population change r' for successive population estimates (N_{t+1}, N_t) is calculated from

$$r' = (\ln N_{t+1} - \ln N_t)/t$$

with t the sampling interval. Generally r' is highest during periods of high reproduction and/or immigration into the population. Irvine *et al.* (1995) report the instantaneous rate of population change r' of *Neomysis integer* in a brackish lake (Hickling Broad) to be +0.06 to -0.10. Positive measurements occurred when the *N. integer* population was highly reproductive. A positive peak in r', measured before the reproductive period (during early spring), reflect the influx of adults into the population through immigration.

4.6 Mortality

Under certain conditions (a.o. that individual growth is described by a von Bertalanffy growth model) the total mortality of a population is equal to the P/B ratio of the population (Allen, 1971). Mortality rate (Z) can also be obtained from a length converted catch curve (Mees et al., 1994) and amounted from 3.15 to 4.41 over the year. Mortality rate was not different between the sexes for the summer cohorts of *Neomysis integer* in the Schelde (Mees et al., 1994).

Instantaneous dead rate d' is estimated as the difference between the instantaneous birth rate and the instantaneous rate of population change. Instantaneous dead rate of a *Neomysis integer* population in Hickling Broad amounts between 0.02 and 0.15 (Irvine *et al.*, 1995), *i.e.* 2 to 15 animals per 100 animals die daily. In wintertime dead rate is minimal. A negative dead rate in early spring indicates the immigration of individuals into the water mass from outside.

4.7 Sex-ratio

A shifted sex ratio (further always expressed males:females) is a well described phenomenon in mysid species (Mauchline, 1980). Differences in the sex-ratio over time can be explained by a differential mortality of one of the sexes, while spatial differences in the sex-ratio may be linked to sexual differential habitat preferences as described for other estuarine crustaceans (like *Palaemon longirostris*, Sorbe, 1983b; Schuchardt *et al.*, 1987). In most *Neomysis integer* populations the sex ratio is close to 1:1 (Mauchline, 1971). The sex ratio in Frisian lakes, ranged between 1:1.5 and 1:0.7; with a mean close to 1:1 (Bremer, 1980; Bremer and Vijverberg, 1982).

In loch Furnace (Parker and West, 1979), the sex ratio was strongly biased towards the females, being greatest in April (1:9). Only in June and August when the breeding females of the spring and summer generation were dying off, males outnumbered the females. Females are always more abundant than males in the Severn estuary (1:2 to 1:6) (Moore *et al.*, 1979). In the Kiel canal sex-ratio is 1:1.9 (Kinne, 1955). In the lower reaches of the Weser estuary significantly more females than males were caught (Schuchardt *et al.*, 1989). This shifted sex-ratio is different for the different generations, respectively 1:6 in the overwintering generation, and 1:2 – 1:4 in summer. In a study in the Tamer estuary (Moffat and Jones, 1992), the proportions of males, females and juveniles were not related to temperature. The sex-ratio ranged between 1:1 and 1:2 for most of the year, except for October when females outnumbered males with a ration of 1:9.

In the Weser and Gironde estuaries, a shifted sex-ratio was observed along the longitudinal axis of the estuary (Sorbe, 1980; Schuchardt *et al.*, 1989). More females (1:5) were caught in the most upstream reaches while in the mesohaline region an almost equilibrated ration was found (1:0.9). Along the longitudinal transect of the Ythan the overall sex-ratio equals 1.0 (Astthorsson, 1980). No information is available on this segregation of sexes along the salinity gradient for other estuaries.

4.8 Field-based growth curves

Growth curves of all cohorts present over the year have been derived from field data for several estuarine *Neomysis integer* populations (Mauchline, 1977; Astthorsson, 1980; Astthorsson and Ralph, 1984; Mauchline, 1985; Mees *et al.*, 1994), as well as in the Baltic (Arndt and Jansen, 1986) and for brackish lakes (Aaser *et al.*, 1995). Bremer and Vijverberg (1982) and Beattie and de Kruijf (1978) only derived a growth curve of the first summer generation of *N. integer* from Slotermeer and Bergumermeer.

Growth curves can be fitted to a growth model. The generalized von Bertalanffy growth function (Gayanilo *et al.*, 1989) is originally designed for describing fish growth but is recently applied to mysids growth with good results (Mees et al., 1994; Soselisa, 1994; Fockedey, unpublished). To describe the growth stop during the period of coldest temperatures of the winter generation, a seasonally oscillating version of the latter growth model can be used. Mees *et al.* (1994) demonstrated that a good fitting of the von Bertalanffy growth model in *Neomysis integer* was only possible if the differences in growth between the sexes were taken into account. *N. integer* grows almost linearly up to sexual maturity. From then on the growth rate slows down (Astthorsson, 1980).

To date, the field-estimated growth parameters have rarely been validated with laboratory observations. Only Astthorsson (1980), compared the field derived growth curve for *Neomysis integer* from the Ythan estuary with a growth curve derived from laboratory growth experiments at 9 and 16°C, however based on very few observations. Fockedey *et al.* (in press – Chapter 3) compared laboratory-based growth parameters estimates of *N. integer* with those from field studies in the Schelde estuary and the brackish pond Galgenweel.

4.9 Laboratory-based growth curve

Very little detailed information is available on the growth curves and growth rate of *Neomysis integer* cultured under constant laboratory conditions. Bremer and Vijverberg (1982) refer to a study performed by Schrotenboer (1980) who estimated growth and development rate of *N. integer* by means of laboratory culture at 15 °C and 17.5 °C over 110 days. The growth curve at 15 °C was linear and the one at 17.5 °C was curvilinear.

Kuhlmann (1984) described the growth of juvenile *Neomysis integer* (between 3 and 10 mm) to be linear. Astthorsson (1980) constructed average growth curves for *N. integer* based on laboratory length-specific measurements of the intermoult period and growth factor and an initial juvenile length of 2.4 mm TL. Irvine *et al.* (1995) describe post-marsupial growth under constant laboratory conditions (20 °C) as a linear regression: SL = 2.8 + 0.105 days ($n = 52$; $r^2 = 0.92$; $p < 0.001$).

Field observations of the same population (successive peaks in the length-frequency distributions) also suggested a linear growth rate. Fockedey *et al.* (in press – Chapter 3) described growth of *N. integer* under 8 salinity/temperature combination. At all treatments, except the coldest (8 °C) where growth was linear, the growth curves were best fitted with a von Bertalanffy growth model.

4.10 Growth rate

Field- and laboratory-based growth rates of *Neomysis integer* from several investigations are presented in Table 8. However, Astthorsson and Ralph (1984) questioned the validity of growth rates calculated from field data, based on the grounds that it is often difficult to follow the cohorts. On the other hand, growth rates calculated from laboratory experiments may be influenced by the experimental conditions. Arndt and Jansen (1986) and Bremer and Vijverberg (1982) found higher growth rates in a natural population in comparison with the available laboratory growth rates. When comparing the data from Table 8 this statement cannot be confirmed as maximal laboratory growth rates are all higher than those recorded in the field.

The growth rate of *Neomysis integer* kept in laboratory cultures at 20 °C and feeding on copepods and Cladocera was 1 mm per 9.5 days, *i.e.* 0.11 mmTL d^{-1} (Irvine *et al.*, 1995). The mean growth rate of *N. integer* maintained on a diet of *Artemia* nauplii was 0.06 mmTL d^{-1} at 9 °C and 0.09 mmTL d^{-1} at 16 °C (Astthorsson, 1980; Astthorsson and Ralph, 1984). Growth rate of the same population in the field (Ythan) was estimated from the time spent within each 1 mm size class and varied between 0.03 and 0.16 mm d^{-1} in the growth season from May to September, and from 0.03 – 0.13 mm d^{-1} in wintertime, *i.e.* from November to April (Astthorsson, 1980). Other field derived maximal growth rates amount to 0.13 mm d^{-1} in the Schelde (Mees *et al.*, 1994) and 0.16 mm d^{-1} in Slotermeer (Bremer and Vijverberg, 1982). Juveniles, just released from the marsupium, grew between 0.142 and 0.281 mm d^{-1} in laboratory experiments at different temperature/salinity combinations (Kuhlmann, 1984).

The growth rate is related to the length of the mysid and differs between and within the cohorts. In the Schelde (Mees *et al.*, 1994) *Neomysis integer* grows at a rate of 3 – 4 mm $month^{-1}$ in autumn, and ceases completely during wintertime. In spring the mysids regained their fast growth rate that they maintained during summer. In these cohorts the smaller juveniles and subadults grew fastest (3 – 4 mm $month^{-1}$, *i.e.* 0.10 – 0.13 mm d^{-1}), while the larger mysids grew slower (1 – 2 mm $month^{-1}$; *i.e.* 0.03 – 0.06 mm d^{-1}). Aaser *et al.* (1995) formulated semi-log transformed linear relationships between the cohorts-specific growth rate and the (total) length of *N. integer*.

The growth rate of *Neomysis integer* is related to environmental temperature (Kinne, 1955; Astthorsson and Ralph, 1984), although it cannot be seen as the only determining factor. At the same temperature of for example 12 °C, the growth rate of *N. integer* accelerates in spring, but decreases in autumn (Schuchardt *et al.*, 1989). Probably the length of the daylight period also plays an important role (Schuchardt *et al.*, 1989). In the Bergumermeer, *N. integer* living near the warm water discharge of a power plant grows equally fast in spring and summer as in other parts of the lake. However, growth can continue longer into autumn in the warmer water sites (Beattie and de Kruijf, 1978).

Individual production or growth in terms of dry weight was 0.02 mgDW d^{-1} and 0.03 mgDW d^{-1}, respectively at 9 and 16 °C respectively (Astthorsson, 1980). Maciejewska and Opalinski (2002) measured the average body wet weight increase over an 18 days period at 14 °C feeding *ad libitum* on frozen *Daphnia*: 0.057 mgWW ind^{-1} d^{-1} or 0.01 mgWW $mgWW^{-1}$ d^{-1} for the smaller animals (initial length ± 8mm), and 0.0002 mgWW ind^{-1} d^{-1} or 0.0003 mgWW $mgWW^{-1}$ d^{-1} for the larger animals (initial length ± 15 mm). Production rates of *Neomysis integer*, calculated from field based growth curves, amounts 0.611 mgWW $mgWW^{-1}$ d^{-1} (Beattie and de Kruijf, 1978) in Bergumermeer, and 0.283 mgWW $mgWW^{-1}$ d^{-1} in Slotermeer, two Frisian brackish lakes (Bremer and Vijverberg, 1982). In the laboratory experiments at 15 °C performed by Schrotenboer (1978), *N. integer* individuals grew 0.277 mgWW $mgWW^{-1}$ d^{-1}.

Table 8: Growth rates available for *Neomysis integer* in literature (Adapted from Winkler and Greve, 2002)

Field	Temperature Salinity	Period	Stage	Growth rate (mm TL d^{-1})	
Hickling Broad	20 – 22 °C	Jun/Aug		0.18	Irvine et al., 1995
	?	Sept/Oct		0.08-0.11	
	?	Nov/Apr		0.04	
	?	Apr/May		0.14	
Schelde estuary	17 °C	Autumn		0.10-0.13	Mees et al., 1994
	9 °C	Winter		0	
	18 °C	Spring/Summer	Juvenile	0.10-0.13	
	18 °C	Spring/Summer	Adult	0.03-0.06	
Slotermeer	15 – 20 °C	May-Oct	2-14 mm TL	0.13-0.16	Bremer and Vijverberg, 1982
Ythan estuary	?	Summer	Juvenile	0.13-0.16	Astthorsson, 1980; Astthorsson and Ralph, 1984
	?	Summer	Adult	0.03-0.06	
	?	Winter	Juvenile	0.10-0.13	
	?	Winter	Adult	0.03-0.06	
Lake Ferring	?	Spring/Summer	3.14 x 0.567^{TL} (n=5; r^2=0.82; p<0.03)		Aaser et al., 1995
		Winter cohort (< winterstop)	2.41 x 0.538^{TL} (n=7; r^2=0.97; p<0.001)		
		Winter cohort (> winterstop)	0.024 mm d^{-1} (n=5; p<0.0001)		

Laboratory	Temperature Salinity	Food	Stage	Growth rate (mm TL d^{-1})	
Laboratory	14 °C – 13 psu	Green algae	Juvenile	0.142	Kuhlmann, 1984
	14 °C – 17 psu	*Daphnia* sp.		0.161	
	14 °C – 24 psu	*Artemia* sp.		0.166	
	17 °C – 13 psu			0.229	
	17 °C – 17 psu			0.233	
	17 °C – 20 psu			0.232	
	17 °C – 24 psu			0.189	
	19 °C – 13 psu			0.231	
	19 °C – 17 psu			0.274	
	19 °C – 20 psu			0.224	
	21 °C – 17 psu			0.281	
	21 °C – 20 psu			0.271	
	21 °C – 24 psu			0.186	
	24 °C – 17 psu			0.204	
	24 °C – 20 psu			0.194	
	24 °C – 24 psu			0.193	
Laboratory	20 °C	Copepoda Cladocera	?	0.11	Irvine et al., 1995
Laboratory	9 °C	*Artemia*	3-13 mm	0.02-0.09	Astthorsson, 1980; Astthorsson and Ralph, 1984
	16 °C	*Artemia*	3-12 mm	0.03-0.15	
Laboratory	10 °C	*Artemia*	3-7 mm	0.05 – 0.09	Winkler and Greve, 2002
	15 °C	*Artemia*	3-7 mm	0.12 – 0.19	
	10 °C	*Artemia*	8-12 mm	0.03-0.08	
	15 °C	*Artemia*	8-12 mm	0.03-0.09	

4.11 Moulting

Growth of mysids can be described in terms of intermoult periods (IMP) and growth factors (GF) (Mauchline, 1976; 1977; 1977b). The IMP is the period between two successive moults and the GF is the percentage increase in length at each moult. Generally the intermoult period increases when the animals become larger, while the growth factor decreases steadily at successive moults. Although mysids grow in discrete steps when moulting, the length increase at a moult can also be expressed as the mean length increase within the intermoult period or intermoult growth rate (GR) (Winkler and Greve, 2002).

Detailed information on the growth and moulting of *Neomysis integer* is scarce. Schrotenboer (1980), Astthorsson (1980), Astthorsson and Ralph (1984), Kuhlmann (1984), Irvine *et al.* (1995), Gorokhova (2002) and Winkler and Greve (2002) all performed growth experiments with *N. integer*, but only at very few temperature-salinity combinations or at limited periods within the life cycle.

According to Mauchline (1976; 1977; 1977b) the intermoult period is related in an exponential function to body length and moult number. Astthorsson (1980) and Gorokhova (2002) confirm this log-linear relationship for *Neomysis integer*. The relationship differed between the two experimental temperatures 16 °C and 9 °C (Astthorsson, 1980): the intermoult period ranged from approximately 4 and 8 days in juveniles to 12 and 16 days in adult *N. integer* at 16 and 9°C, respectively. The intermoult period is inversely related to temperature (Astthorsson, 1980). At higher temperatures the moulting occurs more frequently, resulting in a higher growth rate (Astthorsson and Ralph, 1984). However Winkler and Greve (2002) and Fockedey *et al.* (in press – Chapter 3), basing their conclusions on a more extended dataset, could not confirm the exponential relation between IMP and body length or moult number. No differences in IMP were found between the sexes (Gorokhova, 2002; Fockedey *et al.*, in press – Chapter 3).

Mauchline (1976; 1977; 1977b) demonstrated that the growth factor in mysids is related in an exponential function to mysid length and to moult number. The log-linear relationship was confirmed for *Neomysis integer* (Astthorsson, 1980; Astthorsson and Ralph, 1984; Gorokhova, 2002). Temperature (9 and 16°C) did not have an effect on the growth factor in the experiments of Astthorsson (1980) and Astthorsson and Ralph (1984), but was affected by temperature (8°C – 25°C) in the experiments of Fockedey *et al.* (in press – Chapter 3). The growth factor ranged from 14 % in juveniles to 3 % in adult *N. integer* (Astthorsson, 1980). However Winkler and Greve (2002) and Fockedey *et al.* (in press – Chapter 3), basing their conclusions on a more extended dataset at more temperature/salinity combinations, could not confirm the exponential relationship between GF and body length or moult number.

The moulting process can be grouped into 3 major sub-periods (Gorokhova, 2002): the postmoult, intermoult (not to confuse with the IMP (Mauchline, 1976; 1977a; 1977b) and premoult periods. Each period constitutes 34 %, 22 % and 44 % of the intermoult period in *Neomysis integer* (Gorokhova, 2002). Development of the new exoskeleton occurs during the premoult stage and involves the enzymatic digestion of the existing post-ecdysial layer and re-absorption of material from this layer into the new cuticle. At the time of moulting (ecdysis), this pre-ecdysial layer is fully developed. Another portion of the exoskeleton is formed after ecdysis, and the synthesis of this post-ecdysial layer is associated with the incorporation of assimilated nutrients into newly formed matter. Thus the old, shed cuticle contains material synthesized during one moult cycle before the last one (Gorokhova and Hansson, 1997).

Moulting in *Neomysis integer* always occurs at night (Fockedey, personal observation). The removal of exuvia proceeds fast (< 1 min) in three steps: (1) carapace and thoracopods, (2) abdomen with abdominal appendages, and (3) first antennae. Freshly moulted individuals lie on the bottom for a while (5 – 7 min), then swim and behave normally. The formation of the statolyth at the base of the endopod is completed within 3h after ecdysis (Gorokhova, 2002). In experiments, *Neomysis integer* is often seen to eat its own cast moults, even if enough other food is available. Possibly, the mysid can acquire important minerals and organic matter in this way (Astthorsson, 1980).

4.12 Intermoult growth

Mauchline (1973), Childress and Price (1978), Cuzin-Roudy *et al.* (1981) and Hartnoll (1982) report a limited growth increment during the intermoult period of mysids due to the stretching of the abdominal joints. For *Neomysis integer* the increase in length within a moult cycle amounts to 5 – 15 % (Mauchline, 1973). This phenomenon was described for field caught gravid females, which do not moult as long as they carry embryos and larvae in the marsupium. However, females moult in between successive broods and then increase (minimally) in length (Fockedey, unpublished). This was not taken into account by (Mauchline, 1973).

4.13 Response of post-marsupial growth to temperature, salinity, food quality and quantity

Juveniles just released from the marsupium and fed a mixture of green algae, *Daphnia* sp. and *Artemia* nauplii, grew maximally (0.25 mm d^{-1}) at 19 – 21 °C and 16 – 20 psu (Kuhlmann, 1984). However, a limited salinity and temperature range was selected in this study (between 14 – 24 °C and 13 – 24 psu) and the lower limits were far from reached.

Only a limited number of replicates were used per treatment (between 2 and 9 individuals) and no information on the mortality, intermoult period and growth factor was reported in the paper. Effects of temperature and salinity on the growth parameters IMP and GF were described in a previous paragraph 4.11 (Astthorsson, 1980; Astthorsson and Ralph, 1984; Winkler and Greve, 2002; Gorokhova, 2002; Fockedey *et al.*, in press – Chapter 3).

The growth over the whole life span in terms of IMP, GF and GR; and the sexual development of *Neomysis integer* is studied over an environmentally relevant salinity and temperature range by Fockedey *et al.* (in press – Chapter 3). The effect of food quality on these growth parameters is dealt with in Fockedey *et al.* (submitted c – Chapter 4) and in Fockedey *et al.* (submitted a – Chapter 5).

The effect of food quantity on the growth and moulting was studied as well (De Pauw, 1998; Gorokhova, 2002; Fockedey, unpublished). The duration of the IMP is extended in condition of suboptimal food quantity. The animals mainly prolonged their late postmoult and early premoult stages at a suboptimal feeding regime (Gorokhova, 2002). Starvation holds up the moulting process in the intermoult or premoult stage. Ecdysis was observed in some individuals only and was restricted to the first week (Gorokhova, 2002). Temperature affects the duration of the total intermoult period, but does not influence the relative duration of the substages of the intermoult period, as long as food supply is high (Gorokhova, 2002).

4.14 Effect of genotype on life history characteristics

For euphausiids (Haywood and Burns, 2003) it is demonstrated that the rate of development is different between siblings growing under exactly identical experimental conditions. For *Neomysis integer* this variation in growth between siblings resulted to be very small (Fockedey *et al.*, in press – Chapter 3) and thus laboratory-based studies on growth, development, physiological responses and ecotoxicological bio-assays can be performed with a relatively small number of replicates.

Genetically different populations of a species may differ in their growth and the response of their physiological processes towards salinity (Lee, 1999) and temperature (Wittmann, 1984). The phylogeographic patterns of *Neomysis integer* were examined through its distribution range by Remerie *et al.* (submitted a; submitted b), using mitochondrial cytochrome oxidase I sequencing. The *N. integer* population of the Schelde estuary was genetically homogenous along the longitudinal estuarine axis, but a large heterogeneity was observed between the populations from 11 estuaries. The responses of the distinct *N. integer* populations to temperature, salinity and other environmental conditions may be population-dependent and need further study.

5 BIOCHEMICAL COMPOSITION

5.1 Dry weight and ash content

The dry weight of *Neomysis integer* is 22 % of the wet weight for most of the year in Southampton waters (Raymont *et al.*, 1964). A slight reduction in the percentage dry weight was found in December and January (20 – 21 %) (Raymont *et al.*, 1966). Raymont and Krishnaswamy (1960) reported the dry weight as 19.0 – 19.9 % of the wet weight for the same population. The dry weight of *N. integer* from a Baltic population was 22 % of the wet weight (Maciejewska and Opalinski, 2002). In the Schelde estuary, the dry weight of *N. integer* is measured as around 14 – 17 % of the wet weight (Verslycke, 2003). See also Table 2 for more conversions.

Some authors use a correction factor when calculating the dry weight out of the wet weight in formaldehyde-preserved animals and add another 10 % to the calculated dry weight (Beattie, 1982). The length reduction of *N. integer* after a 100 days conservation in a 4 % formaldehyde-seawater solution is4 %, corresponding to a wet weight reduction of 17.4 %. The major shrinkage occurs in the first day after conservation (Kuhlmann *et al.*, 1982).

The wet weight of individual *Neomysis integer* is significantly dependent on the season, since size varies between cohorts (Verslycke *et al.*, 2004). Adult animals collected in spring (± 28 mg) weighed significantly more than adults collected in summer (± 21 mg) and winter (± 14 mg), these data ar ein agreement with the population biology (Mees *et al.*, 1994). The wet weight of *N. integer* is dependent on the location along the estuarine gradient (Verslycke *et al.*, 2004). Animals collected at the most upstream locations of the Schelde estuary have a significantly lower wet weight.

The ash content of *Neomysis integer* from the Ythan was 10.8 % of the dry weight, without sexual differentiation (Astthorsson, 1980). Total ash content of ovigerous females of Southampton Water amounts to 7.9 % of the dry weight (Raymont *et al.*, 1964). Ash and chitin together amounted to 14 % of the dry weight (Raymont *et al.*, 1966). See also Table 2 for more conversions.

The weight of a moult shed is related to the weight of *Neomysis integer* according to the factor 0.1057 (Astthorsson, 1980). For a juvenile *N. integer* the moult is approximately 8 % of the dry weight of the animal that produced it, while for mature individuals this figure is 10 % (Astthorsson, 1980). The ash content of shed moults equals 51.4 % of the DW (Astthorsson, 1980).

The dry weight and ash content of the eggs (*remark: probably meant stage I embryos?*) of *Neomysis integer* are on average 0.04 mg DW and 8.1 % (Astthorsson, 1980). Irvine *et al.* (1995) consider the dry weight of the embryos to be 10 % of their wet weight.

5.2 Chitin content

Chitin content is 7.1 % of the dry weight of ovigerous *Neomysis integer* from Southampton waters (Raymont *et al.*, 1964). The exoskeleton of *N. integer* contains large amounts of protein. Moulting of *N. integer* is temperature-, salinity- and age-dependent (Fockedey *et al.*, in press – Chapter 3). Moulting can thus create large variation in the protein content of *N. integer* (Verslycke and Janssen, 2002).

5.3 Caloric content

The caloric content of 10 – 15 mm sized *Neomysis integer* is 4.95 ± 0.10 cal $mgDW^{-1}$ (Summers , 1980). Astthorsson (1980) obtained a somewhat smaller mean caloric conversion factor of 4.68 cal $mg\ DW^{-1}$. The mean annual caloric value of adult females (4.75 cal $mgDW^{-1}$) was significantly larger than that of adult males (4.62 cal $mgDW^{-1}$), probably related to the (energetically rich) egg production in the ovaries (Astthorsson, 1980). Maciejewska and Opalinski (2002) used the conversion factors of 1.03 cal $mgWW^{-1}$ (4.33 J) as the body energy equivalent for *N. integer*. Kaiser *et al.* (1992) determined the energy content of a *N. integer* individual (body length 14.5 mm) to be 0.15 KJ. In terms of ash free dry weight (ADW) the mean annual caloric values is 5.17 and 5.32 cal $mgADW^{-1}$, respectively for adult males and females (Astthorsson, 1980). The caloric value of *N. integer* shows little seasonal variation (Astthorsson, 1980).

The mean caloric content of *N. integer* is 19.89 J mgDW^{-1} (12.91 J mgDW^{-1} for juveniles and 22.65 J mgDW^{-1} for adults) (Arndt and Jansen, 1986). Shed moults have a mean caloric content of 1.28 cal mgDW^{-1} or 2.63 cal mgADW^{-1} (Astthorsson, 1980). The caloric content of stage I embryos is 7.4 cal mgDW^{-1} or 0.30 cal per embryo (Astthorsson, 1980).

5.4 C, N and P content; C:N ratio

Total nitrogen content of ovigerous female *Neomysis integer* from Southampton is 11.4 % of the dry weight (Raymont *et al.*, 1964) and does not vary significantly over the year (Raymont *et al.*, 1966). The non-protein nitrogen is equivalent to 22 % of the total nitrogen, but varies with environmental salinity (Raymont *et al.*, 1966).

Total organic carbon ranges between 22 and 35 % (mean 30 %) of the dry weight in ovigerous females over the course of a year (Raymont *et al.*, 1964; 1966). Parsons *et al.* (1977) used a general conversion factor of 40 %. The organic matter as the summation of the protein, lipid and carbohydrate content, is highly constant over the year (Raymont *et al.*, 1966). The conversion of organic carbon to total organic matter in *Neomysis integer* is approximately 1:3 (Raymont *et al.*, 1966).

Subadult *Neomysis integer* from the Baltic (mean DW 1.67 mg) contained 42 % carbon and 11 % nitrogen (Gorokhova and Hansson, 1999). No variations in the C:N ratio (3.65 – 3.95, mean 3.78) could be detected between the sexes or between animals from the summer generation of subsequent years (Gorokhova and Hansson, 1999).

The total phosphorous content of *Neomysis integer* is determined by Tundisi and Krishnaswamy (1967). Values were 53.5 µg mgWW^{-1} for mature females, 41.0 µg mgWW^{-1} for adult males and 128.6 µg mgWW^{-1} for juvenile *N. integer*.

5.5 Protein and amino acids content

The total protein content of ovigerous females of *Neomysis integer* is 70 µg mgWW^{-1}, *i.e.* 70 % of the dry weight, 7 % of the wet weight, 80 and 90 % of the total organic matter excluding chitin. Proteins make up the main part of the total N content of the animals and are quantitatively the most important energy fraction of ± 1700 mJ mgWW^{-1} (Raymont *et al.*, 1964; 1966; Srinivasagam *et al.*, 1971; Verslycke and Janssen, 2002; Verslycke *et al.*, 2004). Throughout the year there are no significant changes in total protein levels (Raymont *et al.*, 1966; Verslycke et al; 2004). The protein of *N. integer* has been found to contain 13 % nitrogen (Raymont *et al.*, 1968). Therefore the total N values can be multiplied by a factor 7.7 to obtain an estimate of the protein content (Raymont *et al.*, 1966). The protein in *N. integer* showed a wide but not unusual range of amino acids: in descending order glutamate, aspartate, leucine, serine, glycine, alanine and lysine (Raymont *et al.*, 1968). The major yolk protein in eggs of *N. integer* is vitellin and it is essential to the nutritional needs of the embryo (Ghekiere *et al.*, 2004).

Non-protein N (including free amino acids) is 20 % of the total N, but the proportion varies with the environmental salinity from 14 % to 23 % (Raymont *et al.*, 1966; 1968). Free amino acids constitute up to 80 % of the non-protein N (Raymont *et al.*, 1968). The non-protein amino acids mainly consist of glycine, alanine and glutamate (Raymont *et al.*, 1968; Srinivasagam *et al.*, 1971). They are more prominent in individuals living at higher salinities and are responsible for the osmoregulatory mechanism of the species (Raymont *et al.*, 1968).

The most dominant amino acids in *Neomysis integer* are aspartate, glutamate and lysine (together accounting for 33 %), while alanine, serine, valine, glycine and praline represent a further 31 % (Armitage *et al.*, 1978). Glycine, taurine, alanine, proline, aspartate, glutamate, threonine, arginine, tyrosine, lysine, phenyl-alanine, isoleucine, leucine, valine, serine, cysteic acid and ornithine appeared to be non-essential to *N. integer* as they could be synthesised by the species or/and its digestive micro-organisms in the gut (Armitage *et al.*, 1981). The first 4 or 5 amino acids of this series are involved in the osmoregulation of the species (Armitage and Morris, 1982; Moffat, 1996).

The very high frequency of the incorporation of glycine and taurine underlines their importance to *N. integer* (Armitage *et al.*, 1981). Methionine and histidine are not synthesised by *N. integer*.

Since lipid and carbohydrate reserves in *Neomysis integer* are small (see following paragraphs), and only used as short-term energy sources, the species can use its own body proteins during nutritional stress (Armitage *et al.*, 1978). Starvation of 6 days (on kaolin clay) significantly decreased the protein content of *N. integer* (Morris *et al.*, 1977). When fed on a starch diet, the total protein and most amino acid concentrations were also drastically reduced (Armitage *et al.*, 1977). When fed pure protein (albumin), the mysids total protein was reduced as well (-39 %), probably because some nutritive requirements (*e.g.* cofactors or vitamins) were not met by the diet (Armitage *et al.*, 1978).

Neomysis integer takes up more ^{14}C from the food into their free and protein amino acids from a starch based diet (100 % glucose, aspartate or glutamate) than from a protein based diet (70 % egg yolk + 20 % cod liver oil + 10 % starch) (Armitage *et al.*, 1981). Probably, in the absence of proteins the metabolism of tissue protein of *N. integer* is increased and incorporation of food ^{14}C is more rapidly transferred into the tissues, while in protein-fed animals nitrogen and amino acids are supplied in the diet and catabolism of tissue protein is not necessary (Armitage *et al.*, 1981). In comparison with another mysid species (*Gnathophausia* sp.), *N. integer* metabolises diet proteins at a high rate and relies to a great extent on protein as a metabolic substrate (Armitage *et al.*, 1981). The differential uptake of ^{14}C from the food illustrates the higher uptake efficiency across the intestine membrane when fed starch based diets in comparison to a protein-based diet (Armitage *et al.*, 1981).

5.6 Lipid content

The lipid content of ovigerous *Neomysis integer* is 13 % of the dry weight (Raymont *et al.*, 1964). The lipid content of adults is on average 37 µg $mgWW^{-1}$ or 4 % of the WW and represents an energy equivalent of 1600 mJ $mgWW^{-1}$ (Verslycke and Janssen, 2002; Verslycke *et al.*, 2004). Mysids are capable of storing lipids in the R and B-cells of the digestive glands (Molloy, 1958; Raymont *et al.*, 1968; Brunet *et al.*, 1994). In comparison to other mysids (Adare and Lasenby, 1994; Azeiteiro et al., 2001; Richoux et al., 2004), the lipid content of *N. integer* is relatively small (Raymont *et al.*, 1968; Morris and Sargent, 1973) and lipids are not a very important energy reserve for *N. integer* (Raymont *et al.*, 1964). The problem of food shortage in *N. integer* may not be so acute for an estuarine omnivore exploiting a wide range of feeding methods and habits and always has a choice of dietary sources.

The total lipid content varies moderately over the year – between 8.5 and 15.6 % of the organic matter excluding chitin – and shows significant decreases in winter time in Southampton waters (Raymont *et al.*, 1966; Morris, 1971), while in the Schelde estuary *Neomysis integer* has lower lipid contents in summer and winter as compared to spring (Verslycke *et al.*, 2004). These patterns can be associated with local conditions of breeding, food supply and metabolic rates. Along the estuarine gradient of the Schelde estuary, the average lipid concentration increases from downstream to upstream locations (Verslycke *et al.*, 2004).

The eggs of *Neomysis integer* contain large quantities of lipid material (Linford, 1965). Females have a higher lipid content than the males or juveniles, resulting from a larger triglyceride fraction (Morris, 1973). The lipid metabolism of ovigerous females is assumed to be different from males and is probably slower in winter when the demand for lipid for gamete production comes to halt (Linford, 1965; Verslycke and Janssen, 2002; Verslycke *et al.*, 2004). It has been demonstrated that adult mysids have a lower O:N ratio than juveniles, as adults rely relatively more on protein substrates, which results in a higher relative lipid content of the adults than juveniles (McKenney, 1998).

When held at a high temperature, high salinity and low dissolved oxygen concentration, lipid content of *Neomysis integer* decreases (Verslycke and Janssen, 2002). Morris (1971) found significant changes in the lipids fatty acid composition of *N. integer* in a series of experiments to assess the effects of temperature and salinity.

A decreasing temperature leads to a build-up of the long-chain polyunsaturated acids at the expense of short-chain low unsaturated acids. Salinity does not have an effect on the fatty acid composition.

Starvation for 96h did not show any statistically significant decrease in the total lipid level of *Neomysis integer* (Linford, 1965), although a starvation period of 6 days (on kaolin) did decrease lipid levels significantly (Morris *et al.*, 1977). A diet of carbohydrate (starch) is not adequate for the maintenance of a normal lipid composition in *N. integer* on the long term, causing a reduction in the total lipid, triglyceride, and long-chain polyunsaturated fatty acids (Morris *et al.*, 1977). A diet of detritus and phytoplankton, taken from the mysids natural marsh habitat, caused a significant total lipid loss of 25 % after 7 days and of 45 % after 12 days (Morris, 1971). Incorporation of dietary ^{14}C into the lipid fraction of *N. integer* was highest on a diet of glucose and glutamate (Armitage *et al.*, 1981).

The lipids of *Neomysis integer* (Linford, 1963; Raymont *et al.*, 1968; Morris, 1971) contain 3 – 18 % non-saponifiable material, 50 % phospholipids, 30 % triglycerides, hydrocarbon, diglycerides and traces of monoglycerides, and low levels (< 10 %) of sterols. The dominant lipid class in *N. integer* is thus fatty acids (86 %), the next abundant class is sterols. *N. integer* lacks sterol esters, wax esters and fatty alcohols (Morris, 1971; Bradshaw *et al.*, 1989; 1990). The fatty acid:sterol ratio in *N. integer* equals 1.8 – 2.7 (Bradshaw *et al.*, 1989; 1990). Triglycerides are thought to function primarily as an energy store, being metabolized fairly rapidly, whereas phospholipids are considered more as a structural lipid, its metabolism being slower (Morris, 1971; Morris *et al.*, 1977). *N. integer* was found to be capable of converting dietary starch or short-chain saturated fatty acids into long-chain polyunsaturated fatty acids and incorporating them mainly in the triglyceride and phospholipid fractions (Morris *et al.*, 1973; 1977). The species' requirements for triglycerides are easily met by biosynthesis from a range of diets within 3 – 4 days. To obtain all needed phospholipids, *N. integer* needs more time to biosysnthesize them from diets not containing polyunsaturated acids (Morris *et al.*, 1973). When starved, the lipid metabolism was maintained for over 1 week, but the long-chain polyunsaturated fatty acids gradually declined (Morris *et al.*, 1977).

The **fatty acid composition** is relatively constant over the year, and is dominated (51 %) by poly-unsaturated fatty acids or PUFAs (Morris, 1971; Bradshaw *et al.*, 1989). The fatty acid content is 3.2 $\mu g\ mgWW^{-1}$ (Bradshaw *et al.*, 1989). In summer and autumn, these PUFAs increase in concentration at the expense of short-chain low unsaturated acids (Morris, 1971). An increase in short-chain fatty acids in early summer can be related to the feeding of *Neomysis integer* on the phytoplankton bloom containing high amounts of these fatty acids (Morris, 1971).

The fatty acid composition of *Neomysis integer* differs between sexes and between developmental stages. Mono- and long chain PUFAs are present in higher concentrations in adult females, mainly due by a high concentration in the triglyceride fraction (Morris, 1973). Probably these differences can be related to the egg production or embryo formation in females, with the high levels of triglycerides in ovigerous females being used as an energy source for the eggs (Morris et al, 1981). Saturated fatty acids remain at constant levels, irrespective of sex or age, and can be explained by their presence as stable fractions within glycerides and phospholipids (Morris, 1973).

The **sterols** of *Neomysis integer* are dominated by cholesterol (85 – 90 %). The fairly simple sterol composition is affected to some degree by the sex and the level of maturity (Morris *et al.*, 1981), with juveniles having a different composition in comparison to adult females. This may be the result of the juveniles having a very different diet from the adults or of the juveniles having less capacity for the bioconversion of their other dietary sterols to cholesterol (Morris *et al.*, 1981). Environmental temperature does not have any effect on the sterol composition of *N. integer*, while subtle changes are observed as salinity changes, especially lower than 10 psu (Morris *et al.*, 1981; 1982).

When food is passing through the gut, the amount and composition of the dietary lipids alters. *N. integer* decreases the fatty acids and increases the sterols during herbivory (Bradshaw *et al.*, 1990). *N. integer* also significantly contributes lipids to its faecal pellets, mainly cholesterol and fatty acids when gut epithelium cells are added to the faecal material.

The enteric microbes also contribute to the fatty acids of the faeces of *N. integer*. All the contributed lipids are modified and/or reabsorbed by digestive processes while still in the gut system (Bradshaw *et al.*, 1989).

5.7 Carbohydrate content

The amount of carbohydrates in *Neomysis integer* is very low: 0.20 – 0.42 % of the wet weight (Raymont and Krishnaswamy, 1960; Verslycke and Janssen, 2002) or 1.06 – 1.30 % of the dry weight (Raymont and Krishnaswamy, 1960). Using another technique, Raymont *et al.* (1964) obtained a value of 2.4 % of the dry weight for ovigerous *N. integer*.

Over the year the carbohydrate levels are between 2 and 3 % of the total organic matter excluding chitin (Raymont *et al.*, 1966) or 1 – 2 % of the total energy reserve (Verslycke *et al.*, 2004). In the Schelde estuary, adult *Neomysis integer* contains on average 2µg $mgWW^{-1}$ sugars (Verslycke *et al.*, 2004). Sugar content is significantly lower in winter than in spring and summer (Raymont *et al.*, 1966; Verslycke *et al.*, 2004). This can be explained by a higher energy demand and/or reflects the lower food availability or quality in winter (Verslycke *et al.*, 2004).

The carbohydrate content in fed *Neomysis integer* tended to be somewhat higher than in starved animals, indicating that carbohydrates are stored during feeding (Raymont and Krishnaswamy, 1960). Mysids (*N. integer*) are capable of storing glycogen in the R and B-cells of the digestive glands (Molloy, 1958; Raymont *et al.*, 1968; Brunet *et al.*, 1994). However, the generally low carbohydrate content of *N. integer* implicates that glycogen, making up 25 – 30 % of the total carbohydrates (Raymont *et al.*, 1968), cannot be a significant energy storage material (Raymont *et al.*, 1964). The problem of food shortage in *N. integer* may not be so acute for an estuarine population and may explain the lack of energy reserves (Raymont *et al.*, 1964). Sugars are probably only used as a short-term fast energy source (Raymont *et al.*, 1968) and preferred over lipid and protein as the fuel for metabolic processes (Morris, 1999).

6 ENERGY BUDGETS

There is a general lack of information on the quantities of energy consumed by *Neomysis integer* in the field and the role of the species in the trophic web. However, it is often difficult to directly determine the food ration of such small organisms like *N. integer*, especially since they are omnivorous. Indirect studies which measure the respiration, production and egestion are often the only way to estimate the daily food ration or energy requirement of mysids (*e.g.* Rudstam, 1989; Thiel, 1996; Maciejewska and Opalinski, 2002). Bioenergetic models like 'Scope for Growth' (Roast *et al.*, 1999b) or 'Cellular Energy Allocation' (Verslycke *et al.*, 2003; 2004) have recently been adapted for use with *N. integer* and are relatively rapid, alternative measurements of the energy status (fitness) of a *N. integer* population allowing the evaluation of the potential for growth and reproduction or the quality of the environment the population is living in (*e.g.* food availability and quality, pollution).

Despite the role of *Neomysis integer* in the estuarine food web, it is surprising that very little information is available on the parameters which affect their food requirements and how the ingested food is partitioned to meet the animal's requirements (Astthorsson, 1980). Energy is acquired through feeding and food absorption, and lost through respiration, excretion and moulting, with the surplus energy available for somatic growth and reproduction. *N. integer* has little energy reserves and depends mainly on the daily food intake to meet its energy requirements (Raymont *et al.*, 1964; 1966; Linford, 1965; Verslycke *et al.*, 2004b). This stresses the need for information on daily food consumption, daily energy requirements and assimilation efficiencies on different dietary items.

6.1 Energy intake – daily ration

Few studies on *Neomysis integer* give data on the energy intake. Often this is the parameter estimated from energy budgets given all energy expenditure values (*e.g.* Maciejewska and Opalinski, 2002). Generally, mysids need daily approximately 10 % of their total body carbon content to meet their basic metabolic requirements (Froneman, 2000).

Arndt and Jansen (1986) calculated the specific ingestion rate of *Neomysis integer* feeding on *Chlorella vulgaris* to be 108 µgDW d^{-1}. The daily energy intake of a juvenile *N. integer* was estimated as 13 % of the body weight at 10 °C and as 28 % of the body weight at 20 °C (Arndt and Jansen, 1986). Specific consumption rate (daily ration) was 7 – 13 % for juvenile *N. integer* feeding on *Artemia* nauplii (Kuhlmann, 1982) at 10 – 19 °C.

Astthorsson (1980) estimated energy intake over the complete life span of *Neomysis integer*, using a laboratory-derived growth curve, and a relationship between mysid size and daily food consumption, the latter based on laboratory experiments with *N. integer* feeding on *Artemia* nauplii. Maximum feeding rate was 300 – 450 *Artemia* nauplii for adult *N. integer*. In relation to the DW of the mysid, the intake of *Artemia* increased according to a log-log relation and was highest at higher temperatures (Astthorsson, 1980). The average daily food consumption of an immature *N. integer* (1mg DW) equals 70 and 129 *Artemia* d^{-1}, at 9 °C and 16 °C respectively. This corresponds to 0.10 and 0.18 mg $DW_{Artemia}$ d^{-1} or 10 and 18 % of the mysid's body DW. Adult mysids (6 mg DW) consumed 265 and 378 Artemia d^{-1}, at 9 °C and 16 °C respectively. This corresponds to 0.37 and 0.53 mg $DW_{Artemia}$ d^{-1} or 6 and 9 % of the mysid's body DW. Throughout its life from juvenile (2.4 mm TL) to a mature 15 mm sized animal (after 277 days), *N. integer* consumed 305 cal at 9 °C and 370 cal at 16 °C.

6.2 Specific dynamic action

The energetic cost to find and process food is defined as the specific dynamic action. If *Neomysis integer* is offered *Artemia* nauplii in a concentration beneath its maximal feeding rate, it is capable of capturing all available prey (Astthorsson, 1980). It is not stopping its feeding activities to minimise the energy loss by the increased searching effort, as was suggested for some copepod species (Frost, 1975). When feeding on calanoid copepodites (*Eurytemora affinis*) in low concentration, *N. integer* makes no attempt to hunt (Irvine *et al.*, 1993). Increased respiration rates, attributable to the dynamic action, usually occur in the first hours after feeding (Kiørboe *et al.*, 1985).

Results from experiments with other crustaceans give values for the specific dynamic action within the range of 17 – 20 % of the assimilated food (Kiørboe *et al.*, 1985; Lampert, 1986). Rudstam (1989) assumes a specific dynamic action of 17 % for *Mysis mixta*. No measurements have been done with other mysids or *N. integer*.

6.3 Assimilation efficiency

The assimilation efficiency or absorption efficiency is the proportion of the organic matter that is absorbed from the ingested food through the gut membrane; thus excluding the amount of organic matter that is egested in the faecal pellets (Conover, 1966). The assimilation efficiency can be measured quantitatively in the laboratory, provided the exact amount of food offered, the amount of food remaining uneaten and the weight of the faecal pellets produced can be estimated (Ferguson, 1973). Often this is not possible and/or very time consuming. The simpler ratio-method can be used as well, were only a sample of the food and a sample of the faeces are needed, and their respective DW and ADW are measured. The latter technique assumes (1) that the faeces contain organic matter derived entirely from the food; (2) that all unassimilated food can be collected and (3) all fraction of the food must be ingested in the same proportion as contained in the food, *i.e.* no preferential selection of certain food items may occur. Both assumptions are contested by Johannes and Satomi (1967), but Ferguson (1973) found both methods to be in good agreement for animal food (bivalve mantle).

The assimilation efficiency of *Neomysis integer* feeding on dead animal food (bivalve mantle, crab hepatopancreas and dead mysids) is 68 – 92 % (Ferguson, 1973), and 57 – 65 % when feeding on *Artemia* nauplii (Astthorsson, 1980). When feeding on monospecific phytoplankton cultures, the assimilation efficiency is 73 – 90 % for dinoflagellates and diatoms, except for *Skeletonema* (58 – 66 %) (Ferguson, 1973). Assimilation efficiency on natural detritus is 9 – 10 % and on laboratory-made detritus (aged algal cultures) 42 – 46 % (Ferguson, 1973). A low absorption efficiency of 35 % was measured in *N. integer* when feeding on sediments with a low organic content (Roast *et al.*, 2000) in comparison with an absorption efficiency of 70 – 90 % and 60 – 90 % when feeding on zooplankton and phytoplankton respectively (Astthorsson, 1980).

Juveniles had a lower assimilation efficiency than adults on animal food and on a diatom diet of *Coscinodiscus* or *Skeletonema* cells (Ferguson, 1973). When feeding on detritus no such trend was visible. The assimilation efficiencies of juvenile *Neomysis integer* on natural phytoplankton assemblages or green alga *Chlorella vulgaris* suspensions however, were significantly higher (respectively 70 and 90 %) than those of adults (respectively 62 and 80 %) (Arndt and Jansen, 1986).

The assimilation efficiency decreased when animals released their young or when they are moulting (Ferguson, 1973). The higher the ash content of the food, the lower the assimilation efficiency (Ferguson, 1973). Assimilation efficiency of *Neomysis integer* increases with increasing temperature between 5 and 25 °C when feeding on animal food (Ferguson, 1973); but is not affected by temperature when feeding on organically poor sediments (Roast *et al.*, 2000). Salinity has little or no impact on the assimilation efficiency of *N. integer* feeding on animal food or sediments; at least in the first 24 hours (Ferguson, 1973; Roast *et al.*, 2000).

Assimilation of carbohydrates by *Neomysis integer* is 75 – 80 %, with the highest assimilation efficiency on diets with the lowest carbohydrate content (Ferguson, 1973). *N. integer* assimilates the protein from animal food with an efficiency of 80 – 90 %, from diatom food with an efficiency of 75 % (Ferguson, 1973). Highest assimilation efficiency of carbohydrates and proteins is observed when *N. integer* is feeding on dead members of its own species, probably because identical or closely resembling proteins and carbohydrates are more easily absorbed (Ferguson, 1973).

6.4 Egestion: faecal pellet production

Maciejewska and Opalinski (2002) determined the daily faeces egestion of *Neomysis integer*, when feeding on frozen zooplankton (at 14 °C), as 0.169 mgDW ind^{-1} d^{-1} or 0.01 mgDW $mgWW^{-1}$ d^{-1}. During the course of the experiment (24 h) however, 22 % of the initial weight of the faecal material is leached into the water and a correction factor was applied. Egestion rate of *N. integer*, when feeding on organically poor sediments, was 0.017 – 0.049 mg faeces mg^{-1} dry weight mysid h^{-1} (Roast *et al.*, 2000). The egestion rate increased with increasing temperature and salinity (Roast *et al.*, 2000). Egestion rates were not affected by gender (Roast *et al.*, 2000). Egestion rate ranged between 0.022 – 0.044 mg faeces mg^{-1} dry weight mysid h^{-1} when feeding on laboratory-made estuarine aggregates (Fockedey et al., submitted d – Addendum 2). Faecal pellet production, and thus feeding activity, slows down when the mysids are releasing their young from the marsupium or when they are moulting (Ferguson, 1973).

The caloric value of *Neomysis integer* faeces (when feeding on frozen zooplankton) was 3.66 cal $mgDW^{-1}$ faeces or 15.37 J $mgDW^{-1}$ faeces (Maciejewska and Opalinski, 2002). The caloric value of faeces when feeding on other dietary items is not reported in literature. The organic content of the faeces is dependent on the organic content of the food (Ferguson, 1973). When feeding on diets with 45 – 65 % organic matter the organic content of faecal pellets decreased little, while feeding on organically rich food diminished the relative organic matter content from 40 up to 70%. When feeding on detrital food sources (< 45 %), the organic content of the faecal pellets contained relatively more carbon than the food (enrichment of organic matter). This is probably due to the preferential selection of the organic fraction of the food supplied (Ferguson, 1973).

6.5 Egestion: excretion of soluble excretory product (N, P)

The excretion of soluble nitrogen and phosphorous by animals is an important pathway for the remineralisation of nutrients in aquatic ecosystems. The measurement of N excretion can give indication of the level of protein turnover (Raymont *et al.*, 1968). Also a link between osmoregulation through free amino acids and the nitrogen excretion has been demonstrated (Raymont *et al.*, 1968). Nitrogen excretion is of significance in the disposal of excess free amino acids and is mainly done in the form of ammonia (Raymont *et al.*, 1968).

Not much information is available on the excretion of soluble products by *Neomysis integer*. The weight-specific mean ammonia excretion is highly temperature dependent and amounts to 5 – 10, 5 – 15, 10 – 25 and 15 – 35 µg NH^{4+} gDW^{-1} h^{-1}, respectively at 6, 10, 15 and 20 °C (Laughlin and Lindén, 1983). Weisse and Rudstam (1989) measured the ammonium excretion of *N. integer* to be 3 – 11 µmol NH^{4+} gDW^{-1} h^{-1} between 6 and 16 °C. At a constant salinity (0.4 – 35 psu at 15 °C), *N. integer* excretes 1.0 ± 0.5 µg NH_3 $mgDW^{-1}$ h^{-1} (Raymont *et al.*, 1968). A reduction in the environmental salinity leads to a rapid but temporary rise in ammonia secretion up to 6 times the basal excretion rate. A transfer from low to high salinity caused little to no effect on the excretion rate (Raymont *et al.*, 1968). Weight-specific mean dissolved inorganic phosphorus (DIP) amounted 0.2 –1.0 µmol PO_4^{3-} gDW^{-1} h^{-1} (between 6 and 16 °C) and was correlated to temperature (Weisse and Rudstam, 1989). Sex and dry weight of the mysids has no effect on the excretion rates of N and P (Laughlin and Linden, 1983; Weisse and Rudstam, 1989). Caloric conversions for ammonia-N and urea-N are respectively 0.00594 and 0.00551 cal $µgN^{-1}$ (Elliott, 1976).

Laboratory rearing conditions tend to increase the ammonia excretion compared to field-collected mysids (Laughlin and Lindén, 1983), probably due to differences in the dietary composition (N-rich food in excess) and feeding frequency in the experimental setup in comparison with the wild mysids.

Although some authors (Clutter and Theilacker, 1971; Lasenby and Langford, 1972; Roast *et al.*, 1999) considered the soluble organic excretion in mysids to be insignificant (< 5 %), Ferguson (1973) indirectly estimated that *Neomysis integer* excreted 15 % of the ingested energy in this form. By assuming that the excretion is a fixed percentage of the energy ingested, this value was used by Astthorsson (1980) to calculate the energy loss by excretion of soluble excretory products as 45 cal at 9 °C and 55 cal at 16 °C.

6.6 Growth

The energy used for growth can be derived from the growth curve. The length can be expressed in terms of weight and subsequently in terms of calories. Astthorsson (1980) converted laboratory growth curves (in length) into energy content curves (in cal). Freshly released juveniles represent 0.19 cal, while mature adults contain 29.22 cal. For data on the caloric conversions factors of *Neomysis integer* see higher.

The gross growth efficiency, *i.e.* the percentage of the ingested food which is used for growth, is between 8 and 10 % for the whole life time of *Neomysis integer* (Astthorsson, 1980), whereas the net growth efficiency, *i.e.* the percentage of the assimilated food used for growth, equals 12 – 17 % taken over its whole life span (Astthorsson, 1980). The gross growth efficiency decreases from 20 – 25 % in juveniles to 5 – 8 % in adults and significantly larger for *N. integer* living at 9°C than at 16°C and feeding on *Artemia* (Astthorsson, 1980). Ferguson (1973) report gross growth efficiencies of *N. integer* on a diet of crab hepatopancreas as 28 %, 19 % and 12 % for animals with a total length of respectively 8 – 10, 10 – 12 and 12 – 14 mm. Net growth efficiencies for the same size classes are respectively, 43 %, 27 % and 17 %. Gross and net growth efficiencies on laboratory-made detritus (aged algal culture) are considerably lower. For animals with a total length of 8 – 10 and 10 – 12 mm, the gross and net growth efficiencies are very similar as 8 and 19 %; larger animals had the lowest gross (3 %) and net (8 %) growth efficiency. All experiments of Ferguson (1973) were performed at 15 °C. Growth conversion efficiencies reported from growth experiments with well fed *N. integer* juveniles on *Artemia* nauplii are 34 % at 10 °C and 38 % at 19 °C (Kuhlmann, 1982).

6.7 Moulting

Organic matter, *i.e.* energy, is lost during moulting. The dry weight of a moult of *Neomysis integer* is linearly related to the dry weight of the animal that sheds the moult. Moults of juveniles and adult *N. integer* respectively weigh about 8 to 10 % of the dry weight of the individuals that produced them (Astthorsson, 1980). The caloric value of moults of *N. integer* is 1.28 cal $mgDW^{-1}$ (Astthorsson, 1980). Over a complete life span, *N. integer* moults on average 23 times (at 9 and 16 °C) and the total energy loss amounts to 6 cal (Astthorsson, 1980).

6.8 Reproduction

The amount of energy used by male mysids for sperm production is probably negligible (Clutter and Theilacker, 1971; Astthorsson, 1980). The energy used by females for egg production can be estimated using field derived data on the length-dependent brood size (Table 6) and knowledge on the number of successive broods produced by one female. The caloric content of 1 egg is estimated to be 0.30 cal (Astthorsson, 1980). In age-dependent energy budgets one need to allocate the total number of energy spend in brood production over the time that females invest energy in the development of the ovaries.

6.9 Respiration

Weight-specific oxygen consumption rates can be used to estimate the daily oxygen consumption of differently sized *Neomysis integer*. Different methods are used (Winkler bottles, electrodes, Gilson respirometers, CO_2 production, pH changes) and respiration is reported in a variety of units (µg-mg, µl, mm^{-3} per mg-gWW, mg-gDW) over a range of time scales (h-day). A summary is given in Table 9. Nothing is known about the respiration of embryos and larvae during intra-marsupial development.

Using data of the laboratory growth curves of *Neomysis integer*, Astthorsson (1980) calculated the overall energy expenditure over the complete life cycle. At 9 °C it takes *N. integer* 277 days to grow from a 2.4 mm juvenile to a 15 mm adult and during this period the total energy expenditure on metabolism (measured as respiration) is estimated to be 95 cal. At 16 °C it takes 166 days to grow to an adult and metabolic cost is 127 cal.

Table 9: Weight-specific respiration rates for *Neomysis integer* available in literature.

Temp	Sal	Method	measurement	Source
10°C	8 psu	Winkler method	3.5-11.1 µgO_2 mgWW day^{-1} 15.9 and 50.4 µgO_2 mgDW day^{-1}	Raymont et al., 1966
18°C	?	CO2 production, pH change	0.10 to 0.62 µlCO_2 mgWW^{-1} h^{-1}	Raymont and Krishnaswamy, 1968
5°C 15°C	0.3-18.7 psu	Respirometer (Gilson)	1.4-1.7 µlO_2 mgDW h^{-1} 1.9-2.1 µlO_2 mgDW h^{-1}	Vlasblom and Elgerhuizen, 1977
6°C 10°C 15°C 20°C	7 psu	Oxygen electrode	0.8-1.0 mgO_2 gDW^{-1} h^{-1} 1.0-1.3 mgO_2 gDW^{-1} h^{-1} 1.3-1.6 mgO_2 gDW^{-1} h^{-1} 1.6-2.8 mgO_2 gDW^{-1} h^{-1}	Laughlin and Lindén, 1983
5-15°C	?	Winkler apparatus	1-3 µlO_2 mgDW^{-1} h^{-1}	Weisse and Rudstam, 1989
5-15°C	1-30 psu	Oxygen electrode	0.14-0.41 µlO_2 mgWW^{-1} h^{-1}	Roast et al., 1999
5°C 10°C 20°C	2-24 psu 2-24 psu 10-15psu <10 – >15	Flow through- Respirometer	0.7-1.8 µlO_2 mgDW^{-1} h^{-1} 1.2-1.8 µlO_2 mgDW^{-1} h^{-1} ± 1.7 µlO_2 mgDW^{-1} h^{-1} 3-4 µlO_2 mgDW^{-1} h^{-1}	Arndt and Jansen, 1986
14°C	2 psu	Oxygen electrode	0.889 mm^3O_2 mgWW^{-1} h^{-1}	Maciejeska and Opalinski, 2002

With **WW**: wet weight; **DW**: dry weight = 19 - 22% WW; density of Oxygen gas = 1.429 kg/m^3)

Several oxycaloric coefficients are available. The conversion factor of 4.8 cal ml^{-1} O_2 suggested by Schmidt-Nielsen (1979) implies a metabolisation of equal mixtures of carbohydrate, fat and protein, as is the case when *Neomysis integer* is offered animal food (Ferguson, 1973). Maciejewska and Opalinski (2002) used an oxycaloric coefficient of 0.0047 cal mm^{-3} O_2. The oxygen consumed is transformed to energetic equivalents using oxyenthalpic equivalents for an average lipid, protein and sugar mixture as 484 kJ mol^{-1} O_2 (Verslycke and Janssen, 2002). Roast *et al.* (1999b) used a heat equivalent of oxygen uptake of 0.02008 J µl^{-1} O_2. Also 13600 J g^{-1} O_2 can be used as oxycaloric conversion factor (Elliott and Davidson, 1975).

6.10 Energy budgets

A preliminary energy budget for 12 – 14 mm sized *Neomysis integer* has been constructed by Ferguson (1973). The quantity of food ingested is allocated to growth, faecal pellets, respiration and excretion. The quantity of food channelled into to latter two functions was found by difference. The allocation percentage to growth, *i.e.* net growth efficiency, is low (16 %) for 12 – 14 mm *N. integer* in comparison with other species (Ferguson, 1973). The growth efficiency was highest (27 %) with animal food (crab hepatopancreas) and lowest (7.5 %) with artificial detritus (Ferguson, 1973). Respiration and excretion are also higher with animal food. When considering the amount of faecal pellets produced however, a much lower percentage of animal food is being egested (23 – 37 %) compared with detrital food (63 – 66 %). Although a much greater quantity of detritus diet (max. 7.2 mgDW) was ingested per animal compared to the animal diet (max. 2.6 mgDW), the latter supported a higher growth efficiency. Thus, *N. integer* can feed far more economically on an animal diet than on de detrital diet.

A simple energetic budget was used to calculate the daily energy requirements of *Neomysis integer* in the Baltic (Maciejewska and Opalinski, 2002) from measurements on production, respiration and egestion. Daily food ration (in mg WW of microzooplankton ind^{-1} d^{-1}) of *N. integer* as a function of mysid size (WW, in mg) is expressed as: $C = 0.66\ WW^{0.61}$ (r^2=0.9992; n=10). For example, the daily ration for an average individual (20mg WW) is 2.86 cal of food daily, *i.e.* 4.22 mg of zooplankton (WW). All supporting experiments were performed at 14 °C and animals were allowed to feed on natural zooplankton assemblage and/or *ad libitum* frozen *Daphnia*.

A more complicated energy budget (Parsons *et al.*, 1977) was used to calculate the energy relations for the entire life span of *Neomysis integer* (Astthorsson, 1980). The energy ingested equals the energy loss due to metabolism, excretion, moulting, growth and gonad production. The energy expenditure in the gonad production is different between the two sexes and energy budget for males and females were calculated separately. In general, 14 % of the assimilated food is used for growth, 3 % is lost by moulting, 50 % was used for respiration and 24 % was presumed to be excreted in a soluble form. In adult females 10 % of the assimilated food is used for egg production. No differences were found for animals kept at winter or summer temperatures (9 and 16 °C).

6.11 Cellular Energy Allocation

Cellular Energy Allocation (CEA) is a relatively new methodology (De Coen and Janssen, 1997) to assess the individual-based energy budget and is used to assess effects of abiotic variables like salinity, temperature and oxygen (Verslycke and Janssen, 2002; Verslycke *et al.*, 2004) and exposure to pollutants (Verslycke *et al.*, 2003; 2004b; 2004c) on the metabolic processes of *Neomysis integer*. The ratio of the total available energy reserves used (decrease in total sugars, lipid and protein content) and the average energy consumption (measured as cellular respiration rate from electron transport activity) indicate the energy available in excess of that required for maintenance and reflects the energy available for growth and reproduction (Verslycke and Janssen, 2002; Verslycke *et al.*, 2004). CEA is predictive of long-term effects on growth and other long-term population effects in the field (De Coen and Janssen, 1997).

Sugar, lipid and protein content is transformed into energetic equivalents using their respective energy of combustion, respectively 17500 mJ mg^{-1} glycogen, 24000 mJ mg^{-1} protein and 39500 mJ mg^{-1} lipid. The oxygen consumed as measured by electron transport activity (ETA) is transformed to energetic equivalents using oxyenthalpic equivalents for an average lipid, protein and sugar mixture as 484 kJ mol^{-1} O_2.

The CEA can be influenced by a large array of factors like diet, reproductive status, sex, age, location, season, hence careful interpretation of the data is required (Verslycke *et al.*, 2004). When starved (4 days) at a higher temperature, energy reserves and CEA of *Neomysis integer* decreased although not significantly (Verslycke and Janssen, 2002). The energetic metabolic processes of *N. integer* were relatively unaffected in the laboratory by short-time changes in salinity, temperature and dissolved oxygen (Verslycke and Janssen, 2002). *N. integer* from the Schelde estuary, on the other hand, expressed a clear seasonal response in their CEA with spring and summer values significantly higher than in winter (Verslycke *et al.*, 2004). Also, important spatial differences were observed in the CEA along the estuarine gradient, with smaller CEA in the (most polluted) upstream stations (Verslycke *et al.*, 2004).

The latter was not confirmed however by more recent CEA measurements (Ghekiere, personal communication). The average total energy content of adult *N. integer* of the Schelde estuary is on average 3200 mJ $mgWW^{-1}$ and was significantly affected by the location along the estuarine gradient, but not by season (Verslycke *et al.*, 2004). Protein was the most important fraction (70 µg $mgWW^{-1}$), followed by lipids (37 µg $mgWW^{-1}$) and sugars (2 µg $mgWW^{-1}$), making proteins and lipids the most quantitative energy sources for the species (Verslycke *et al.*, 2004). The individual fractions were differentially affected by season and location along the estuarine gradient. Energy consumption of *N. integer* in the Schelde was on average 31 mJ $mgWW^{-1}$ h^{-1} (Verslycke *et al.*, 2004) and was not affected by season but increased towards the more upstream sampling locations. CEA values in the *Artemia* fed *N. integer* from laboratory cultures (± 66) was significantly lower than in the field (± 135), since energy content was comparable (3200 – 3300 mJ $mgWW^{-1}$) but energy expenditure was significantly higher in the laboratory (54 mJ $mgWW^{-1}$ h^{-1}) than in the field (31 mJ $mgWW^{-1}$ h^{-1}) (Verslycke and Janssen, 2002; Verslycke *et al.*, 2004).

6.12 Scope for growth

Scope for growth (SFG) is a technique where several physiological responses are integrated into a single bioassay originally designed for bivalves (Widdows and Salkeld, 1993). It has been adopted for *Neomysis integer* by Roast *et al.* (1999b). It provides a rapid, instantaneous measurement of the energy status of an organism, as does the Cellular Energy Allocation technique (Verslycke *et al.*, 2004b). However, SFG integrates respiration, feeding and excretion rates, rather than respiration rate and biochemical composition in CEA. The SFG method is used in *N. integer* for the evaluation of the toxic effect of the pesticide chlorpyrifos on the metabolic processes (Roast *et al.*, 1999b), not yet for the impact of abiotic (*e.g.* salinity, temperature, dissolved oxygen) and biotic variables (*e.g.* gender, age, size, developmental state, food quality and quantity).

7 PHYSIOLOGY

The upper region of the estuarine environment is characterized by strong fluctuating conditions of salinity and temperature. Both are considered dominant 'ecological abiotic master factors', which may act either singly or in concert to modify the population dynamics (survival, development and growth rates), the distribution and physiology and metabolism of estuarine organisms (Kinne, 1970; 1971; McKenney and Celestial, 1995). As a typical estuarine species, the brackish water mysid *Neomysis integer* experiences strong tidal, diel and seasonal changes in temperature and salinity (Moffat and Jones, 1992; Roast *et al.*, 1999).

7.1 Salinity tolerance

Neomysis integer is euryhaline and tolerates a wide salinity range of 1 to 40 psu (Mauchline, 1971; Vlasblom and Elgershuizen, 1977; Arndt and Jansen, 1986; Roast *et al.*, 2001), although survival is low in salinities greater than 35 psu (Ralph, 1965). Kuhlmann (1984) reported however, the upper salinity tolerance limit of adult *N. integer* to range between 25 – 30 psu at 10 °C. No particular preference was shown by *N. integer* within the salinity range from 2 to 12 psu (Arndt and Jansen, 1986). The species possesses considerable powers of adaptation to waters of low salinity (Tattersall and Tattersall, 1951), but is unable to maintain itself in absolute fresh water (Stammer; in Segerstrale, 1945) when summer temperatures become higher than 23 – 24 °C (Merker, 1928). *N. integer* is highly tolerant to large, acute salinity fluctuations between 1 and 30 psu (Moffat and Jones, 1992; Roast *et al.*, 1998). It can attain osmotic balance within 2 hours of exposure to a change in salinity (Moffat, 1996).

In the field *Neomysis integer* can be found at salinities between 0.1 and 38 psu, although it is rare in waters of more than 20 psu (Tattersall and Tattersall, 1951; Vlasblom and Elgershuizen, 1977). In the Schelde estuary, *N. integer* was recorded at salinities ranging from 8 to 25 psu with a maximal abundance at around 15 psu (Mees *et al.*, 1994). Ongoing studies suggest that the population is shifting towards the more oligohaline zone of the estuary (Verslycke *et al.*, 2004; Fockedey, personal observation) as a consequence of improved oxygen conditions in the upstream reaches in winter and early spring (*e.g.* De Brabandere *et al.*, 2002; http://waterbase.nl). In other, more oxygenated Western European estuaries such as the Guadalquivir (Spain), Gironde (France), Tamar (UK), Elbe (Germany) and Ems (The Netherlands) the abundance peak is typically found around 5 psu (Mees et al, 1995; Moffat, 1996; Drake *et al.*, 2002; Fockedey, personal observation).

7.2 Temperature tolerance

Neomysis integer is an eurythermic species that occurs in brackish waters along the Western European coast at longitudes between 36°N and 63°N and in the Baltic Sea (Deprez *et al.*, 2004; http://intramar.ugent.be/NeMys). Within the range Elbe – Guadalquivir, the summer water temperature of the brackish estuarine zone varies from 26 °C in the North to 29 °C in the South, while winter water temperatures range from 0 °C in the North to 10 °C in the South (Drake *et al.*, 2002, Zimmermann, 1997).

Neomysis integer can sustain temperatures from 0 to 33 °C under laboratory conditions (Merker, 1928; Mauchline, 1980), although its optimal resistance tend towards the lower temperature ranges (Arndt and Jansen, 1986). The tolerance of mysids to ambient temperatures may vary **among populations** of the same species (Mauchline, 1980). *N. integer* from the Baltic Sea dies within 2.5 weeks at 20 °C, probably because this population rarely experiences temperatures above 15 °C, and never for periods exceeding a few days at a time (Laughlin and Lindén, 1983). No particular preference was shown by *N. integer* from the Baltic within the temperature range from 4 to 18 °C (Arndt and Jansen, 1986). The tolerance of mysids to ambient temperatures may vary **between generations** within the same population. Kuhlmann (1984) reports a distinct difference in the upper tolerance limit between the winter and summer generations of adult *N. integer* from Kiel Canal as respectively 10 to 12 °C and 20 to 25 °C (at 10 psu). Furthermore, temperature tolerance limits vary **ontogenically**. Juveniles seem to have a different range of temperature tolerance than the adults (Kinne, 1955).

In the coastal water of the western Baltic Sea, the shoals are leaving the shallow littoral zone when water becomes too cold (< 2 °C), or too warm (> 20 °C) (Välipakka, 1992). The fact that it is easy to keep *Neomysis integer* at 0 °C for long periods shows that the species has a good resistance to cooling, whereas its frost resistance to freezing at -10 °C is relatively poor with all animals dying within 8 minutes (Arndt and Jansen, 1986). However, Jansen (1979) described some individuals of *N. integer* to be present in the shallow zone of the Darss-Zingst Peninsula when ice is present in winter time. Espeel (1979) mentions a 'lethargic' behaviour of *N. integer* in very cold winter conditions (< 1 °C) in a brackish lake, with the animals lying at the bottom without any movement.

Temperature is generally thought to overshadow salinity in its effects on growth and reproduction in crustaceans. Still, temperature can influence the salinity tolerance of a species (Vlasblom and Elgershuizen, 1977; Arndt and Jansen, 1986) and interaction effects of both on the survival and growth of a species can change with age (Kinne, 1955; McKenney, 1994; McKenney and Celestial, 1995). *Neomysis integer* is better able to tolerate both low and high salinities at the low temperature range, *i.e.* thermophobic behaviour (Arndt and Jansen, 1986). In freshwater *N. integer* dies rapidly when the temperature is 23 – 24 °C, while in water of a higher salinity they can support temperatures up to 33 °C (Merker, 1928).

The effect of temperature on metabolic rates is commonly expressed as the Q_{10} value. Temperature has a significant effect on the respiration rate of *Neomysis integer*, with a Q_{10} of 1.5 to 3.3 (Clutter and Theilacker, 1971; Astthorsson, 1980; Laughlin and Lindén, 1983; Weisse and Rudstam, 1989; Roast *et al.*, 1999). Temperature also has a significant effect on the ammonia and DIP excretion rate of *N. integer*, with a Q_{10} of respectively 1.4 – 2.9 and 2.6 – 4.9 (Weisse and Rudstam, 1989).

Short term temperature changes of 5 °C (from 15 to 20°C) did not appear to cause an acute temperature chock in *Neomysis integer* (Laughlin and Lindén, 1983). During diel vertical migration *N. integer* can encounter temperatures from 18 °C at the surface to 5 °C at the bottom (in a 30 m deep Baltic station). Since metabolic rates, like respiration and excretion, are strongly affected by temperature, these rates can vary with a factor 2 – 3 during a 24h cycle (Weisse and Rudstam, 1989).

7.3 Oxygen tolerance

The abundance of *Neomysis integer* is affected by the temperature in relation to the oxygen content of the water (Jorgensen, 1929). The scarcity of the species in the field is particularly well marked when oxygen content drops below 40 %, *i.e.* 3.3 – 5.1 mg l^{-1} at 5 – 25 °C (Jorgensen, 1929; Mees *et al.*, 1993; 1995; Margonski and Maciejewska, 1999). Also in (organically) polluted waters the oxygen is more quickly depleted and has its impact on the relative abundance of *N. integer*. In enclosed waters where a permanent halocline is present under which an anaerobic stagnant water mass (hypolimnion), the *N. integer* populations are confined to the oxygenated surface layers (*e.g.* Parker and West, 1979). However, *N. integer* can sustain low oxygen-tensions under laboratory conditions. An oxygen saturation decreasing to 20 % had no influence on the survival and behaviour of adult *N. integer* under laboratory conditions at 18 °C and 18 psu (Kuhlmann, 1984). From 20 % on, their behaviour became abnormal (not further described) and the lethal threshold of oxygen tolerance was at 13 % O_2 saturation. In the complete absence of oxygen, *N. integer* can survive for 20 minutes (Arndt and Jansen, 1986).

7.4 Ammonium tolerance

The toxic threshold of adult *Neomysis integer* to increased ammonia concentration (at 16 °C and 16.5 psu) lies at 0.2 mg NH3 l^{-1}; the 96h LC_{50} is measured at 1.7 mg l^{-1} (Kuhlmann, 1984). This value can be considered as high in comparison with other crustaceans (*Daphnia*), freshwater fish or marine fish larvae (Kuhlmann, 1984).

7.5 Osmoregulation

The isosmotic point of *Neomysis integer*'s blood is 16 psu at 15 °C (Southampton waters, Ralph, 1965) to 19 psu at 5 °C (Loch Etive - Scotland, McLusky and Heard, 1971). Moffat (1996) described the isosmotic point of *N. integer* to be higher than 20 psu at 15 °C for a population in the Looe estuary. It is not unusual for the blood concentration at a given salinity to vary between different populations of the same species (Moffat, 1996).

Neomysis integer is an extremely efficient hyper-hypo-osmoregulator. It is capable of maintaining the concentration, composition and volume of its body fluids such that the metabolic functioning of the cells can continue normally. It can maintain its blood concentration hyperosmotic to the medium when living in diluted sea water environments in the range 0.5 to 20 psu and hyposmotic at salinities between 20 and 40.6 psu (Ralph, 1965; McLusky and Heard, 1971; Moffat, 1996). In fact, the blood concentration itself varies between 14.5 and 24 psu (McLusky and Heard, 1971).

Neomysis integer can rapidly respond to acute changes in salinity and attains osmotic balance within 2 hours of experiencing a change in salinity (Moffat, 1996). This osmoregulatory ability is correlated with changes in (mainly non-essential) free amino acid concentrations. Glutamine, glycine, taurine and alanine were identified as important osmo-effectors in *N. integer* (Moffat, 1996), while Armitage and Morris (1982) report glycine, alanine and proline to be involved in the osmoregulation of this species. Armitage and Morris (1982) report major changes in the free amino acid concentrations within the first 4 hours after an abrupt salinity change. In the field, the adjustment of free amino acid concentration in *N. integer* to salinity change occurs at the changing of the tide at either high or low water (Armitage and Morris, 1982).

Alternating high and low salinity leads to a net decrease in protein in *Neomysis integer* (Austin, 1965), suggesting that the proteins, relatively rich in glycine, alanine and glutamine (Raymont *et al.*, 1968), are the direct, irreversible source for the free amino acids needed for osmoregulation. The proteins are broken down and the free amino acids excreted when no longer required. The discovery of several intracellular transaminases in *N. integer* provides another possible mechanism (by extensive amino acid conversion) for the mobilisation of those large quantities of free amino acids needed in function of osmoregulation (Raymont *et al.*, 1967; Raymont *et al.*, 1968).

Subtle changes in the structural membrane sterols of *Neomysis integer* do appear when environmental salinity changes, especially when salinity drops below 10 psu (Morris *et al.*, 1982). This may be the result of the animal requiring to modify its membrane structure (*i.e.* orientation of the lipid layers) in order to cope with the changing external salinity. These changes occur (in the laboratory) in less than 48 hours. In the field such changes happen regularly during the tidal cycle and are part of *N. integer*'s mechanisms to cope with it sliving in fluctuating environmental salinity (Morris *et al.*, 1982).

The isosmotic point of *Neomysis integer* is a little lower in comparison with the coexisting species *Praunus flexuosus* (25 psu). *N. integer* is a better osmoregulator and thus better adapted to live in more oligohaline waters than *P. flexuosus*, since the range of salinities experienced by the body tissues of *N. integer* is less than in *P. flexuosus* over the same range of media (McLusky and Heard, 1971). The isosmotic point of the other coexisting species *Mesopodopis slabberi* is not know in literature.

7.6 Respiration

Mysids oxygen consumption is dependent on several abiotic (*e.g.* temperature, salinity, season) and biotic (like generation, gender, weight, age and reproductive status) factors. Each factor may have a solitary effect or several factors may act in concert to modify the oxygen consumption (Roast *et al.*, 1999). The respiratory physiology of *Neomysis integer* is considered to be adapted for inhabiting a highly (acutely and longer term) variable environment (Roast *et al.*, 1999). The specialized respiratory physiology, taken with the broad salinity tolerance and an efficient osmoregulatory mechanism explains the presence of *N. integer* in the upper regions of European estuaries.

The impact of salinity, temperature and adaptation salinity on the respiration rate were studied by Vlasblom and Elgershuizen (1977), but no firm conclusions could be made. More recently, also Verslycke and Janssen (2002) measured oxygen consumption by electron transport activity (ETS) at varying salinity, temperature and dissolved oxygen combinations in the laboratory, but the small variations in respiration could not be explained by a single abiotic factor within the ranges tested, suggesting that biotic factors such as weight, age, and gender probably have a larger influence on the respiration rates.

7.6.1 Temperature effect

Several studies (Astthorsson, 1980; Laughlin and Lindén, 1983; Weisse and Rudstam, 1989; Roast *et al.*, 1999) proved that the weight-specific respiration rate of *Neomysis integer* is highly temperature dependent. The temperature dependency of the respiration of *N. integer* is moderate though (Q_{10} between 1.5 and 3.3) in comaprsion to other species, indicating a significant degree of temperature compensation.

The oxygen consumption of *Neomysis integer* was affected more by temperature changes at high than at low salinity (Roast *et al.*, 1999), as demonstrated in higher Q_{10} values at higher salinity. A temperature of 20 °C cannot be considered as optimal for Baltic *N. integer* (Arndt and Jansen, 1986), as is reflected in the high O_2 consumption in comparison with 5 and 15 °C; and especially the low (2 psu) and high (22 psu) salinities have a striking effect on the respiration rate. It can explain why mysids migrate from the littoral zone to deeper (and cooler) water in the summer.

In general there was little difference between male and female oxygen consumption in response to temperature changes (Roast *et al.*, 1999), with males increasing their respiration to a somewhat higher extent than females. Temperature has a significant effect on the O_2 consumption of *Neomysis integer* from the same generation, but respiration is also significantly influenced between seasons or generations by other factors than temperature (Astthorsson, 1980).

7.6.2 Salinity effect

The respiration of *Neomysis integer* is susceptible to changes in salinity as well, but the effect of salinity on physiological processes is less predictable. After all, temperature has a stronger effect on the oxygen consumption than salinity (Roast *et al.*, 1999). In experiments performed by Arndt and Jansen (1986), the salinity had no effect on the respiration at the low temperatures of 5 and 10 °C. At 20 °C respiration is generally higher, but is minimal at the intermediate salinities of 10 – 15 psu and highest at the low (2 psu) and high (24 psu) salinity treatments. In contrast to the former study, Vlasblom and Elgershuizen (1977) found the respiration of *N. integer* to be affected by salinity at 5 and 15°C. At any salinity tested (0.3 – 18 psu, except 2 psu) the respiration was always lower than at the adaptation salinity (12.8 psu). A change in salinity cause greater changes in the oxygen consumption at low (5 °C) than at high (15 °C) temperatures (Roast *et al.*, 1999). Salinity effects were not modified by the mysid gender (Roast *et al.*, 1999).

7.6.3 Body size effect

The respiration of *Neomysis integer* is strongly related to the body size, body surface or body weight (Astthorsson, 1980; Arndt and Jansen, 1986) and are therefore experessed as weight-specific respiration rates (Table 9). The oxygen consumption (R) increases with increasing body weight (DW) according to the following regression $R = 3.21\ DW^{0.6}$ (Arndt and Jansen, 1986).

7.6.4 Gender effect

At most temperature/salinity combinations, male *Neomysis integer* consumed significantly more oxygen than females (Roast *et al.*, 1999). Gender differences in respiration rates have been reported, but may also result from the reproductive status of the test organisms (Raymont *et al.*, 1966; Simmons and Knight, 1975) or from morphological differences between male and female mysids affecting weight-specific oxygen consumption rates (Smith and Hargreaves, 1985).

7.6.5 Season effect

According to Raymont *et al.* (1966) and Astthorsson (1980), the respiration rates of *Neomysis integer* are significantly affected by season. The weight-specific oxygen consumption, measured in the laboratory at 10 °C with animals from the field, showed to have a peak in March and in August, and a marked decline in September/October while respiration stays low during winter months. The respiration of similar sized animals at a specific temperature was found to be higher in summer than in winter (Astthorsson, 1980).

In contrast to the former studies, Verslycke *et al.* (2004) and Roast *et al.* (1999) found no seasonal effect (mainly temperature) in the respiration of *Neomysis integer* from the Schelde and East Looe River estuary, probably because temperature changes occur gradually and the mysids can acclimate to the changing conditions.

7.6.6 Other effects

In the Schelde the respiratory energy consumption of *Neomysis integer* increased upstream (Verslycke *et al.*, 2004) and can be explained by stress caused by decreased salinity and dissolved oxygen or increased pollution (Verslycke *et al.*, 2004).

Laboratory rearing conditions showed to increase oxygen consumption compared to field-collected mysids (Laughlin and Lindén, 1983), probably due to the dietary differences and feeding frequency between the two situations.

7.6.7 Field validation

Laboratory measurements on the effect of salinity and temperature on respiration rate of *Neomysis integer* were related to the field conditions the species is living in (East Looe River estuary) by Roast *et al.* (1999), and where high tidal fluctuations are experienced in temperature (10 °C) and salinity (33 psu); in order to evaluate the adaptive nature of temperature and salinity responses in *N. integer*. *N. integer* disposes of relative good temperature compensation (to the moderate temperature changes experienced in the field over a tidal cycle). The salinity response measured in the laboratory (higher respiration at lower salinity) cannot be seen to have an adaptive nature, since living at the low salinity reaches implies high metabolic costs due to high oxygen consumption (Kinne, 1971; Roast *et al.*, 1999). After all, combining the salinity and temperature responses together, the respiration is high at high water in comparison with low water (Roast *et al.*, 1999). It would be worthwhile to repeat this exercise in estuaries with less extreme tidal fluctuations in salinity and temperature.

On a seasonal basis the oxygen consumption of *Neomysis integer* is predicted to be higher in summer, when temperatures are higher (Roast *et al.*, 1999). At lower winter temperatures the effect of changing (tidal) salinity conditions are more distinct than in summer (Roast *et al.*, 1999). On the other hand, the seasonal temperature increase occurs gradually over a longer period of time and a gradual adaptation might occur, causing a minimal effect on the respiration of *N. integer* (Roast *et al.*, 1999). Also, Raymont *et al.* (1966) and Astthorsson (1980) report the respiration rates of *N. integer* to be significantly affected by season in itself. Predictions based on measurements of one sampling occasion like the one of Roast *et al.* (1999) would be invalid to extrapolate to other seasons in such a case.

8 ECOTOXICOLOGY

Mysids are sensitive to chemical contaminants at environmentally relevant concentrations and have been used in regulatory toxicity testing for more than 20 years (*e.g.* Nimmo and Hamaker, 1982; Gaudy *et al.*, 1991; Harmon and Langdon, 1996; Brandt *et al.*, 1993; Roast *et al.*, 1998; Veslycke *et al.*, 2004 and references herein). The U.S. Environmental Protection Agency and the American Society for Testing and Materials both have adopted the subtropical *Americamysis bahia* (formerly *Mysidopsis bahia*) as a key testing species for coastal and estuarine monitoring, and standard guides for conducting life--cycle toxicity tests with this species have been developed (USEPA, 2002). Although a relatively large amount of published toxicity data is available for *Americamysis* species, relatively limited data are available on the sensitivity of other mysid species to toxicants (Roast *et al.*, 1999c). However, the available evidence suggests that mysids are generally more sensitive to toxic substances than many other test species (Morton *et al.*, 1997; Roast *et al.*, 1998b; Verslycke *et al.*, 2003b).

Ideally, chemical risk assessment should be assessed by standardized endpoints that cover the molecular, individual and population level. For mysids, this implies that, in addition to evaluating mortality, acute, chronic and multigenerational bio-assays have to be developed for testing chemical effects on growth and moulting, reproduction, biochemical composition, metabolism, physiological processes, behaviour and morphologic aberrations (as reviewed by Verslycke *et al.*, 2004). Also, field studies and caging experiments with mysids have been published (Clark et al., 1986; Rand and Clark, 2000; Fossi et al., 2001; Verslycke, 2003). Because of their ecological importance, wide geographic distribution, year-round availability in the field, ease of transportation, ability to be cultured in the laboratory, and sensitivity to contaminants, mysids are appropriate toxicity test organisms. Clearly, field validation of the biomarkers is a strong research need for the future.

Recently, there has been increasing interest in using the brackish water mysid *Neomysis integer* (Leach, 1840) as a toxicological test species for estuarine systems (Emson and Crane, 1994; Roast *et al.*, 1998b; Verslycke *et al.*, 2004 – Addendum 3). It is an alternative to *Americamysis bahia* for use in European water quality testing (Roast *et al.*, 1998a; Verslycke *et al.*, 2004). Due to its relatively high temperature requirements, the subtropical species *A. bahia* can not be used in temperate regions and its low tolerance for low salinities of 0.1 to 5 psu makes it an inappropriate test species to use in the turbid upper reaches of estuaries or oligohaline inland water bodies (Roast *et al.*, 2000a; 2001).

Next of being applied in acute toxicity tests (von Oertzen *et al.*, 1988; Emson and Crane, 1994; Wildgust and Jones, 1998; Roast *et al.*, 1999c; 2001; Verslycke *et al.*, 2003b), *Neomysis integer* have been used successfully in various sublethal tests for evualuating swimming ability (Roast et al., 2000b; 2000c; 2001b; 2002; 2002b), energy budget (Roast et al., 1999b; Verslycke et al., 2003; 2004b; 2004c), testosterone metabolism (Verslycke et al., 2002; 2003c; 2004c), respiration (Laughlin and Linden, 1983; von Oertzen *et al.*, 1988), ammonia-excretion (Laughlin and Linden, 1983), growth and moulting (Ghekiere et al., submitted), vitellogenesis (Ghekiere et al., 2004), and intra-marsupial development (Ghekiere et al., in preparation).

9 CONCLUSIONS

The present work aims to gather all literature available on the brackish water mysid *Neomysis integer*, with focus on its distribution, feeding ecology, life history aspect, behaviour, physiology, biochemical composition, bioenergetics and ecotoxicology. It aims to identify gaps in our knowledge of the species.

Because *N. integer* is often used as a model species to study the ecology of brackish water crustaceans, and because the species is easy to sample (qualitatively) in shallow water and keep in the laboratory, many studies and data are available concerning the species. The older studies (< 1980) are often superficial or based on a limited number of observations; while their data are often unpublished (as Ph.D. theses or reports) or published in local journals. Information extracted from this *'grey'* literature has been integrated in the review. In the last 10 years, quite some in-depth studies have been published concerning aspects of the feeding ecology, population dynamics, physiology, bioenergetics, behaviour, and ecotoxicological use of the species. One should consider this chapter as a reference work, to grab to when specific information of one of the topics is needed. The author's contributions (results presented in this thesis and some unpublished work) are highlighted in the text.

Abundant information is available on the distribution patterns of *Neomysis integer* in enclosed brackish waters and estuaries, although on has to keep in mind that the swarming behaviour, vertical and horizontal migration, segregation of life stages and escape behaviour of *N. integer* (all not fully understood yet) can handicap the quantification of the density and biomass, and may hamper the calculation of the production and the study of the life history of the species.

There is a great need for the description of the feeding ecology of key species – like *Neomysis integer* – in estuarine environments for the development of accurate C-flux models and the description of detritus based food web patterns, including the quantification of transfer coefficients. Although *N. integer* is described as an important food item for many demersal and pelagic fish, larger epibenthic crustaceans and wading bird species, quantitative information is still lacking on its own diet, feeding rates, feeding patterns and selectivity (especially for populations living in estuarine conditions).

Numerous data are available on the life history of *Neomysis integer* over a wide geographical and habitat range, although southern populations (< 51°N) are more poorly known. Variations are observed between these populations in the number of cohorts, size-at-maturity, fecundity and growth rate. Growth and reproduction are affected by prevailing environmental conditions as generally observed in Crustacea. However, in the eurythermic and euryhaline *Neomysis integer*, typically living in the highly dynamic estuarine environment, this is not thoroughly studied yet. Details on how intra- and post-marsupial development, moulting processes and reproduction are affected by a wide range in salinity, temperature, food quantity and quality are still lacking.

The biochemical composition and the ecophysiology of *Neomysis integer* are well known and several methodologies to calculate the energy budget have been applied to the species.

There has been an increasing interest in using the brackish water mysid *Neomysis integer* as a toxicological test species for Western European estuarine systems. Mortality, respiration, swimming behaviour, testosterone metabolism and energy budgets are well established endpoints for bioassays with the species. However, more data on its growth, moulting, development and reproductive processes are needed (at the individual- and population-level). The influence of prevailing environmental variables on these processes, as well as their optimal range have to be known in order to develop optimal laboratory cultures and to differentiate between chemically-induced variability and natural variability in toxicity testing.

Still, some literature published on the species *Neomysis integer* is not dealt with in the present literature review as its falls out of the scope of the present Ph.D and cover fields like environmental contamination, biomanipulation of brackish lakes, use of the species for drug detection, molecular, phylogenetic and phylogeographic work on *N. integer*, detailed morphologic descriptions of the cuticle, statocyst, sensory systems and the intra-marsupial development, visual sensitivity of the species, presence of intersexuality, culturing of the species, and use as food for other trophic levels. All references are grouped in Table 10 with an indication of the topics not treated in this review (*).

Table 10: All literature on *Neomysis integer* (* falling out of the scope of the present overview)

Taxonomy	Mauchline and Murano, 1977; Deprez *et al.*, 2004; http://www.vliz.be/vmdcdata/nemys; www.iorbis.org
Morphology – External (general)	Tattersall and Tattersall, 1951; Mauchline, 1980; Hayward and Ryland, 1995; http://ip30.eti.uva.nl/bis/crustacea.php; http://www.marlin.ac.uk/species/taxon_Neomysisinteger.htm
Morphology – Feeding appendages and gut structure	Gelderd, 1909; Lucas, 1936; Molloy, 1958; Tattersall and Tattersall, 1951; Haffer, 1965; Astthorsson, 1980; Mauchline, 1980; Armitage *et al.*, 1981; Espeel, 1982; Bradshaw *et al.*, 1989; Maciejewska, 1992; Brunet *et al.*, 1994; Kobusch, 1998; Remerie, 1999; Roast *et al.*, 2004
* **Morphology** – Cuticle	Putz and Buchholtz, 1991
* **Morphology** – Statocyst	Lowenstam and McConell, 1968; Espeel, 1984; 1985; 1986; 1987; Wittmann et al., 1993
* **Morphology** – Olfactory system	Guse, 1979; Guse, 1983; Hallberg et al., 1992; Johansson and Hallberg, 1992; 1992b
* **Morphology** – Sensilla	Guse, 1978; 1980; 1980b
* **Morphology** – Intra-marsupial development	Rathke, 1839; Wagner, 1896; 1998; Needham, 1937; Kinne, 1955; de Kruijf, 1977; Mauchline, 1980; Scholtz, 1984; Scholtz et al., 1993; Fockedey *et al.*, submitted b – Chapter 6
Morphology – morphometric regressions	Schuchardt et al., 1989; Mees et al., 1994
Morphology – length/weight regressions	de Kruijf, 1977; Beattie and de Kruijf, 1978; Astthorsson, 1980; Summers, 1980; Beattie, 1982; Bremer and Vijverberg, 1982; Jansen, 1985c; 1985c; Arndt and Jansen, 1986; Mees *et al.*, 1994; Aaser *et al.*, 1995; Irvine et al., 1995; Gorokhova and Hansson, 1999; Maciejewska and Opalinski, 2002; Winkler and Greve, 2004
Density & Biomass – Estuaries	Percival, 1929; Moore et al., 1979; Sorbe, 1980; O'Sullivan, 1984; Milner, 1986; Rodriguez and Dauvin, 1987; Schuchardt et al., 1989; Haesloop, 1990; Apel, 1992; Hough and Naylor, 1992; Mees and Hamerlynck, 1992; Moffat and Jones, 1992; Mees et al., 1993; 1993b; San Vicente, 1993; Bamber and Henderson, 1994; Bernát et al., 1994; Cattrijsse et al., 1994; Mees et al., 1994; 1995; Köpke and Kausch, 1996; Moffat, 1996; Mouny et al., 1996; San Vicente, 1996; Drake et al., 1997; Mouny et al., 1998; Zouhiri et al., 1998; Cunha et al., 1999; Dauvin et al., 2000; Mouny et al., 2000; Drake et al., 2002; Hampel et al., 2003; 2003b; David *et al.*, 2005; Fockedey, unpublished – EU MATURE
Density & Biomass – Baltic Sea	Muus, 1967; Rasmussen, 1973; Kotta and Simm, 1979; Weslawski, 1981; Arndt and Jansen, 1986; Rudstam *et al.*, 1986; Hansson, 1990; Köhn, 1992; Rudstam *et al.*, 1992; Thiel, 1992; Välipakka, 1992; Margonski and Maciejewska, 1999

Density & Biomass – Ponds and lakes	Barnes *et al.*, 1971; Beattie and de Kruijf, 1978; Parker and West, 1979; Bremer, 1980; Bremer and Vijverberg, 1982; Espeel, 1982; Platenkamp, 1983; Bales *et al.*, 1993; Hosper and Meijer, 1993; Irvine *et al.*, 1993; Jeppesen, *et al.*, 1994; Meijer *et al.*, 1994; Soselisa, 1994; Aaser *et al.*, 1995; Irvine *et al.*, 1995; Verslycke *et al.*, 2000
Diet of *Neomysis integer* – description	Lucas, 1936; Tattersall and Tattersall, 1951; Vorstman, 1951; Kinne, 1955; Mauchline, 1971; 1980; Bremer and Vijverberg, 1982; Sorbe, 1980; Astthorsson, 1980; Jansen, 1985b; Haesloop, 1990; Uitto *et al.*, 1995; Speirs *et al.*, 2002; Vilas and Fockedey, unpublished
Diet of *Neomysis integer* – quantitative stomach analysis and fullness index	Astthorsson, 1980; Sorbe, 1980; Bremer and Vijverberg, 1982; Jansen, 1985b; Arndt and Jansen, 1986; Haesloop, 1990; Irvine *et al.*, 1993; Soselisa, 1994; Remerie, 1999; Speirs *et al.*, 2002; Fockedey and Mees, 1999; Fockedey, unpublished – EU MATURE; Fockedey, unpublished; Vilas and Fockedey, unpublished
Diet of *Neomysis integer* – isotope fractionation	Rolff, 1998; Gorokhova, 1999; Gorokhova and Hansson, 1999
Diet of *Neomysis integer* – Feeding rate (ingestion, egestion, gut evacuation rate, assimilation efficiency)	Lucas, 1936; Molloy, 1958; Ferguson, 1973; Astthorsson, 1980; Kuhlmann, 1982; Arndt and Jansen, 1986; Irvine *et al.*, 1993; 1995; Aaser *et al.*, 1995; De Pauw, 1998; Viitasalo *et al.*, 1998; Roast *et al.*, 2000; Maciejewska and Opalinski, 2002; Winkler and Greve, 2004; Bergström and Englund, 2004; Albertsson, 2004; Fockedey *et al.* submitted a – Chapter 5; Fockedey *et al.*, submitted c – Chapter 4; Fockedey *et al.*, submitted d – Addendum 2; Fockedey, unpublished
Diet of *Neomysis integer* – Selectivity and structuring effects on prey populations	Espeel, 1982; Moss and Leah, 1982; Jansen *et al.*, 1983; Jansen and Heerklos, 1983; Van De Vijver, 1983; Jansen, 1985b; Arndt and Jansen, 1986; Rudstam *et al.*, 1986; 1992; Hansson *et al.*, 1990; Thiel, 1992; Irvine *et al.*, 1993; 1995; Bernát *et al.*, 1994; Jeppesen *et al.*, 1994; Aaser *et al.*, 1995; Fockedey and Mees, 1999 – Chapter 2
Diet of *Neomysis integer* – Feeding modes	Lucas, 1936; Tattersall and Tattersall, 1951; Raymont *et al.*, 1964; Parker and West, 1979; Astthorsson, 1980; Mauchline, 1980; Bremer and Vijverberg, 1982; Espeel, 1982; Irvine *et al.*, 1993; Bales *et al.*, 1993; Roast, 1997; Roast *et al.*, 2000; Roast *et al.*, 2004
Diet of *Neomysis integer* – diet overlap with other species	Kinne, 1955, Sanina, 1961, Jansen, 1985b; Maciejewska, 1992; Thiel, 1992; 1996; Remerie, 1999; Maciejewska and Opalinski, 2002; Winkler and Greve, 2004; Vilas and Fockedey, unpublished
Diet of *Neomysis integer* – Starvation	Raymont and Krishnaswamy, 1960; Raymont and Conover, 1961; Linford, 1965; Raymont *et al.*, 1964; 1967; 1966; 1968; Morris *et al.*, 1977; Vlasblom and Elgershuizen, 1977; Armitage *et al.*, 1977; 1978; Parker and West, 1979; Murtaugh, 1984; Weisse and Rudstam, 1989; Gorokhova and Hanssen, 1999; Winkler, 2000; Gorokhova, 2002; Verslycke and Janssen, 2002
Diet of *Neomysis integer* – Faecal pellets and coprophagy	Molloy, 1958; Ferguson, 1973; Parker and West, 1979; Bradshaw *et al.*, 1989; Weisse and Rudstam, 1989; Roast *et al.*, 2000; Maciejewska and Opalinski, 2002; Fockedey *et al.*, submitted d – Addendum 2

Predation on *Neomysis integer*	Patterson, 1905; Kemp, 1910; Redeke, 1941; Healey, 1972; Cramp, 1977; 1983; Kislalioglu and Gibson, 1977; Morawski, 1978; Van den Broek, 1978; Mauchline, 1980; Summers, 1980; Timola, 1980; Marchand, 1981; Sorbe, 1981; 1983b; Bremer and Vijverberg, 1982; Van De Vijver, 1983; Heeste, 1984; Van Densen, 1985; 1988; Arndt and Jansen, 1986; Janssen and Spannhof, 1987; Franek, 1988; 1989; Debus, 1989; Kostrzewska Szlakowska and Szlakowsk, 1990; Costa and Elliott, 1991; Leonardsson, 1991; Assis et al., 1992; Costa et al., 1992; Moreira *et al.*, 1992; Aarnio and Bonsdorff, 1993; Houthuijzen et al., 1993; Irvine *et al.*, 1993; Cattrijsse, 1994; Cattrijsse *et al.*, 1994; Holker and Hammer, 1994; Thiel, 1996 and references herein; Van Densen et al., 1996; Lazauskiene et al., 1996; Cattrijsse et al., 1997; Larsson and Berglund, 1998; Mouny *et al.*, 1998; Hostens and Mees, 1999; Thyrel et al., 1999; Søndergaard *et al.*, 2000; Thiel, 2000; Temming and Herrmann, 2001; Hostens, 2003; Maes *et al.*, 2003; Granqvist and Mattila, 2004; Hampel and Cattrijsse, 2004; Winkler and Greve, 2004; Dean *et al.*, 2005
Behaviour – Swarming	Percival, 1929; Mauchline, 1971c; Arndt and Jansen, 1986; Walesby, 1973; Parker and West, 1979; Espeel, 1982; Arndt and Jansen, 1986; Rudstam *et al.*, 1986; Thiel, 1992; Köpcke and Kausch, 1996; Roast *et al.*, 2004
Behaviour – Segregation of life stages	Tattersall and Tattersall, 1951; Kinne, 1955; Ralph, 1965; Beattie and de Kruijf, 1978; Parker and West, 1979; Astthorsson, 1980; Sorbe, 1980; Platenkamp, 1983; Milner, 1986; Schuchardt *et al.*, 1989; Hough and Naylor, 1992; Välipakka, 1992; Cattrijsse *et al.*, 1994; Moffat, 1996
Behaviour – Position maintenance	Hough and Naylor, 1992; Moffat and Jones, 1993; Köpcke and Kausch, 1996; Roast *et al.*, 1998; 1998b; 2000b; 2000c; 2001b; 2002; 2002b
Behaviour – Swimming	Parker and West, 1979; Hough and Naylor, 1992; Roast *et al.*, 1998; 1998b; Lawrie *et al.*, 1999; Roast *et al.*, 2000b; 2000c; 2001b; 2002; 2002b
Behaviour – Predator avoidance	Mauchline, 1971c; Debus *et al.*, 1992; Kaiser *et al.*, 1992b; Rademachers and Kils, 1996; Lindén *et al.*, 2003
Behaviour – Vertical migration	Jansson and Källander, 1968; Beattie and de Kruijf, 1978; Moore *et al.*, 1979; Bremer and Vijverberg, 1982; Jansen, 1985; Arndt and Jansen, 1986; Rudstam *et al.*, 1986; Debus *et al.*, 1992; Irvine *et al.*, 1993; Bernát *et al.*, 1994; Aaser *et al.*, 1995; Köpcke and Kausch, 1996; Zouhiri *et al.*, 1998; Dauvin *et al.*, 2000; Fockedey, unpublished – EU project MATURE; Mees, unpublished – EU Project JEEP
Behaviour – Horizontal migration	Vorstman, 1951; Kinne, 1955; Ralph, 1965; Muus, 1967; Kühl and Mann, 1969; Barnes *et al.*, 1977; Beattie and de Kruijff, 1978; Jansen, 1979; Moore *et al.*, 1979; Astthorsson, 1980; Sorbe, 1980; Bremer and Vijverberg, 1982; Jansen, 1985; Arndt and Jansen, 1986; Rudstam *et al.*, 1986; Schuchardt *et al.*, 1989; Hough and Naylor, 1992; Thiel, 1992; Välipakka, 1992; Jansen, 1993; Mees *et al.*, 1993b; 1994; Cattrijsse *et al.*, 1994; Köpcke and Kausch, 1996; Speirs *et al.*, 2002; Allen *et al.*, 2003; Hampel *et al.*, 2003; 2003b

Life history – field data (number of cohorts, life span, size-at-maturity, sex-ratio)	Vorstman, 1951; Tattersall and Tattersall, 1951; Kinne, 1955; Wiktor, 1961; Raymont et al., 1966; Mauchline, 1971; 1971b; de Kruijff, 1977; Beattie and de Kruijf, 1978; Borghouts, 1978; Espeel, 1979; 1982; Parker and West, 1979; Astthorsson, 1980; Bremer, 1980; Jansen et al., 1980; Sorbe, 1980; Bremer and Vijverberg, 1982; Platenkamp, 1983; Astthorsson and Ralph, 1984; Arndt and Janssen, 1986; Jansen, 1986; Rudstam et al., 1986; Schuchardt et al., 1989; Weisse and Rudstam, 1989; Haesloop, 1990; Moffat and Jones, 1992; Tehn, 1992; Irvine et al., 1993; 1995; Mees et al., 1994; Soselisa, 1994; Aaser et al., 1995; Fockedey, unpublished; Mees et al., unpublished
Life history – annual production	Bremer, 1980; Bremer and Vijverberg, 1982; Kuhlmann, 1982; Arndt, 1985; Arndt and Jansen, 1986; Thiel, 1992; Mees *et al.*, 1994; Soselisa, 1994; Aaser *et al.*, 1995; Irvine *et al.*, 1995; Fockedey, unpublished
Life history – fecundity (breeding season, brood size, number of broods, intra-marsupial mortality, hatching success, development time, size and growth, birth rate)	Vorstman, 1951; Tattersall and Tattersall, 1951; Kinne, 1955; Raymont *et al.*, 1966; Mauchline, 1971; 1972; Vlasblom and Elgershuizen, 1977; Beattie and de Kruijf, 1978; Borghouts, 1978; Parker and West, 1979; Moore *et al.*, 1979; Astthorsson, 1980; Bremer and Vijverberg, 1982; Arndt and Jansen, 1986; Schuchardt *et al.*, 1989; Haesloop and Scheffel, 1991; Hough and Naylor 1992; Mees et al., 1994; Soselisa, 1994; Irvine *et al.*, 1995; Moffat, 1996; Fockedey *et al.*, submitted b – Chapter 6; Fockedey and Mees, unpublished; Fockedey, unpublished; Janssen, unpublished; Mees *et al.*, unpublished
Life history – mortality	Mees et al., 1994; Irvine *et al.*, 1995
Life history – growth (field and laboratory-based growth curves, growth rate, moulting,)	Kinne, 1955; Mauchline, 11973; 976; 1977; 1977b; 1985; Beattie and de Kruijf, 1978; Astthorsson, 1980; Schrotenboer, 1980; Bremer and Vijverberg, 1982; Astthorsson and Ralph, 1984; Kuhlmann, 1984; Arndt and Jansen, 1986; Schuchardt *et al.*, 1989; Mees *et al.*, 1994; Soselisa, 1994; Irvine *et al.*, 1995; Aaser *et al.*, 1995; Gorokhova and Hansson, 1997; De Pauw, 1998; Gorokhova, 2002; Maciejewska and Opalinski, 2002; Winkler and Greve, 2002; Fockedey *et al.*, in press – Chapter 3; Fockedey *et al.*, submitted a – Chapter 5; Fockedey *et al.*, submitted c – Chapter 4; Fockedey, unpublished
Biochemical composition – dry weight, ash content, Chitin content	Raymont and Krishnaswamy, 1960; Raymont *et al.*, 1964; 1966; de Kruijf, 1977; Astthorsson, 1980; Summers, 1980; Jansen, 1985c; Arndt and Jansen, 1986; Mees *et al.*, 1994; Irvine *et al.*, 1995; Aaser *et al.*, 1995; Gorokhova and Hansson, 1997; Maciejewska and Opalinski, 2002; Verslycke, 2003; Winkler and Greve, 2004
Biochemical composition – caloric content	Summers , 1980; Astthorsson, 1980; Arndt and Jansen, 1986; Kaiser *et al.*, 1992; Maciejewska and Opalinski, 2002
Biochemical composition – C, N and P content	Raymont *et al.*, 1964; 1966; Tundisi and Krishnaswamy, 1967; Gorokhova and Hansson, 1999
Biochemical composition – proteins, amino acids	Raymont *et al.*, 1964; 1966; 1968; Srinivasagam *et al.*, 1971; Morris *et al.*, 1977; Armitage *et al.*, 1977; 1978; 1981; Armitage and Morris, 1982; Moffat, 1996; Verslycke and Janssen, 2002; Verslycke *et al.*, 2004; Ghekiere *et al.*, 2004

Biochemical composition – lipids	Molloy, 1958; Raymont *et al.*, 1964; 1966; 1968; Linford, 1963; 1965; Morris, 1971; 1973; Morris and Sargent, 1973; Morris *et al.*, 1973; 1977; 1981; 1982; Armitage *et al.*, 1981; Bradshaw et al., 1989; 1990; Brunet *et al.*, 1994; Verslycke and Janssen, 2002; Verslycke *et al.*, 2004
Biochemical composition – carbohydrates	Molloy, 1958; Raymont and Krishnaswamy, 1960; Raymont *et al.*, 1964; 1966; 1968; Brunet *et al.*, 1994; Morris, 1999; Verslycke and Janssen, 2002; Verslycke *et al.*, 2004
Energy budgets	Astthorsson, 1980; Rudstam, 1989; Thiel, 1996; Roast *et al.*, 1999b; Maciejewska and Opalinski, 2002; Verslycke and Janssen, 2002; Verslycke *et al.*, 2003; 2004; 2004b; 2004c
Physiology – Tolerance salinity	Merker, 1928; Stammer; in Segerstrale, 1945; Tattersall and Tattersall, 1951; Ralph, 1965; Mauchline, 1971; Vlasblom and Elgershuizen, 1977; Kuhlmann, 1984; Arndt and Jansen, 1986; Moffat and Jones, 1992; Mees *et al.*, 1994; 1995; Moffat, 1996; Roast *et al.*, 1998; 2001; Drake *et al.*, 2002; Verslycke *et al.*, 2004
Physiology – Tolerance temperature	Merker, 1928; Kinne, 1955; Vlasblom and Elgershuizen, 1977; Espeel, 1979; Jansen, 1979; Mauchline, 1980; Laughlin and Lindén, 1983; Kuhlmann, 1984; Arndt and Jansen, 1986; Välipakka, 1992
Physiology – Tolerance oxygen	Jorgensen, 1929; Parker and West, 1979; Kuhlmann, 1984; Arndt and Jansen, 1986; Mees *et al.*, 1993; 1993b, 1994; 1995; Margonski and Maciejewska, 1999; Roast *et al.*, 2000
Physiology – Tolerance ammonium	Kuhlmann, 1984
Physiology – Osmoregulation	Austin, 1965; Ralph, 1965; Raymont *et al.*, 1967; 1968; McLusky and Heard, 1971; Armitage and Morris, 1982; Morris *et al.*, 1982; Moffat, 1996
Physiology – Respiration	Raymont et al., 1966; Raymont and Krishnaswamy, 1968; Simmons and Knight, 1975; Vlasblom and Elgerhuizen, 1977; Astthorsson, 1980; Laughlin and Lindén, 1983; Smith and Hargreaves, 1985; Arndt and Jansen, 1986; Weisse and Rudstam, 1989; Roast et al., 1999; Maciejeska and Opalinski, 2002; Verslycke and Janssen , 2002; Verslycke *et al.*, 2004
Physiology – Excretion	Raymont *et al.*, 1968; Ferguson, 1973; Laughlin and Lindén, 1983; Weisse and Rudstam, 1989
Physiology – Visual sensitivity	Halberg, 1977; Kurnaty, 1979; Hallberg et al., 1980; Lindström, 1992; 2000
* **Culturing protocol**	Mauchline, 1971; Astthorsson, 1980; Kuhlmann, 1984; Arndt and Jansen, 1986; Haesloop, 1990; Roast *et al.*, 1999; Verslycke et al., 2003b
Ecotoxicology – General	Roast et al., 1998b; Verslycke et al., 1994 – addendum 3
Ecotoxicology – Metals	von Oertzen et al., 1988; Emson and Crane, 1994; Wildgust and Jones, 1998; Roast et al., 1999c; 2000b; 2001; 2002; 2002b; Verslycke et al., 2003b

Ecotoxicology – Oil pollution	Laughlin and Lindén, 1982; 1983; Lindén et al., 1982
Ecotoxicology – Pesticides	Zmudzinski, 1975; Zandmane and Stasulane, 1987; Zandmane, 1988; Zandmane and Zelcans, 1988; Davies et al., 1997; Roast et al., 2000c
Ecotoxicology – Endocrine disruption	Verslycke, 2003; Verslycke et al., 2003; 2003c; 2004c; 2004d; 2005
* **Environmental contamination**	Beattie and de Kruijf, 1978; Vobach and Felt, 1981; Foekema et al., 1998; Loizeau et al., 2001; 2001b
* **Biomanipulation in lakes**	Dietrich and Hesse, 1990; Hosper and Meijer, 1993; Meijer et al., 1994; Jeppesen et al., 1994; Moss et al., 1996
* **Detection anabolic drugs**	De Wasch et al., 2002; Verslycke et al., 2002; Van Hoof, 2004; Poelmans et al., 2005
* **Phylogeny & Phylogeography**	Kobusch, 1998; Remerie, 2005; Remerie et al., 2004
* **Molecular work**	Suomalainen, 1954; Salemaa, 1986; Nunn et al., 1996; Remerie, 2005; Remerie et al., 2004; Remerie et al., submitted a; submitted b
* **Parasitism**	Tatterssal and Tattersall, 1951; Gibson, 1972; Astthorsson, 1980; Espeel, 1984; Koie, 1993; Marcogliese, 1996
* **Intersexuality**	Hough et al., 1992; Mees et al., 1995b

Appendix

Records of *Neomysis integer*

approx. Latitude	approx. Longitude	Location name	Sytem	Source
71°03'N – 63°50'N	32°09'E – 44°04'E	? White Sea and Murman Seas	?	Wagner, 1885 (Jarzynsky); Zimmer, 1909
68°29-10'N	14°12E – 15°28'E	Lofoten, Norway	Fjord – Loch	Holmquist, 1957
67°14'N – 64°58'N	11°50'E – 15°43'E	Helgeland coast, Norway	Fjord – Loch	Holmquist, 1957
63°26'N – 58°00'N	4°37'E – 10°23'E	Norwegian coast, Christiania to Trondheim	Fjord - Loch	Wagner, 1885 (Sars); Zimmer, 1909
60°34'N – 53°40'N	9°28'E – 30°16'E	Baltic Sea (Estonian coastal waters, Gdansk Bay, Isefjord, Mecklenburg Bay, Vistula lagoon, Bay of Riga, Gulf of Bottnia, Finnish coastal area, Baltic proper, Swedish coast, Darss/Zingst Peninsula, coast Poland, Vislinsky Bay, Danish estuaries and lagoons)	Baltic	Wagner, 1885 (Lindström, Lilljeborg, Cajander, Kröyer); Blegvad, 1922; Dahl, 1944; Segerstrale, 1945; Wiktor, 1961; Järvekülg, 1965; Muus, 1967; Rasmussen, 1973; Kotta and Simms, 1979; Kotta 1979; 1980; 1984; Wiktor et al., 1980; Lumme et al., 1980; Salemaa, 1981; Laughlin and Lindén, 1983; Jansen, 1985; Arndt and Jansen, 1986; Chojnacki and Ciupinski, 1986; Rudstam et al., 1986; Arndt, 1989; Weisse and Rudstam, 1989; Rudstam and Hansson, 1990; Tehn, 1991; 1991b; 1992; Salemaa et al., 1990; Kohn, 1992; Välipakka, 1992; Petryashov, 1992; Pentti, 1992; Witek et al., 1993; Witek, 1995; Razinkovas, 1993; 1996; Thiel, 1996*; Margonski and Maciejewska, 1999; Lindström, 2000; Maciejewska and Opalinski, 2002 and references herein; Lindén et al., 2003; Bergström and Englund, 2004
54°24'N – 53°54'N	9°09'E – 10°13'E	Nordostseekanal/ Kiel canal, Germany	Brackish canal	Kinne, 1955; Schütz, 1969; Kuhlmann, 1984
60°51'N - 59°51'N	2°07'W - 0°47'W	Shetland Islands, Scotland, UK	Brackish pond	Scott and Duthie, 1895
59°23'N – 58°43'N	3°26'W – 2°22' W	The Orkneys, Scotland, UK	Fjord - Loch	Nicol, 1939
58°26'N	3°05'W	Loch Wester, Wick, Scotland, UK	Fjord - Loch	Scott, 1891
58°21-19'N	6°30-35'W	Loch Arnol, Loch Bravas and inland water, Island of Lewis, Outer Hebrides, Scotland, UK	Fjord - Loch	Elton, 1937; Tattersall and Tattersall, 1951*
57°43-40'N	3°16'W	Loch of Spynie, Scotland, UK	Fjord - Loch	Gordon, 1852
57°41-30'N	7°31-06'W	North Ulst, Scotland, UK	Fjord - Loch	Nicol, 1936
57°39-37'N	3°38-34'W	Bay of Findhorn, Scotland, UK	Estuary	Gordon, 1852
57°21-18'N	2°00W	Ythan, England, UK	Estuary – subtidal	Astthorsson, 1980; Astthorsson and Ralph, 1984

approx. Latitude	approx. Longitude	Location name	Sytem	Source
57°03'N - 56°56'N	7°23-32'W	Several lochs, Island Barra, (e.g. Loch St. Clair), Outer Hebrides, Scotland, UK	Fjord - Loch	Scott, 1894; Crichton and Young, 1936
56°42'N	2°28'W	North Esk, Scotland, UK	Estuary - subtidal	Tattersall and Tattersall, 1951*
56°34-32'N	8°07-10'E	Lake district (o.a.Lake Ferring), Denmark	Brackish lake	Aaser et al., 1995; Jeppesen et al., 1994; Søndergaard et al., 2000
56°27'N	3°04'W	Quarry near Tay, Scotland, UK	Brackish pond	Tattersall and Tattersall, 1951
56°34-11'N	5°03-37'W	Loch Craignish, Feochan, Etive, Dunstaffnage Bay, Crenan, Shuna, Linnhen, Eil, Torridon, Ardmaddy Bay, Scotland, UK	Fjord - Loch	Mauchline, 1971; McLusky and Heard, 1971; Kaiser et al., 1992
56°16'N-55°24'N	5°28'W-4°28'W-	Firth of Clyde, at head of lochs Striven, Riddon, Fyne, Gilp and Ranza; Bubh loch, Southannan and Hunterston sands and Kames Bay, Scotland, UK	Fjord - Loch	Mauchline, 1971; 1971b
56°00'N	2°51'W	Aberlady, Scotland, UK	Estuary – marsh	Nicol, 1936
55°23'N-51°25'N	10°26'W - 6°05W	Ireland (Shannon, Lee, Dodder, Cork, Dublin Bay, Galway, Mayo, Wicklow, Youghal; Loch Leam, Loch Foyle, Loch Furnace)	Estuary Brackish lake/pond Fjord - Loch	Rankin, 1907; Kemp, 1910; Tattersall, 1912; Thompson, 1828; Thompson, 1845; Thompson, 1847; Kinahan, 1857; Melville, 1857; MacDonnald and MacMillan, 1951; Murray, 1977; Parker, 1978; Parker, 1979; Parker and West, 1979; O'Sullivan, 1984
55°21-20'N	1°36-34'W	Coquet, England, UK	Estuary	Jorgensen, 1924
54°59-57'N	1°36-25'W	Tyne, England, UK	Estuary	Jorgensen, 1929
54°18-15'N	9°54-59'E	Flemhuder See, Germany	Brackish lake	Rademacher and Kils, 1996
53°44-30'N	0°58-04'W	Humber, England, UK	Estuary – subtidal	Budd, 2002
53°44-43'N	2°51-50'W	Ponds on Hutton Marsh, England, UK	Estuary - marsh	Tattersall, 1919
53°26-17'N	3°12'W - 2°55'W	Pools in Wirral Peninsula, England, UK	Brackish pond	Tattersall, 1919; Standen, 1922; Tattersall and Tattersall, 1951
53°18'N	3°44'W	Landlocked pool at Colway Bay, Wales, UK	Brackish pond	Walker, 1895
53°55-32'N	8°48'W-10°00'W	Elbe, Germany	Estuary – subtidal	Kraepelin, 1886; Dahl, 1891; Kraefft, 1908; Schlienz, 1924; Caspers, 1951; Kühl, 1964; 1972; 1973; Fiedler, 1991; Bernat et al., 1994; Mees et al., 1995b; Köpcke and Kausch, 1996; Winkler., 2000
53°33-05'N	8°45-34'E	Weser, Germany + tributaries and marsh ditches	Estuary – subtidal and intertidal	Klie, 1914; Schlienz, 1922; 1924; Schräder, 1941; Friedrich, 1960; Kühl and Mann, 1969; Michaelis, 1973; Teufert, 1980; Vobach and Feldt, 1981; Grotjan and Michaelis, 1985; Haesloop, 1990; Haesloop and Scheffel, 1991; Kolbe and Michaelis, 2001

approx. Latitude	approx. Longitude	Location name	Sytem	Source
53°40-28'N	8°05-12'	Jade estuary, Germany	Estuary - subtidal	Apel, 1992
53°33-05'N	8°45-34'E	Bremen, Germany Port and gravel pits (e.g. Hegemannsee) connected to the Weser, last course of rivers Lesum and Ochtum, Wümme (Borgfeld). Canals and waterways connected to the Ochtum (e.g. Krimpelfleet, Hucht-inger fleet, Arsten-Habenhauser-fleet,) and Kleine Wumme (e.g. Machinenefleet, HemmstraSSen-graben)	Brackish inland waters and ponds	Haesloop, 1990; Haesloop and Scheffel, 1991
53°02'N - 52°51'N	5°25-53'E	Brackish lakes in Friesland, The Netherlands (Tjeukemeer, Slotermeer)	Brackish lake	Otto, 1934; Vijverberg, unpublished; Bremer and Vijverberg, 1982
53°05'N - 52°31'N	5°02-39'E	IJselmeer (Zuiderzee) en Barnegat, The Netherlands	Brackish lake/pond	De Vos, 1941; Vorstman, 1951; Macan, 1974;
52°45-35'N	1°33-42'E	Hickling and Cockshoot Broad, England, UK	Brackish lake	Moss, 1991; Bales et al., 1993; Irvine et al., 1993; 1995; Moss et al., 1996
52°29-13'N	7°35'-11°44E	Weser-Elbe canal, Germany	Brackish canal	Munkemüller and Herhaus, 1978
52°26-12'N	6°50'E-7°24'E	Ems – Dollard, The Netherlands & Germany	Estuary – subtidal	Mees et al., 1995; 1995b
52°54-45'N	1°44-24E	Norfolk Broads, England, UK	Brackish pond	Gurney, 1904
?51°57-33'N	? 0°36E – 1°18'E	Lagoon in Essex, England, UK	Brackish lake	Howes, 1939
51°57-52'N	4°05-15'E	Brielse Maas, The Netherlands	Brackish lake	Leentvaar, 1955
51°48-31'N	3°37'E-4°24'E	Brackish lakes and ditches in Zeeland, The Netherlands (Grevelingen, Veere, Den Ingel, Ouwerkerk)	Brackish lake/pond	Tesch, 1911; Vlasblom and Elgershuizen, 1977; Borghouts, 1978; Platenkamp, 1983
51°36-13'N	3°06'W-2°37'W	Severn, England, UK	Estuary – subtidal	Moore et al., 1979; Bamber and Henderson, 1994
51°33'N	0°32'E	Thames, England, UK	Estuary - marsh	Lambert, 1930; Budd, 2002
51°18-14'N	3°48-51'W	Conwy estuary, Wales, UK	Estuary – subtidal	Hough and Naylor, 1992
51°25-21'N	0°28-23'E	Medway, England, UK	Estuary - subtidal	Van den Broek, 1978*
51°26-13'N	4°00-23E	Schelde, brackish part, The Netherlands & Belgium	Estuary – subtidal	Tesch, 1910; Mees and Hamerlynck, 1992; Mees et al., 1993; 1993b; 1994; 1995; 1995b; Hostens and Mees, 1999; Fockedey and Mees, 1999; Maes et al., 2003*; Hostens, 2003*; Verslycke, 2003; Verslycke et al., 2004; 2005
51°25-20'N	4°03-12'E	Schelde, salt marshes Saeftinghe, Waarde and Sieperda, The Netherlands	Estuary – salt marsh	Cattrijsse, 1994; Cattrijsse et al., 1994; 1997*; Hampel et al., 2003; 2003b; Hampel and Cattrijsse, 2004; Hampel, 2003

approx. Latitude	approx. Longitude	Location name	Sytem	Source
51°20-13'N	3°32'E-4°23'E	Brackish ponds, left bank Schelde estuary, East Flanders/Antwerpen Belgium & The Netherlands: Hollandersgat (St-Margriete), Boerenkreek (St-Jan-in-Eremo), Kleine Geul en Rode Geul (Assenede), St-Elooiskreek (Wachtebeke), Groot Gat (Doel), Galgenweel, Kanaaldok, Het Grote Gat, Plas van Steenland, Plas aan Boutweg, Burchtse Weel and Blokkersdijk, Braakman, Schuddebeurs	Brackish pond	Dumont and Gysels, 1971; Vlasblom and Elgershuizen, 1977; Van de Vijver, 1983; Soselisa, 1994; Mees et al., 1995b; Verslycke and Janssen, 2002; Verslycke, 2003; Verslycke et al., 2002; 2003; 2003b; 2004b; 2004c; Ghekiere et al., 2004; Fockedey et al., in press
51°30-06'N	2°25'E - 3°22'E	Continental shelf, Belgium	Coastal sea	Kramp, 1910; Dewicke, 2002; Tattersall and Tattersall, 1951(Oostende?)
51°22-05'N	2°32'E - 3°22'E	Sandy beaches, Belgium	Sandy beach	Van Beneden, 1861; Lock et al., 1999, Beyst, 2001; Beyst et al., 2001
51°12-14'N	2°56-57'E	Spuikom, Oostende, Belgium	Brackish lake	Polk, P., 1963
51°05'N	2°48'E	Clay pits, Stuyvekenskerke, Belgium	Brackish pond	Espeel, 1979; Espeel, 1982
51°00'N – 50°22'N	1°33'E – 2°05'E	Boulonnais, France	?	Wagner, 1885 (Giard)
50°55-53'N	1°23'W	River Itchen, Northam Bridge, England, UK	Estuary – intertidal	Raymont et al., 1964
50°53'N	1°24'W	River Test, Tottem Marsh, Redbridge, England, UK	Estuary – salt marsh	Ralph, 1965; Ferguson, 1973; Armitage, 1979; Raymont et al., 1964; 1966; 1968; Morris, 1971; Morris et al., 1981; 1982b; Armitage et al., 1981
50°48'N	1°19'W	Calshot, Hampshire	Estuary - marsh	Barnes and Jones, 1972
50°48'N	1°05'W	Artificial pond near Porthsmouth, England, UK	Brackish pond	Morris et al., 1977; 1981; 1982
50°30-26'N	4°11-12'W	Tamar, England, UK	Estuary – subtidal	Percival 1929; Tattersall, 1938; Milner, 1986; Bradshaw et al., 1989; 1990; Moffat and Jones, 1992; 1993; Moffat, 1996
50°25-24'N	4°17-18'W	Lynher, England, UK	Estuary – subtidal	Percival 1929
50°23-21'N	4°27-31'W	East Looe, England, UK	Estuary - intertidal	Roast et al., 1998; 1999, 1999b, 2000; Moffat, 1996
50°21'N	4°07'W	Plym, Chelson Meaddows landfill, England, UK	Estuary	Molloy, 1958
50°20-18'N	4°05-01'W	Yealm	Estuary	Molloy, 1958
50°09'N	5°04'W	Swanpool, Falmouth, England, UK	Brackisch pond	Barnes et al., 1971; 1977

approx. Latitude	approx. Longitude	Location name	Sytem	Source
49°28-25'N	0°07-29'E	Seine, France	Estuary - subtidal	Wagner, 1885 (Bonnier, de Kerville); Zouhiri et al., 1998; Mouny et al., 1996; 1998, 2000; Dauvin et al., 2000
48°41-38'N	1°29-21'W	Mont Saint Michel Bay, France	Estuary - marsh	Laffaille et al., 2001*
47°52'N	3°55W	Concarneau, Brittany, France	Estuary	Wagner, 1885 (Bonnier)
47°22-16'N	2°10'W - 1°30'W	Loire, France	Estuary	Marchand, 1981*
45°15-03'N	0°38-44'W	Gironde, France	Estuary - subtidal	Sorbe, 1980; Castel, 1993; Mees et al., 1995; 1995b; David et al., 2005
44°40'N	1°01'W	Arcachon Bay – L'Eyre, France	Estuary - intertidal	Bachelet and Dauvin, 1993
43°21-17'N	3°05'W – 1°55'W	Rias Guipuzcoa (Deba, Urola, Oria, Uremea), Spain	Estuary - subtidal	San Vicente, 1993; 1996
39°06'N-38°41'N	9°09'W-8°42'W	Tagus, Portugal	Estuary - subtidal	Salgado et al., 2004*
37°09-07'N	8°37-34'W	Ria de Alvor, Portugal	Estuary - subtidal	Rodrigues and Dauvin, 1987
36°34-27'N	6°10-12'W	Bay of Cádiz, tidal channels, Spain	Estuary - subtidal	Drake et al., 1997
37°28'N-36°46'N	6°21-00'W	Guadalquivir, Spain	Estuary - subtidal	Drake et al., 2002
43°20-41'N	4°37-40'E	? Bouche-du-Rhone and canal d'Arles, Mediterranean, France	Estuary	Bacescu, 1941

*: recorded from fish and decapod stomach contents.
Historical records not included (location not specified): Friedrichs, 1904; Redeke et al., 1923; Redeke, 1932; 1933; 1935; 1948; Dorgelo, 1928; Makings, 1977.

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