

# Marshes as sources or sinks of an estuarine mysid: demographic patterns and tidal flux of *Neomysis kadiakensis* at China Camp marsh, San Francisco estuary

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## Abstract

The population characteristics, seasonal abundance and tidal flux of *Neomysis kadiakensis* were studied to determine if tidal marshes serve as sources or sinks for mysids in China Camp, located in the San Francisco estuary. Monthly surveys of the zooplankton community were conducted during spring tide periods between May 2002 and May 2003, using a fyke net (500  $\mu\text{m}$  mesh) fixed at the mouth of a fourth order tidal channel system in a tidal marsh. Mysids were collected and preserved hourly throughout full tidal cycles. *Neomysis kadiakensis* was the dominant mysid species, comprising 94–100% of mysids throughout the year. Monthly mean abundance of *N. kadiakensis* ranged from 14 mysids  $\text{m}^{-3}$  in January 2003 to 244 mysids  $\text{m}^{-3}$  in March 2003. Length frequency distributions indicated that reproduction and recruitment were nearly continuous, with abundance peaks occurring throughout the year (e.g., spring, summer and early fall). The resulting flux estimates during this period suggested that China Camp marsh was a sink for *N. kadiakensis*. The mean daily (ca. 24.8 h) fluxes of *N. kadiakensis* corresponded to an instantaneous daily population mortality rate within the marsh channel of  $0.29 \text{ d}^{-1}$ . Although all sizes and stages experienced a net import to the marsh, a significant positive relationship was observed between mysid length and mean annual flux, indicating that larger, mature mysids experienced a greater degree of tidal import to the marsh than smaller, juvenile mysids. These analyses suggest that size-specific predation, perhaps from fishes, shrimp, and/or birds may have had a disproportionate impact on large, mature mysids. Mortality rates in the marsh greatly exceeded the overall population growth rates, indicating that predation pressure on mysids was greater in the marsh than in the subtidal estuary. Mysids, therefore, supply a net flux of energy from the subtidal estuary to the marsh during spring tide series; however, the ultimate fate of this energy is unknown (remaining within the marsh system vs. export back to the estuary via trophic relay or other processes).

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## 1. Introduction

Tidal marshes can play an important trophic role within broader estuarine ecosystems as sources or sinks

of materials, energy, and organisms (Dame and Allen, 1996; Kneib, 2000; Odum, 2000). Tidal marshes have commonly been considered sources of production for neighboring estuaries through the pulsing export of materials such as organic matter and nutrients (Odum, 1980; Dame et al., 1986). These material exports, however, are not universal across marsh-estuarine systems and will often vary with regard to marsh age, tidal range, subsystem area, and distance to the ocean

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(Childers et al., 2000; Valiela et al., 2000). Nekton movements are also considered to have a role in the export of marsh production, via a chain of predator–prey interactions, to the open estuary, e.g., the trophic relay concept (Kneib, 1997).

Marshes are an important nursery habitat for many estuarine species (Kneib, 1997; Minello et al., 2003), and can function as sources of invertebrates and fish. Some decapod crustaceans, whose reproductive strategies are associated with dispersal and recruitment, utilize marshes during ebbing tides to release larvae, resulting in the net export of larvae from tidal creeks and channels into subtidal areas (Christy and Stancyk, 1982; Dittel et al., 1991). It has been argued that mysids may similarly favor marsh channels for the release of their broods (Cattrijsse et al., 1994).

Alternatively, tidal marshes may be sinks for estuarine fauna (Carlson, 1978). Because flooded intertidal channels are closer to sources of marsh plant production and detritus than subtidal areas, herbivorous and detritivorous prey species such as mysids migrate into the marsh channels during flooding tides to forage for food (Kneib and Wagner, 1994). Heavy predation (particularly of crustaceans) by resident marsh fauna, can result in a net import of prey to the marsh (Carlson, 1978; Feyrer and Matern, 2000). Currently, there are few data to support this relationship.

Mysids (Crustacea: Mysidacea) are of particular interest in this context for two reasons. First, they are common, often highly abundant members of the hyperbenthos in estuaries (Orsi and Knutson, 1979). They also occupy and occasionally dominate the hyperbenthos in estuarine-marsh channels (Johnston and Northcote, 1989; Cattrijsse et al., 1994; Cunha et al., 1999). Although tidal migrations of mysids between the marsh and the subtidal estuary occur (Hampel et al., 2003), few studies report flux estimates of mysids between these areas.

Second, mysids are important trophic links in estuarine food webs (Orsi and Knutson, 1979; Mees et al., 1994; Mees and Jones, 1997), serving as both consumers and prey. In general, mysids are omnivores, feeding on detritus, phytoplankton and zooplankton (Mauchline, 1980). Mesozooplankton are the most common prey items of many estuarine mysids (Fockede and Mees, 1999; Winkler et al., 2003), however, most mysids utilize organic detritus to a considerable extent as well (Mees and Jones, 1997). Within salt marshes, stable isotope and diet analyses have demonstrated that mysids consume detritus derived from salt marsh vegetation (Zagursky and Feller, 1985; Froneman, 2001). As prey, mysids are important components in the diets of many fishes and shrimp species (Mauchline, 1980). These mysid predators periodically utilize estuarine marshes as nursery habitats or as foraging sites (Cattrijsse et al., 1994; Feyrer et al., 2003).

Historically, in the San Francisco estuary, mysids were significant components in the diets of estuarine fishes, such as juvenile Pacific herring *Clupea pallasii*, and striped bass *Morone saxatilis* (Heubach et al., 1963; Turner, 1966). Recent declines in the abundance of mysids and the closely correlated declines in the abundance of their predators further point to the trophic importance of mysids in the San Francisco estuary (Feyrer et al., 2003).

To properly evaluate whether marshes serve as a source or a sink of a mysid species, an understanding of the basic demography and life history patterns of that species is necessary. Such data are rarely available. In the San Francisco estuary, *Neomysis kadiakensis* is the most euryhaline and widespread native mysid. It inhabits areas with salinities ranging from 0 to 28, is distributed throughout the estuary year-round (Gewant and Bollens, in press), and is known to occupy marsh channels in the northern San Francisco estuary (Carlson and Matern, 2000; J. Orsi, personal communication). However, there are no published life history data for this species.

This study has two major objectives. First, we aim to describe the life history and seasonal abundance patterns of *Neomysis kadiakensis* in an estuarine tidal marsh. Second, we wish to determine fluxes of mysids between the marsh and the neighboring subtidal estuary. Such data are necessary to fully address the overall goal of assessing the trophic role of tidal marshes as sources or sinks for mysids.

## 2. Materials and methods

### 2.1. Study area

China Camp marsh is located on the southwestern edge of San Pablo Bay, a northern embayment of the San Francisco estuary, California, USA (Fig. 1). This ancient and centennial salt marsh complex drains an area of 38.2 ha (Williams and Orr, 2002). China Camp marsh is a brackish intertidal wetland that has experienced relatively little anthropogenic impact, due in part to its protection as a state park for the last 25 years. Tides are mixed semi-diurnal with diurnal ranges of approximately 2 m. The Sacramento and San Joaquin Rivers to the northeast are the main sources of fresh water to China Camp during the summer and fall. In winter and spring months, additional sources of fresh water include smaller rivers entering the northern San Francisco estuary, Gallinas Creek to the west, and rain runoff from upland areas.

All samples were collected in a fourth order intertidal channel system on the west end of China Camp marsh. This channel system drains an area of 11 ha and is approximately 2800 m in length (Visintainer et al.,

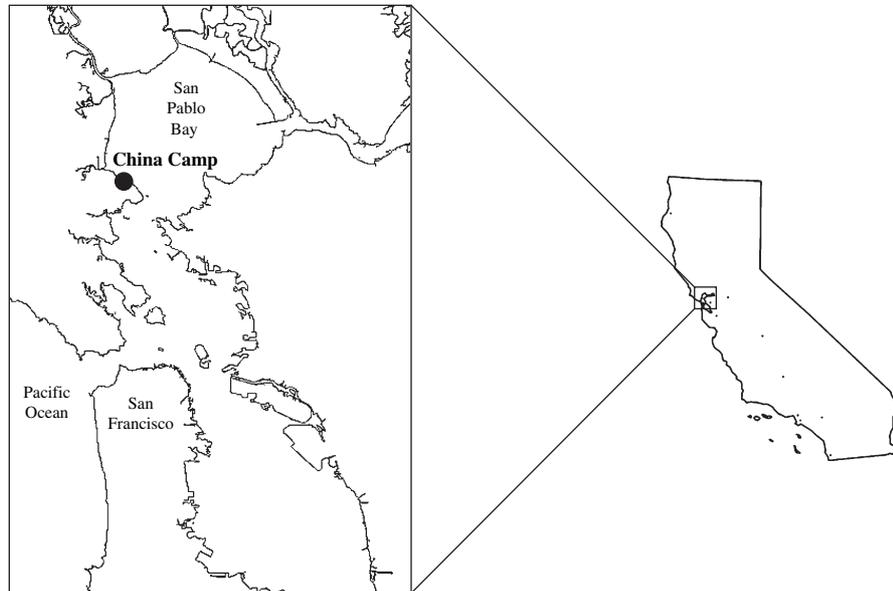


Fig. 1. Location of China Camp marsh in the San Francisco estuary, California, USA.

submitted for publication). The channel is approximately 2 m deep and 10 m wide at mean higher high water (MHHW) at the sampling site. Water routinely floods the marsh plain during extreme spring tides and is confined to the channel during neap and moderate–low spring tides (percentage of time that marsh plain floods = 1.3% annually) (Visintainer et al., submitted for publication). The channel dewateres almost completely during the spring tide series.

## 2.2. Sampling

Mysids were sampled monthly between May 2002 and May 2003. Sampling was conducted during moderate spring tides, those not exceeding 2 m in height, ensuring that water did not flood the marsh plain during sampling, while allowing for nearly complete dewatering of the channel at lower low water (LLW). Each monthly sampling was conducted over a complete tidal cycle to estimate the flux of mysids across the tidal channel mouth. However, storms and equipment failure in December 2002 allowed sampling during only the first half of the tidal cycle.

Samples were collected with a fyke net affixed to galvanized steel poles in the center of the channel. The net (0.35 m wide, 500  $\mu\text{m}$  mesh) spanned approximately 5% of the cross-sectional channel width at mean high water (MHW), approximately 20% of the cross-sectional width at mean low water (MLW), and sampled the entire depth of the water column throughout sampling, between MHW and MLW.

Each month, the complete (24.8 h) tidal cycle was sampled in two discrete 12-h segments. All sampling

began at LLW after the tide had ebbed, when the channel was nearly dewatered, and continued during flood tide for approximately 6 h to lower high water (LHW). At this time, the fyke net was reversed to sample the ebbing tide for ca. 6 additional hours to higher low water (HLW). After a break in sampling for ca. 25 h, sampling continued for ca. 12 h, from HLW to LLW, to complete the tidal cycle. Samples were retrieved hourly from the cod end of the net and were immediately preserved in a 10% formalin/seawater solution and stained with Rose Bengal.

Hydrographic measurements were made hourly throughout the tidal cycle. Water temperature and salinity were measured at the surface and near bottom using digital instruments (YSI 85, YSI Inc.). Water flow was measured using a digital flowmeter (model 2030, General Oceanics, Inc.) positioned at mid-water just in front of the center of the net opening. Water depth was measured by visual reference to a ruled stage gauge installed directly in the center of the mouth of the net.

Because net clogging was reported to be an issue in previous studies (e.g., Carlson, 1978; Houser and Allen, 1996), we sampled only for 15 min each hour during the first four monthly samplings (May–August 2002). We did not encounter significant clogging and made continuous hourly collections throughout the tidal cycle during all subsequent sampling (September 2002–May 2003).

## 2.3. Sample processing and data analysis

Samples exceeding 200 mysids were subsampled with a Folsom splitter until a target of 100–200 individuals

was obtained. Mysids were subsequently counted, identified with the aid of a guide for San Francisco Bay mysids (J. Orsi, unpublished), sexed, categorized by life stage, and measured (apex of the rostrum to the posterior end of the telson) to the nearest micrometer under a dissecting microscope. Sex and maturity life stages were categorized according to Mauchline (1980) and Mees et al. (1994) as neonate, juvenile, immature male, immature female, mature male, mature female, brooding female, and empty female. Male mysids were distinguished by their elongated fourth pleopods and well-developed, setose lobus masculinis. Female mysids were characterized by the presence of a marsupium located between the thoracic legs. Females with developing marsupia that were too small to be seen in lateral view were classified as immature. Adult females were further subdivided into mature (developed marsupium present but not yet filled with young), brooding (marsupium containing a brood of larvae), or empty (distended or irregular lamellae of marsupium indicating the brood had already emerged) female categories. When it was difficult to distinguish between mature and empty females, these stages were grouped together as “non-brooding females”.

Length frequency distributions were analyzed to estimate periods of recruitment. Juveniles 1–3 mm in length were considered recruits. Growth was determined by modal progression analysis (Bollens et al., 1992) for the overwintering generation (November 2002–March 2003), but the lack of distinct modes during other times of the year prevented growth estimates for those seasons.

Absolute and relative monthly fluxes of mysids between the marsh channel and the open waters of the estuary were estimated based on Ferrari et al. (1982, 1985). Absolute net flux ( $N_{\text{net}}$ ) was estimated as the sum of total mysids migrating into the marsh ( $N^-$ ), being negative, and those leaving the marsh ( $N^+$ ), being positive, as measured by those mysids passing through the net over a given tidal cycle. Similarly, net volumes filtered ( $V_{\text{net}}$ ) were determined by calculating the difference between the volume of water entering the marsh ( $V_{\text{fld}}$ ) and leaving the marsh ( $V_{\text{ebb}}$ ) through the net. When  $V_{\text{net}} \neq 0$ , it was necessary to adjust the net flux of mysids ( $N_{\text{net}}$ ) by adding the following value: ( $V_{\text{net}} \times N \text{ m}^{-3}$ ), where  $N \text{ m}^{-3}$  represents the total density of mysids per sampling. The relative flux, termed the ‘Ferrari index’ ( $I$ ) was calculated as:

$$I = \frac{N^- + N^+}{|N^-| + |N^+|}$$

where  $|N^-|$  and  $|N^+|$  are the absolute values of  $N^-$  and  $N^+$ , respectively. This index varies from  $-1$  (sink) to  $+1$  (source), where positive values represent a net flux of mysids out of the marsh into the estuary, and negative

values represent a net flux of mysids into the marsh (Ferrari et al., 1982, 1985).

Annual fluxes are reported as both mean and cumulative fluxes. Mean annual fluxes were determined by calculating the mean of the monthly Ferrari index values ( $\bar{I}$ ) by size and stage. Cumulative fluxes were determined by summing the total incoming individuals and total outgoing individuals across monthly samplings,  $\sum(N^\pm)$ , and subsequently calculating an annual flux using the Ferrari index equation:

$$I_c = \frac{\sum(N^-) + \sum(N^+)}{|\sum N^-| + |\sum N^+|}$$

### 3. Results

#### 3.1. Environmental conditions

Large seasonal variations in temperature and salinity occurred in the study area (Fig. 2). Sampling commenced during a relatively dry year and proceeded through a relatively wet year (<http://www.wrh.noaa.gov>), exhibited by salinities at the start and finish of the sampling year (Fig. 2). Salinity ranged from 27 (August–October 2002) to 6 (January 2003). Temperature of the tidal channel ranged from 25 °C (August 2002) to 10 °C (February 2003).

Current speed in the marsh channel was highly variable both within and between tidal cycles. However, water flowed at its highest rate after HHW, at a mean speed of  $2 \text{ m s}^{-1}$ . Discrete flooding and ebbing current maxima typically occurred 3 h after slack water, with the exception of the flooding current between LLW and LHW, when the mean current maxima occurred during the first hour of the tidal cycle.

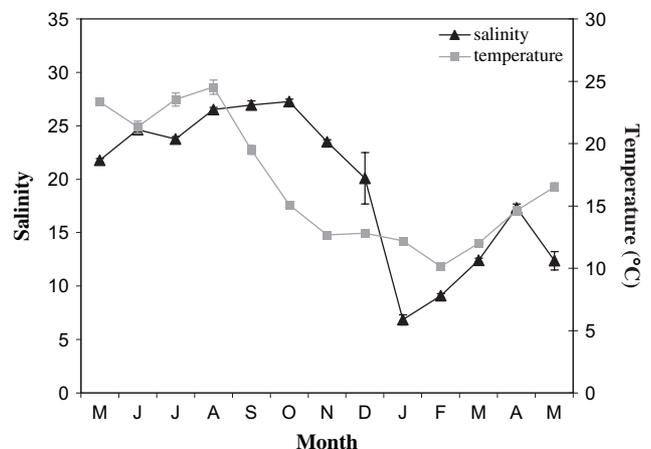


Fig. 2. Mean ( $\pm$ SE) water temperature and salinity at the study site (May 2002–May 2003).

### 3.2. Mysid taxa of San Pablo Bay

All seven described species of San Francisco estuary mysids were captured during the sampling period, including the rare *Deltamysis holmquistae*. *Neomysis kadiakensis* was the dominant species year-round and comprised between 94 and 100% of the mysid assemblage at China Camp throughout the year (Table 1). The remaining species, dominated by the non-native *Acanthomysis aspera* and native *Alienacanthomysis macropsis*, were captured principally between October 2002 and April 2003 and were most abundant in November 2002, at a maximum density of 2.3 individuals  $m^{-3}$ . All subsequent results will refer only to *N. kadiakensis*.

### 3.3. Seasonal abundance, length and stage composition

Maximum *Neomysis kadiakensis* density, of 244 individuals  $m^{-3}$ , occurred in the spring (March 2003) (Fig. 3A). Smaller peaks in density occurred in summer and fall (July and September 2002). The summer peak in density of recruits (1–3 mm) occurred one month prior to the summer peak in density of brooding females (Fig. 3B). During the winter months, densities remained low, never exceeding 42 individuals  $m^{-3}$ .

Overall population growth rates, assuming exponential growth and calculated for the period between each monthly sampling, varied from  $-0.037 d^{-1}$  (December–January) to  $0.093 d^{-1}$  (February–March). Monthly population growth rates were 0.011, 0.020,  $-0.020$ , 0.022,  $-0.012$ ,  $-0.035$ , 0.003,  $-0.037$ , 0.013, 0.093,  $-0.008$ , and  $-0.31 d^{-1}$ , from May 2002 to May 2003, respectively.

Length and stage composition of *Neomysis kadiakensis* indicated that recruitment was nearly continuous throughout the year and juveniles dominated the population, comprising  $>34\%$  of the total population throughout the year and  $>80\%$  of the population in the spring and late fall (Fig. 4). However, reproduction and recruitment declined considerably during winter months; brooding females comprised  $<2\%$  of the population

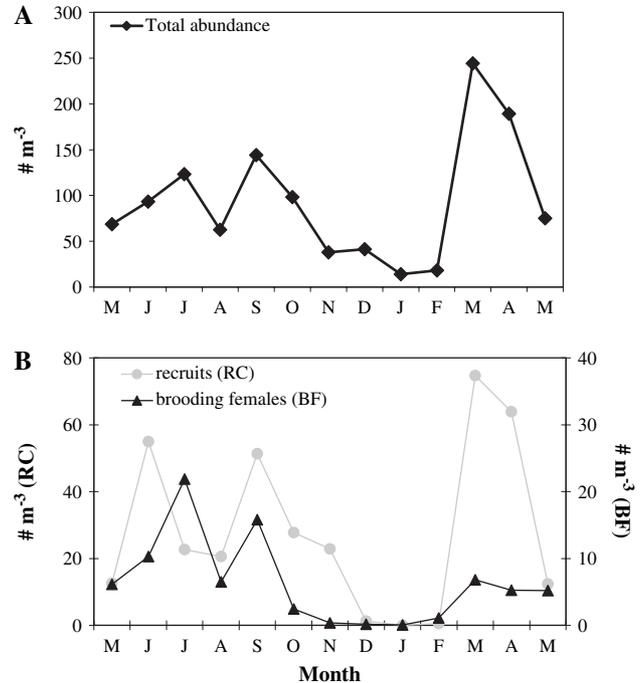


Fig. 3. Seasonal abundance of *Neomysis kadiakensis* (May 2002–May 2003): (A) total abundance, (B) abundance of recruits (1–3 mm) and brooding females.

(November 2002–January 2003) and recruits comprised  $<3\%$  of the population (December 2002–February 2003).

Generally, adult *Neomysis kadiakensis* reached maturity at 7–8 mm and reached a maximum length of 13 mm. Adults of the overwintering generation matured later (10–11 mm) and grew to a maximum length of 17 mm. Modal progression analysis of the overwintering generation indicated that individual *N. kadiakensis* grew more slowly ( $0.07 mm d^{-1}$ ) from November through January and progressively faster from January–February 2003 and February–March 2003 ( $0.10 mm d^{-1}$  and  $0.13 mm d^{-1}$ , respectively). Modal progressions in length frequency distributions were not apparent during other times of the year, and thus individual growth rate estimates were not possible.

Table 1  
Percent composition of mysid taxa at China Camp (May 2002–May 2003)

	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
<i>Neomysis kadiakensis</i>	99.86	100.00	99.99	100.00	100.00	99.51	93.94	95.04	93.94	94.60	99.43	99.23	99.91
<i>Alienacanthomysis macropsis</i>	0.07	0.00	0.00	0.00	0.00	0.00	1.66	1.55	4.78	4.52	0.46	0.62	0.01
<i>Acanthomysis aspera</i>	0.01	0.00	0.00	0.00	0.00	0.45	4.31	3.05	1.21	0.04	0.06	0.14	0.00
<i>Neomysis mercedis</i>	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.04	0.83	0.06	0.02	0.07
<i>Deltamysis holmquistae</i>	0.00	0.00	0.01	0.00	0.00	0.00	0.09	0.07	0.02	0.00	0.00	0.00	0.00
<i>Acanthomysis hwanhaiensis</i>	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Acanthomysis bowmani</i>	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
N	3498	3292	2315	3123	4297	2097	2299	1037	2307	1365	3238	3206	2497

N = the total number of individuals identified to species per month.

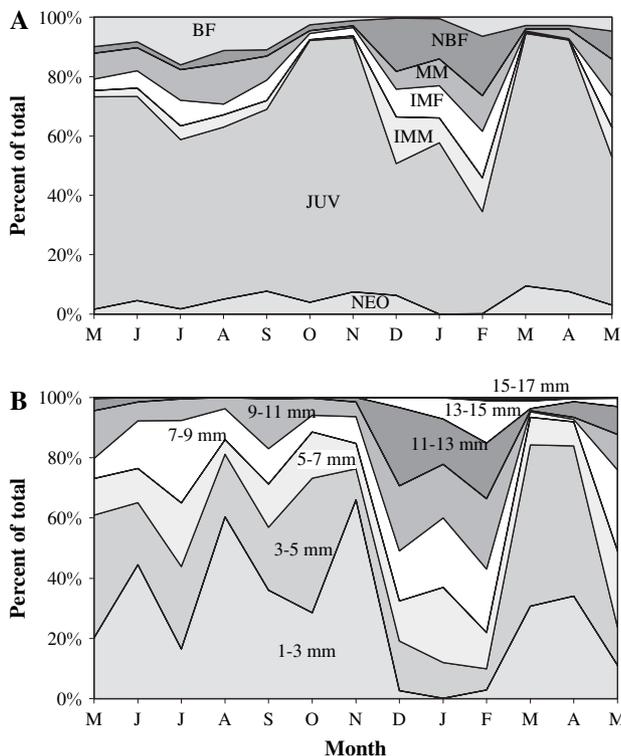


Fig. 4. Percent composition of *Neomysis kadiakensis* (May 2002–May 2003) by: (A) stage, (B) size class. Stage abbreviations are as follows: NEO – neonates, IMM – immature males, IMF – immature females, MM – mature males, NBF – non-brooding females, BF – brooding females.

Overwintering and spring cohorts were identified from distinct modes in the length frequency distributions. Modes produced in the spring and summer were quickly muted by the continued recruitment of new individuals, making the identification of additional generations difficult. We interpreted the following *Neomysis kadiakensis* life history patterns using a combined analysis of length frequency distributions, seasonal abundances, and composition data. Overwintering adults reproduced in the spring and persisted in low abundance through the month of May. Peak abundances of recruits in June 2002 (Fig. 3B) may have been a result of young produced from both overwintering and spring generations. Abundance of brooding females declined in late summer (August 2002), suggesting the death of spring generation females. A sharp decline in the abundance of adults and brooding females in November 2002 suggests that the majority of adults produced in the summer had died, leaving predominantly fall recruits in the overwintering generation.

### 3.4. Tidal flux

Flux estimates indicate that the marsh is a net sink for *Neomysis kadiakensis*. The total flux of individuals

into the marsh exceeded the total flux of individuals out of the marsh during all tides sampled with the exception of January 2003 (Fig. 5E). The average daily (ca. 24.8 h) fluxes of the population indicated an instantaneous daily mortality rate within the marsh channel of  $0.29 \text{ d}^{-1}$ .

Net flux varied by mysid size both within and across months (Fig. 5A–D). Across months, recruits and juveniles were exported from the marsh more frequently, imported to the marsh less frequently, and experienced comparatively smaller fluxes than larger mysids during months of net import. The largest size class (9–13 mm) commonly experienced periods of very high net import, with instantaneous mortality rates occasionally exceeding  $0.99 \text{ d}^{-1}$  (May 2002, March 2003, and April 2003).

Annual fluxes, calculated from monthly flux estimates, indicated that although individuals of all sizes and stages tended toward an annual net import of mysids ( $\bar{I} < 0$ ), annual fluxes were not equal across size and stage. Mysid size and mean annual flux were significantly related ( $r^2 = 0.83$ ,  $p < 0.001$ ), with smaller mysids tending towards zero net flux, and larger mysids tending towards a Ferrari index value of  $-1$  (Fig. 6). Mysid size and annual cumulative flux were also significantly related ( $r^2 = 0.46$ ,  $p < 0.05$ ). A relationship between annual flux and life stage was apparent, with mature mysids experiencing a greater net import to the marsh than neonates, juveniles and immature mysids (Fig. 6B and D). The cumulative flux of neonates ( $I_c = -0.25$ ,  $\bar{I} = -0.14$ ) was comparatively lower than their annual mean flux.

## 4. Discussion

### 4.1. Sources of potential sampling bias

Our sampling regime had two obvious sources of potential bias (spatial and temporal) that merit some discussion. With regard to the former, our estimates of tidal flux are contingent on the assumption that mysids are distributed uniformly across the tidal channel cross-section on both the incoming and outgoing tides. Thus, the fyke net collections of mysids captured from the center of the channel (the only position in which we could capture mysids throughout the tidal cycle) are by definition representative of all other positions in the water column. However, there is no literature to validate this assumption. Hough and Naylor (1992) found that *Neomysis* concentrated in the slow-flowing waters along the channel edge during ebbing tides, and, in this study, mysids were also often observed along the shallow, vegetated edge of the channel during ebbing tides. Thus, if mysid transport varied along the cross-sectional width of the channel, and if mysids behaved differently on the incoming tides than they did on the outgoing tides, our estimates of abundance, stage composition, and fluxes

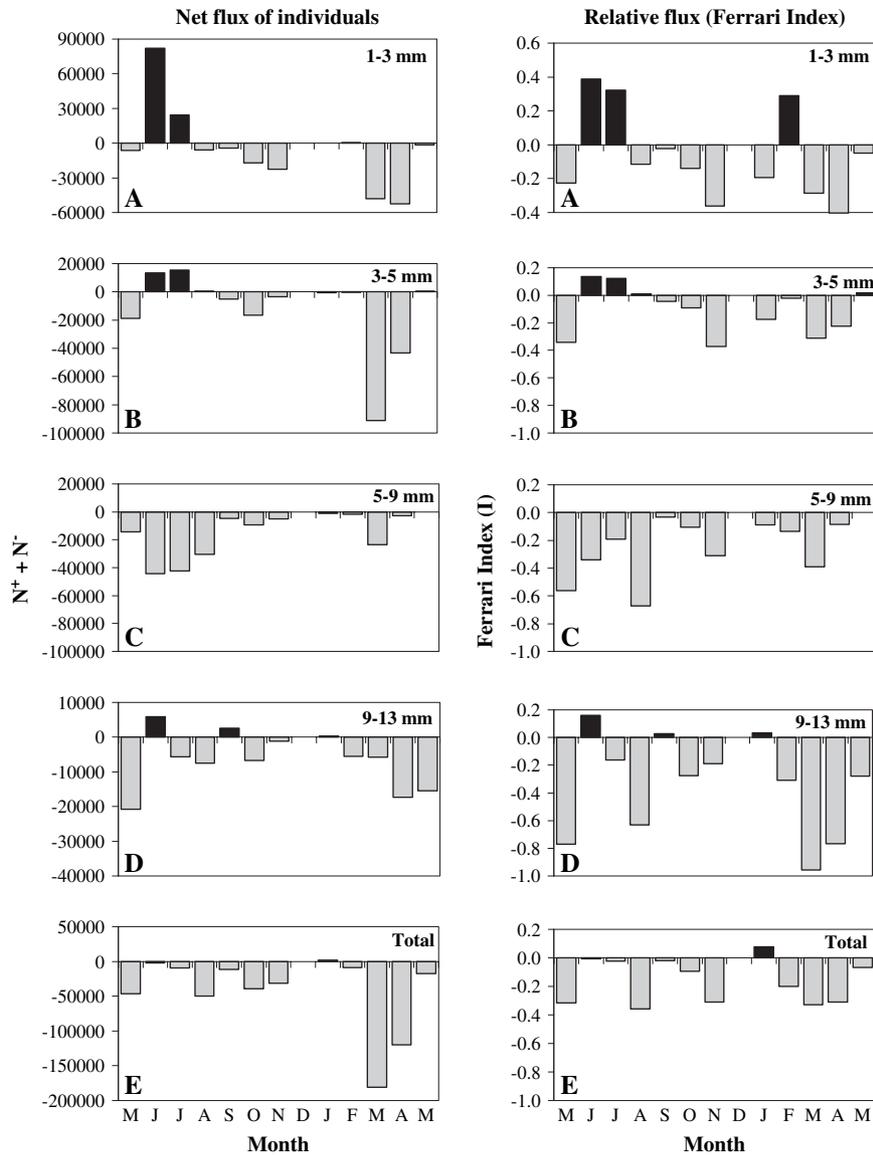


Fig. 5. Net tidal flux of individuals (left panels) and relative flux,  $I$ , (right panels) for *Neomysis kadiakensis*: (A) 1–3 mm, (B) 3–5 mm, (C) 5–9 mm, (D) 9–13 mm, and (E) total *N. kadiakensis*. Sampling did not occur in December 2002. Positive values represent a net flux out of the marsh, negative values represent a net flux into the marsh.

would be affected. More specifically, a greater preference by the mysids for the shallows on the ebb vs. the flood tides would result in a biased estimate of net flux into the marsh, thereby affecting our conclusion that marshes serve as a sink for mysids.

With regard to potential temporal bias, we assumed that fluxes of mysids were similar during spring and neap tide series. We chose to sample exclusively during the spring tide series to ensure that the channel was almost completely dewatered. However, the channel never dewatered during the intervening neap tides, providing habitat within the marsh where mysids could potentially remain and reproduce. Therefore, it is possible that our flux estimates are not representative of the other half of the lunar tidal series, when the channel

does not dewater, and a reverse trend (i.e. a net efflux of mysids) could occur during these periods. However, it is hard to imagine what biological or physical processes would lead to a reversal of the direction of the flux in each lunar cycle. Nevertheless, our annual flux estimates and estimated mortality rates, and our conclusion that marshes act as an overall sink for mysids throughout the year, would be affected if fluxes vary with respect to spring and neap tide series.

#### 4.2. Life history and abundance patterns

*Neomysis kadiakensis* is highly abundant at China Camp marsh (mean annual abundance = 100 individuals  $m^{-3}$ ). Comparatively high mysid abundances have

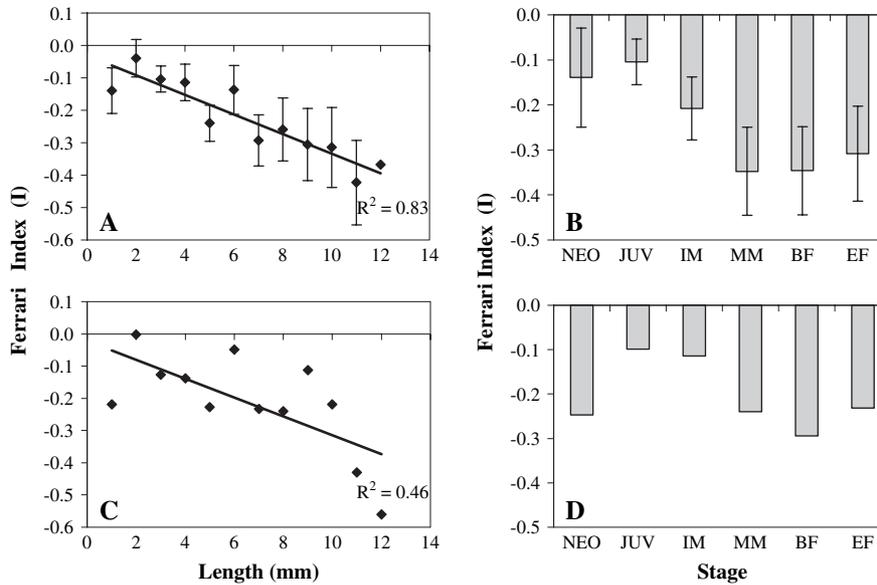


Fig. 6. Relationship between annual mean ( $\pm$ SE) flux ( $\bar{I}$ ) of *Neomysis kadiakensis* as a function of (A) size and (B) stage. Relationship between annual cumulative net flux as a function of (C) size and (D) stage ( $n = 12$ ). Positive values represent a net flux out of the marsh, negative values represent a net flux into the marsh. Stage abbreviations are as follows: NEO – neonate, JUV – juvenile, IM – immature, MM – mature male, BF – brooding female, EF – empty female.

been reported in few marshes worldwide (*Mesopodopsis slabberi* in the marshes of the Westerschelde Estuary, NW Netherlands (Hampel et al., 2003) and *Neomysis mercedis* in the oligohaline marshes of the northern San Francisco estuary prior to 1986 (Orsi and Mecum, 1996; Feyrer et al., 2003)), as well as in many European estuaries (Mees and Jones, 1997). Currently, the mean annual abundances of mysids in marshes of the northern San Francisco estuary are  $<2$  individuals  $m^{-3}$ . Estuary-wide abundances are similarly low (W. Mecum, personal communication). Abundance of *N. kadiakensis* at China Camp marsh is strikingly higher, by comparison, than reported mysid abundances anywhere else in the estuary, perhaps due to the use of different sampling gear and/or sampling of different water depths (habitats). This high, localized mysid abundance at China Camp marsh remains unexplained.

The spring (March 2003) peak in abundance from this study is consistent with Carlson and Matern (2000), who reported peak abundances of *Neomysis kadiakensis* in Suisun marsh, San Francisco estuary, during February and March, 1999. Gewant and Bollens (in press) identified annual peaks in abundance of *N. kadiakensis* between January and April throughout the lower San Francisco estuary; however, due to the large mesh size of their net (3 mm), their abundance estimates are likely biased toward the largest overwintering adults.

The *Neomysis kadiakensis* population at China Camp marsh exhibits life history characteristics common among *Neomysis* species in temperate estuaries (Mauchline, 1980; Johnston and Northcote, 1989; Mees et al., 1994). These include the production of three generations

per year, seasonal variability in abundance, and seasonal differences in size at maturity. Our data confirm the latter two life history characteristics in *N. kadiakensis*. However, our length frequency data suggest nearly continuous reproduction and recruitment with pulses (or episodes) of enhanced reproductive intensity throughout much of the year (e.g., spring, summer, and early fall), rather than three distinct generations. This substantiates Mauchline's (1980) interpretation that species producing three generations per year usually exhibited more or less continuous breeding, with periods of seasonal maxima occurring throughout the year.

Our estimate of individual growth rate of overwintering adults in early spring of ca. 4 mm per month was markedly higher than the 1–2 mm per month estimate in other studies of *Neomysis* spp. adults (Astthorsson and Ralph, 1984; Mees et al., 1994). Our estimates of growth rates in early winter were also higher than the estimated rates in the above studies (ca. 2 mm and  $<1$  mm per month, respectively). These differences may be due, in part, to the higher water temperatures in the San Francisco estuary (e.g., 10–13 °C vs. 1–9 °C in the Netherlands), but other factors, such as food limitation, may also affect growth rates.

#### 4.3. Tidal flux

Existing studies indicate that flux of planktonic and motile invertebrates varies seasonally (Christy and Stancyk, 1982; Dame et al., 1986), by species (Christy and Stancyk, 1982; Ferrari et al., 1985; Sutherland and

Closs, 2001), or by life stage (Christy and Stancyk, 1982; Schlacher and Wooldridge, 1994), or does not occur at all (Houser and Allen, 1996; Taylor, personal communication). These conflicting conclusions may be due, in part, to the lack of repeated ( $n < 3$ ) measures and continuous sampling in these studies and to the general dissimilarities between the subsystems sampled. Few studies have reported a net import of invertebrates to marsh systems (Carlson, 1978; Macdonald et al., 1990), while net export from estuarine-marsh systems has been well documented for stage I zoea of various decapod species (Christy and Stancyk, 1982; Dittel et al., 1991; Lago, 1993).

Our study provides evidence and estimates of faunal fluxes between salt marsh and estuarine ecosystems and is the first to do so in the San Francisco estuary. Our results are in agreement with the findings of Carlson (1978) and MacDonald et al. (1990) and, by the consistent import of *Neomysis kadiakensis* from the estuary to the marsh, indicate that China Camp marsh was a sink for mysids during the spring tide series throughout the year we sampled. The average specific mortality rate ( $m = 0.29 \text{ d}^{-1}$ ) of *N. kadiakensis* in the marsh channel was unusually high and far exceeded the estimated mortality rates ( $0.03\text{--}0.05 \text{ d}^{-1}$ ) of the estuary-wide population of *Neomysis integer* in the Westerschelde estuary (Mees et al., 1994). In addition, the mortality rates of *N. kadiakensis* within the marsh far exceeded the relatively low and stable population growth rates ( $r < 0.09 \text{ d}^{-1}$ ) of the overall population. We, therefore, conclude that for the population to persist, mortality of *N. kadiakensis* in the subtidal estuary must be significantly lower than mortality inside the marsh.

What might have caused such high rates of mysid mortality at China Camp marsh? Predators can account for a considerable proportion of mortality in some mysid populations (Mauchline, 1980), and it seems likely that our findings are the result of heavy predation pressure within the marsh channel. Mysids can be important components in the diets of many juvenile fish species that utilize tidal marshes as nurseries and feeding grounds (Feyrer et al., 2003). Generally, in the marshes of the San Francisco estuary, mysids were found to occur in the diets of resident demersal fishes (e.g., yellowfin goby *Acanthogobius flavimanus* and Pacific staghorn sculpin *Leptocottus armatus*) and transient planktivores (e.g., Atlantic silverside *Menidia beryllina* and topsmelt *Atherinops affinis*) (Visintainer et al., submitted for publication; Simenstad and Toft, unpublished). When they are highly abundant, mysids have comprised up to 43% of the diet of all fishes in Suisun marsh, San Francisco estuary (Feyrer et al., 2003), and have comprised greater than 50% of the diet of juvenile fishes of sub- and intertidal zones of the Westerschelde estuary (Hostens and Mees, 1999).

Birds and shrimps are also possible predators of mysids at China Camp marsh. Birds are common predators of mysids in sandy-beach and open-water pelagic systems (Moran and Fishelson, 1971; McLachlan et al., 1980; Cairns, 1987; Steele and Montevecchi, 1994); however, it is unknown whether birds are predators of mysids in tidal marshes. Epibenthic crustaceans such as amphipods and cumaceans do occur in the diets of migrant shorebirds in tidal marshes (MacNeil et al., 1999; Sutherland et al., 2000), and it is therefore possible that mysids, being similar in size and benthopelagic distribution, may also serve as prey for birds in these habitats. However, predation by birds in relatively steep-sided, higher order channels such as the one sampled at China Camp may be less than that in more open, accessible habitats. Caridean shrimp are also important predators of mysids in some estuaries (Cattrijsse et al., 1994; Hostens and Mees, 1999). In the San Francisco estuary, Sitts and Knight (1979) found that caridean shrimp (*Cragnon franciscorum* and *Palaemon macrodactylus*) consumed up to 6% of the daily standing crop of *Neomysis mercedis*.

Although temporal variations in estimates of invertebrate tidal fluxes have been reported previously (Christy and Stancyk, 1982; Ferrari et al., 1985; Dame et al., 1986), these fluxes have varied in both direction (import vs. export) and magnitude. Our results show that the magnitude of mysid fluxes varied temporally (monthly), but did not vary with regard to direction. The period of greatest net import, corresponding to the spring peak in the abundance of *Neomysis kadiakensis*, might be explained by density-dependent predation within the channel. Density-dependent predation of mysids during periods of peak prey abundance has been documented in other marshes and estuaries (Hostens and Mees, 1999; Feyrer et al., 2003).

Generally, we found annual tidal flux estimates to vary by stage and size, with larger and mature individual mysids experiencing a greater net import to the marsh than small, juvenile and immature individuals. These size- and stage-specific differences in fluxes may be the result of size-specific predation, which has been found to contribute importantly to overall prey mortality patterns in freshwater crustaceans (Wellborn, 1994). Predatory fishes and invertebrates typically select the largest individuals within their prey “specialty”, especially when prey are highly abundant (Wellborn, 1994; Luo et al., 1996; Saint-Jacques et al., 2000). Therefore, predators within the channel at China Camp marsh may be preferentially selecting the largest *Neomysis kadiakensis* as prey.

One exception to this trend in size- and stage-specific flux is our estimate of a high net cumulative import of neonates to the marsh ecosystem (Fig. 6D). Neonates, when released from the marsupium, are unable to swim until after the molt that terminates larval development,

and as a result, are subject to heavy predation until molting occurs (Mauchline, 1980). Predators may therefore be exploiting the immobile neonates while within the marsh channel.

Our monthly neonate flux estimates also indicate that female mysids may occasionally utilize marsh channels for the release of their broods. Net export of neonates occurred during the months of June, July, October, and February; however, the annual flux of neonates remained one of net import. Based on our results, brooding females do not appear to consistently prefer marsh channels for the dispersal of neonates, and the occasional export of neonates from the channel may be circumstantial.

In conclusion, China Camp marsh was found to serve as a significant sink for mysids, at least during spring tide series. Although we did not directly study predation on mysids, it is reasonable to expect that predation is a principal cause of high mortality rates of *Neomysis kadiakensis* within the marsh system. These unusually high mortality rates are important because predator–prey interactions within marshes can be viewed as mechanisms that ultimately drive the trophic retention (i.e. by resident marsh predators) or trophic export of energy from marshes to subtidal areas (e.g., the “trophic relay” concept of Kneib, 1997). Quantification of resident and transient nekton, as well as their diet and consumption rates on important prey such as *N. kadiakensis*, are suggested avenues of future research to extend and clarify these results.

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