

Biology of the introduced copepod *Pseudodiaptomus inopinus* in a northeast Pacific estuary

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ABSTRACT: Compared to other regions, estuaries and coastal bays along the west coast of North America have experienced the largest number of invasions by nonindigenous planktonic copepods. Eight species of copepods from Asia, including 2 species of the genus *Pseudodiaptomus*, have been reported in coastal bays of northern California, and a third species of Asian *Pseudodiaptomus* (*P. inopinus*) has become established in the Columbia River estuary and many smaller estuaries in the northeast Pacific Ocean. It can dominate the plankton in fresh and oligohaline tidal waters of estuaries that are utilized as rearing grounds for a variety of larger invertebrates and fishes. In July 1998 we initiated a 16 mo study of *P. inopinus* in the Chehalis River estuary, Washington State, USA, to document its biology, ecological relationships with other holoplankton, and importance as prey for fish and invertebrate planktivores. In 1998 *P. inopinus* reached peak densities in the late summer/early autumn period of low river flow but a similar peak was not seen in the same period in 1999, when densities of the copepod were significantly lower. These interannual density differences did not appear to be caused by between-year differences in predation or river flooding, but could have resulted from cooler temperatures and higher river flows that occurred in the Chehalis River in 1999. Other abundant planktonic copepods were separated from *P. inopinus* either temporally (*Eurytemora affinis*) or spatially (*Acartia* spp., *Eurytemora americana*) within the estuary, over a relatively short segment of the estuary spanning salinities of 0 to 10 psu. This separation may imply that *P. inopinus* experienced little competition when it was introduced; alternatively, it may have altered the distribution of other copepods in the estuary. *P. inopinus* was rare in the diets of estuarine fishes, but comprised an important and sometimes dominant prey for mysid shrimp *Neomysis mercedis* and juvenile caridean shrimp *Crangon franciscorum*. In turn, *N. mercedis* was an important prey item for estuarine fishes, and thus the main impact of *P. inopinus* on the estuarine food web was via this pathway.

KEY WORDS: Estuary · Northeast Pacific · Copepoda · *Pseudodiaptomus* · Invasive species · Planktivores

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INTRODUCTION

It has been well demonstrated that invasions by introduced species in terrestrial and marine benthic ecosystems have caused profound economic and environmental damage. While such severe impacts have been less often reported for planktonic invaders, in several cases ecological changes caused by introduced

plankton have been shown or hypothesized to be large. In the Black and Azov Seas, invasion by the northwestern Atlantic ctenophore *Mnemiopsis leidyi* coincided with huge decreases in commercially important fishes, presumably contributing to their decline through predation and competition (Shiganova & Bulganova 2000, Kideys 2002, Bilio & Niermann 2004). This invasion was accompanied by other ecological

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changes, including shifts in chlorophyll patterns and concentrations. In a number of large North American lakes and reservoirs, recent invasions by at least 3 species of non-native cladocerans have occurred (Dzialowski et al. 2000, MacIsaac et al. 2000, Therriault et al. 2002). Two of them, the predators *Bythotrephes longimanus* and *Cercopagis pengoi*, appear to have negatively affected native planktonic species and their fish predators (Yan & Pawson 1997, Benoit et al. 2002, Boudreau & Yan 2003).

The largest number of documented invasions by planktonic marine/estuarine species have occurred in estuaries on the west coast of North America. The most striking example of this is in the Sacramento-San Joaquin estuary (including San Francisco Bay), which has seen the introduction of the Asian planktonic calanoid copepods *Pseudodiaptomus marinus*, *P. forbesi*, *Sinocalanus doerrii*, *Acartiella sinensis* and *Tortanus dextrilobatus*, and the cyclopoids *Limnithona sinensis*, *L. tetraspina*, and *Oithona davisae*. The copepod fauna there is now primarily East Asian in some parts of the bay (Orsi & Ohtsuka 1999, S. M. Bollens & J. R. Cordell unpubl.). One species, *T. dextrilobatus*, appears to have the capacity to severely impact the remaining native copepods in San Francisco Bay through predation (Hooff & Bollens 2004). At least 3 of the introduced copepod species established in San Francisco Bay have also recently been introduced to the Columbia River estuary, *L. tetraspina*, *P. forbesi* and *S. doerrii*, and the latter 2 have become abundant there. They were apparently introduced to the Columbia River either from San Francisco Bay or by transoceanic transport (Sytsma et al. 2004). In the Columbia River and a number of other estuaries in Washington and Oregon, a different Asian copepod not found in San Francisco Bay, *Pseudodiaptomus inopinatus*, has become a dominant planktonic tidal brackish-oligohaline species (Cordell et al. 1992, Cordell & Morrison 1996, Bollens et al. 2002). Despite the extensive nature of these invasions in both regional distribution and post-invasion densities, little is known of the biology or ecological effects of these copepods in their invaded habitats.

In this study we examine the biology and ecology of a population of *Pseudodiaptomus inopinatus* that has invaded the Chehalis River estuary, Washington. This copepod was first recorded there in 1992 (Cordell & Morrison 1996), where it remained extremely abundant at least until summer 2004 (J. R. Cordell unpubl. data). There have been few studies of the biology of *P. inopinatus* in Asia, and

none in invaded systems, so the main goal of this work was to provide basic biological and ecological information about this species. The questions addressed in this study were: (1) what are the overall patterns of seasonal abundance of *P. inopinatus* in the Chehalis River estuary, how do they relate to river conditions, and how do they compare to those found in its native range; (2) what are the distribution patterns of *P. inopinatus* within the estuary in relation to season and river conditions; and (3) does *P. inopinatus* enter the estuary's food web as a prey resource for fish and invertebrate predators?

MATERIALS AND METHODS

The Chehalis River is located in southwestern Washington, USA, where it enters a coastal embayment, Gray's Harbor (Fig. 1). We sampled invertebrates and measured salinity and temperature twice-monthly at 3 salinity-based stations likely to span the highest densities of *Pseudodiaptomus inopinatus*, determined from earlier studies (Cordell & Morrison 1996). These stations were located at bottom salinities of ~1, 3, and 6 psu, and occurred at different locations in the estuary on different dates, depending on seasonal conditions (Fig. 2). We began sampling on 10 July 1998 and ended on 3 November 1999. Stations were located using a YSI portable salinity-temperature meter; beginning on 21 August 1998, station coordinates were recorded using a hand-held global positioning system unit. Sampling occurred within 1 h of flood slack tide. River flow data from the Chehalis River at Porter, Washington, USA, which is located ca. 25 river km upstream of the study site, were obtained from the United States Geo-

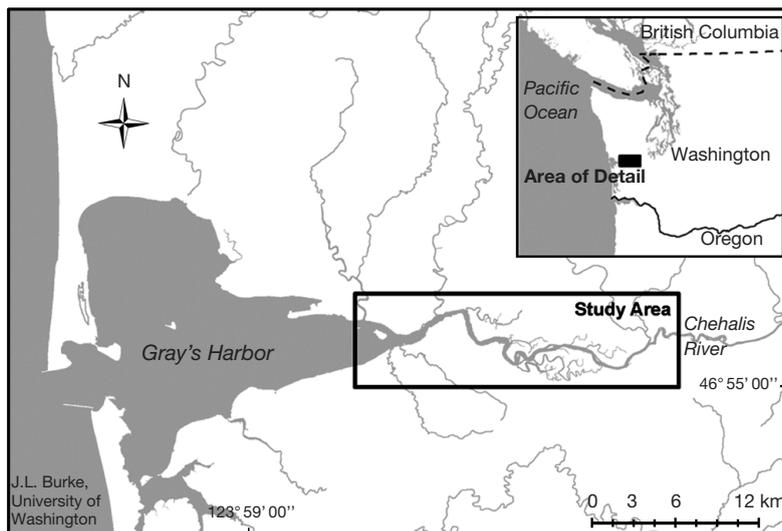


Fig. 1. Location of Chehalis River estuary, Washington, USA, and study area

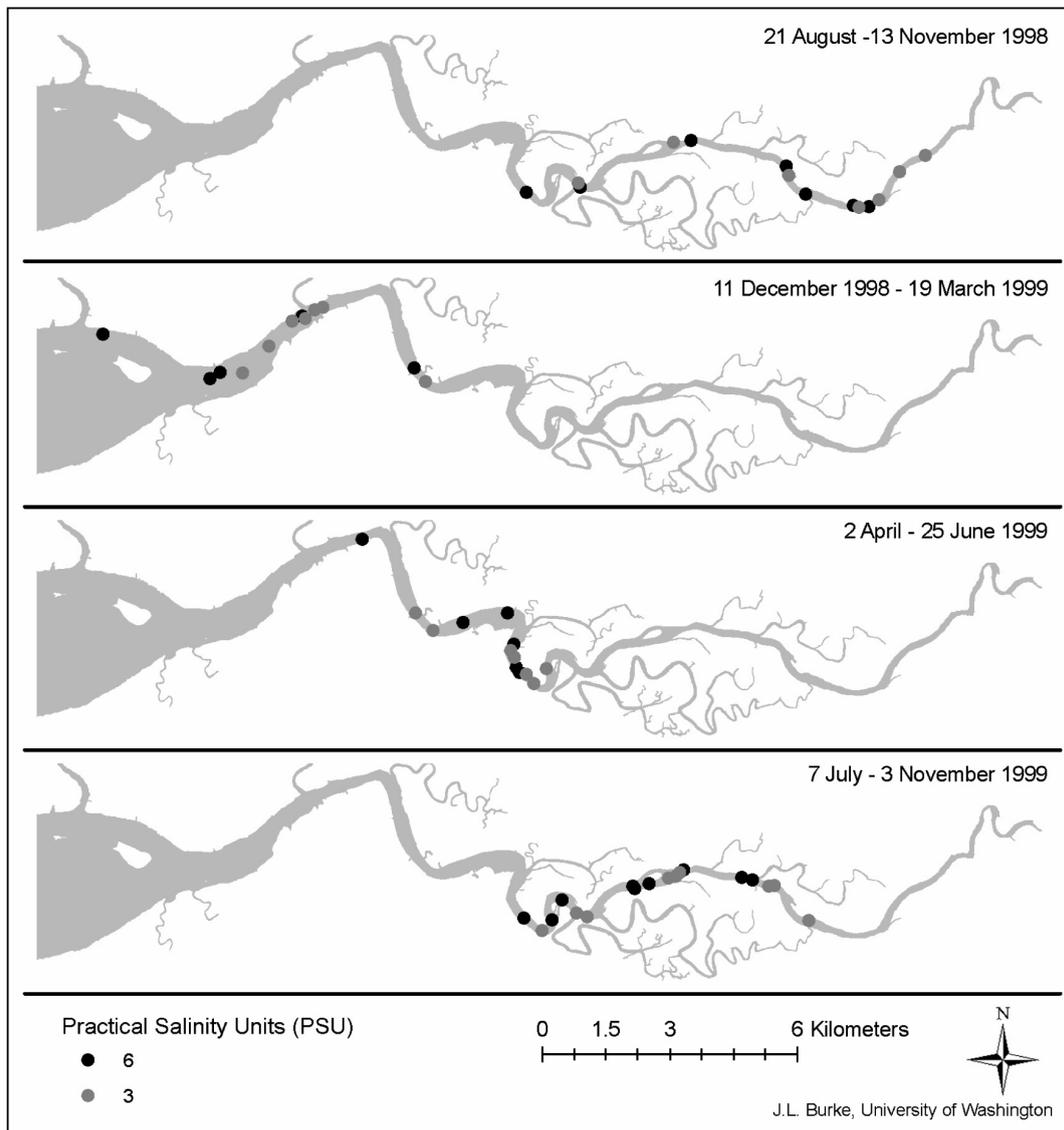


Fig. 2. Location of 3 and 6 psu sampling stations in Chehalis River estuary in 4 seasons during 1998 and 1999. Station coordinates for Figs. 2 & 3 are available from the corresponding author

logical Survey National Water Information System (<http://waterdata.usgs.gov/nwis/>).

At each station, 3 replicate vertical plankton tows were taken from a small (5 m) boat, using a plankton net of 0.5 m diameter and 0.073 mm mesh. The net was lowered to the bottom, depth was recorded, and the vertical orientation of the line was maintained by maneuvering the boat. After ca. 30 s the net was pulled to the surface at a speed of ca. 0.5 m s^{-1} . Additional stations were sampled on 17 October 1998 ($n = 10$) and 6 August and 3 November 1999 ($n = 8$) to document the upstream and downstream distribution of *Pseudodiaptomus inopinus* and other abundant copepods in the Chehalis River estuary during periods of low river

flow and high *P. inopinus* densities. The additional stations were distributed between 0 to 22.9 psu at ca. 3 psu intervals, from several km below the mouth of the river in Gray's Harbor to ca. river km 24 (Fig. 3). Samples were fixed in 10% buffered formalin solution.

To obtain larger epibenthic invertebrate predators, we sampled qualitatively with a $38 \times 17 \text{ cm}$ mouth opening epibenthic sled sampler with 0.6 mm mesh on each zooplankton sampling date at each of the 3 regularly sampled salinity-based stations. The sled was lowered to the bottom and towed slowly for about 5 min, paying out line as needed to keep it on the bottom. If few or no invertebrates were obtained, one additional sample was attempted. Invertebrates were fixed as for

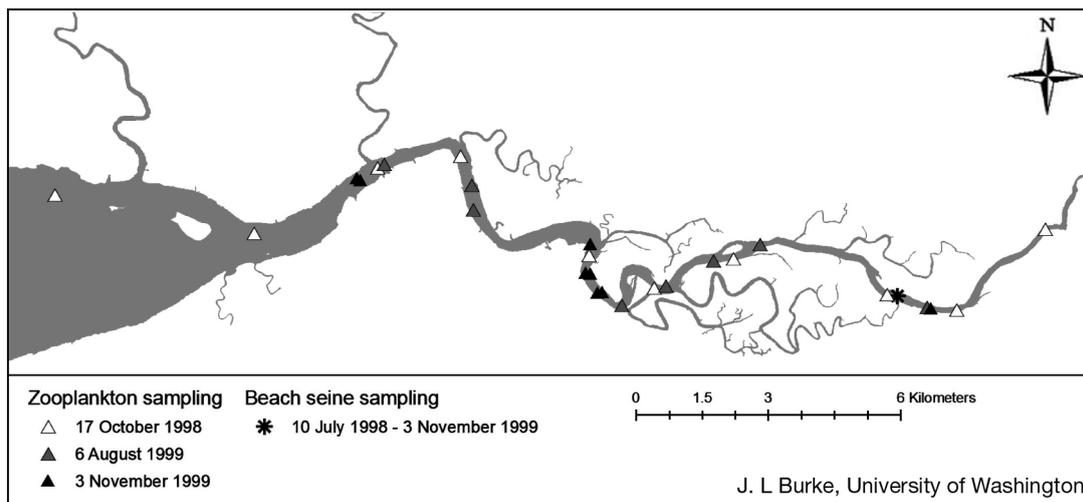


Fig. 3. Extended salinity zooplankton stations and beach seine sampling location

the zooplankton. For one predator, the mysid *Neomysis mercedis*, the full range of life-history stages was collected by the sled, and in the laboratory up to 25 adults and 20 juveniles were measured (from tip of telson to anterior margin of carapace) and the adults were sexed.

Fish were collected for gut content analysis on each sampling date, at 1 station located in the brackish-oligohaline region (0 to 6 psu bottom salinity) of the estuary at river km 21 (Fig. 3). Samples were taken with a 37 m floating beach seine consisting of two 18 m panels made of 3 cm mesh with a $2 \times 2.4 \times 2.3$ m bag made of 6 mm mesh. The net was deployed with a small boat, parallel to shore in water deeper than 2 m, and slowly retrieved to shore. For each fish species caught, up to 10 individuals from each 10 mm size class were retained. Retained fish were killed in a solution of ms-222 (tricaine) before fixation. Additional beach seine sampling was conducted on 15 and 30 April, 14 and 28 May, 11 June, 9 July, 5 August, and 3 September 1999 at up to 5 additional stations both up- and downstream from the regular fish sampling station. The purpose of this more extensive sampling was to obtain additional information about the feeding of commercially and culturally important juvenile salmon on introduced vs. native copepods during the time in which salmon outmigrated through the estuary. Fish were preserved as for zooplankton.

In the laboratory, plankton samples were quantitatively subsampled, if necessary, using a Hensen's Stempel pipette to obtain ca. 200 of the most abundant copepod taxon. Plankton taxa were enumerated and all adult copepods

were identified to species. Life history stages of abundant taxa were also designated: for *Pseudodiaptomus inopinus*, nauplii and copepodid stages were identified (i.e. nauplius, copepodite I-V, adult male, adult female, gravid female); other copepods were identified to more general life history stage (i.e. copepodid, adult male, adult female, gravid female). We also separated 2 distinct morphotypes of male *P. inopinus* based on the shape of the left side of their fifth legs: in one type this appendage is paddle-shaped and in the other it is thumb-shaped (Fig. 4).

For known or hypothesized planktivorous fishes, up to 10 individuals (if available) of each species from each sample date/station were analyzed for gut contents. Each individual was weighed (damp weight) to the nearest 0.01 g, and length was measured (fork length for juvenile salmon, total length for others). The stomach was excised and contents were removed and

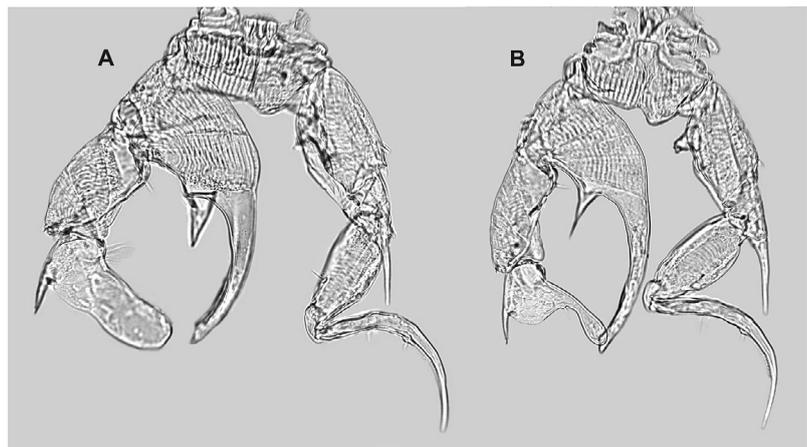


Fig. 4. *Pseudodiaptomus inopinus*. Photomicrographs of fifth legs of 2 morphotypes of male. A: paddle-shaped; B: thumb-shaped

weighed in their entirety. Prey taxa were separated into categories as specific as digestion would allow and each prey category was enumerated and weighed to the nearest 0.0001 g. Diet contents of 2 abundant invertebrate predators, *Neomysis mercedis* and juveniles of the caridean shrimp *Crangon franciscorum*, were also analyzed. Up to 20 adult and 20 juvenile individuals were sexed (male, female, gravid female) and measured for total length (tip of rostrum to end of telson). Stomachs were removed using fine needles (mounted insect pins) and each stomach was teased open in a drop of water on a plastic petri dish. Prey were enumerated at 60 \times magnification with a dissecting microscope, by counting them using one diagnostic characteristic for each prey type, e.g. caudal rami or fifth legs for copepods, dactyls of second gnathopod for amphipods.

To compare river temperatures and densities of *Pseudodiaptomus inopinus* life history stages between the 2 sampling years, we log-transformed the data and conducted 3-way ANOVAs with station, year, and month as factors, and all 2-way interactions, using SPSS version 11.5. These analyses were only performed on data from July to November as these months were sampled in both years.

RESULTS

River hydrography

In both years, highest mean river temperatures corresponded with late summer/early autumn periods of low flow (Figs. 5 & 6). With the onset of late autumn and winter floods, temperatures dropped and remained relatively low throughout the January to April period of high river flows. River flow was significantly higher in 1999 than in 1998 (paired *t*-test, $p = 0.011$) (Fig. 5). Mean temperatures ranged from a high of $20.9^{\circ}\text{C} \pm 0.1$ (SD) on 7 August 1998 to a low of $6.4^{\circ}\text{C} \pm 0.2$ on 19 February 1999. During the low flow period from early July to mid-October mean river temperature was ca. 2°C warmer in 1998 ($19.1^{\circ}\text{C} \pm 1.7$) than in 1999 ($17.4^{\circ}\text{C} \pm 1.6$) at all 3 sampling stations (Fig. 6), and this difference was statistically significant (3-way ANOVA, $p = 0.005$). The location of the 3 and 6 psu sampling stations varied among seasons: in summer and autumn 1998, these stations occurred from river km 12 to 23, in winter 1998-99 from river km 0 to 8, in spring 1999 from river km 5 to 13, and in summer and autumn 1999 from river km 12 to 20 (Fig. 2).

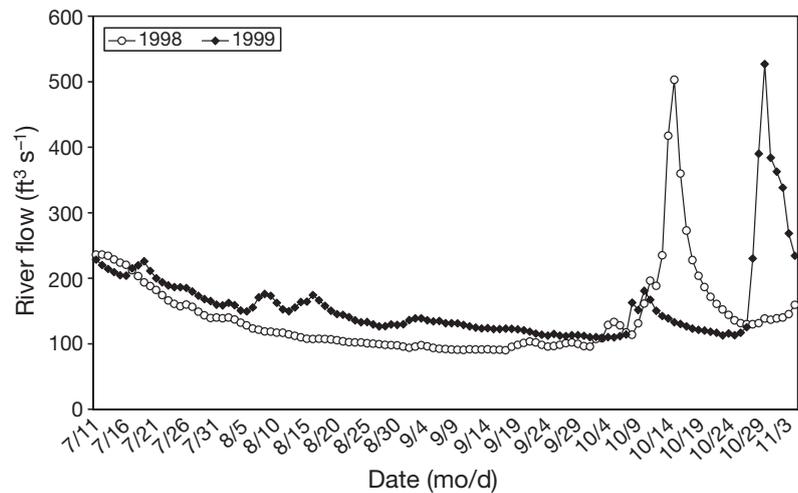


Fig. 5. Chehalis River flows: comparison of 1998 and 1999 for periods sampled in both years, measured at Porter, Washington. $1 \text{ ft}^3 = 0.0283 \text{ m}^3$

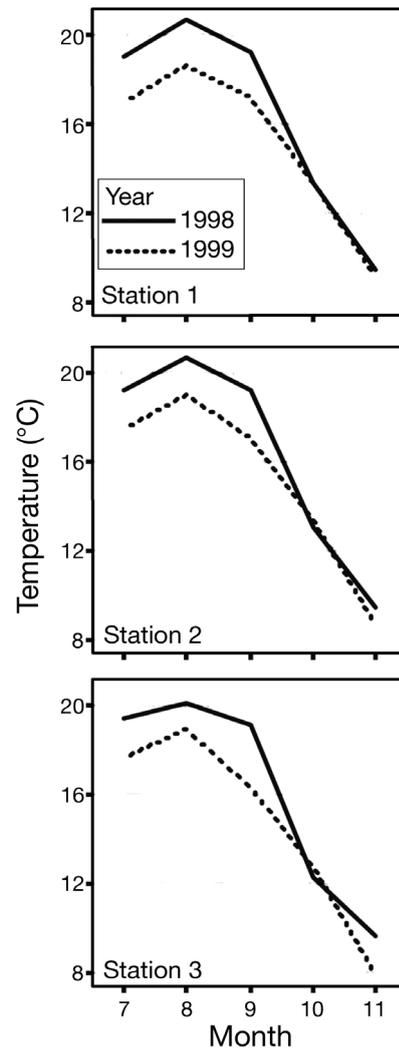


Fig. 6. Temperature of Chehalis River at 3 sampling stations: comparison of 1998 and 1999 for periods sampled in both years

Copepod abundance and distribution

Total *Pseudodiaptomus inopinus* densities increased rapidly between the first sampling date on 10 July 1998 and peak densities (exceeding 10 000 ind. m⁻³) that occurred from late August through mid-September 1998 (Fig. 7). After this, densities quickly declined to <1000 ind. m⁻³, and stayed low until increasing in January 1999. Densities were quite variable in 1999, reaching peaks in April and May. Unlike 1998, total densities in 1999 never approached 10 000 ind. m⁻³ and there was no large abundance peak in late summer/early autumn. Grouped by month, densities of each life history stage (female and male adults, copepodids, nauplii) were greater in 1998 than in 1999 July to September (Fig. 8). These between-year density differences were statistically significant for each life history stage (3-way ANOVA, $p < 0.0003$). In 1998, nauplii and copepodid stages dominated the *P. inopinus* population from July to October, including during peak den-

sity periods, whereas adults dominated from late October through mid-December. In 1999, nauplii and copepodids were the dominant stages throughout the year, except on the last sampling date in November, when densities were very low. Total densities of the calanoid copepod *Eurytemora affinis* were very low during periods of peak *P. inopinus* density in 1998. Densities of *E. affinis* increased in December–January to densities >1000 m⁻³ that persisted from late January–late May 1999. After this, densities decreased rapidly and *E. affinis* was nearly absent from the samples from August–November 1999.

Gravid female *Pseudodiaptomus inopinus* were present throughout the study period, except on the 23 July 1999 sampling date, when no females were found (Fig. 9A). Both gravid and non-gravid females were most abundant in late summer 1998 and again in winter 1999. Gravid females comprised >50% of the female numbers on several sampling dates in late summer/early autumn 1998 but dropped to <25% from late autumn through December 1998 (Fig. 9C). In 1999 they comprised >50% of total females on most sampling dates from late February through May 1999 and then dropped to much lower percentages from June to September before increasing in proportion again in October 1999. Male *P. inopinus* of both fifth leg morphotypes had peak densities similar to those for females in late summer 1998 and winter 1999 (Fig. 9B). On these and most other sampling dates the thumb-shaped type was more abundant than the paddle-shaped type. Relative composition of the paddle-shaped type was similar to that for gravid females, comprising larger percentages of total males only in late winter/early spring, when copepod densities were very low (Fig. 9D). Other than during this period, the thumb-shaped morphotype usually comprised higher percentages of the male numbers.

During peak abundances in 1998, *Pseudodiaptomus inopinus* was most abundant at Station 3 (0 psu) on 2 of the 3 sampling dates, with densities approaching or exceeding 100 000 ind. m⁻³ (Fig. 10C). There were several other, lower peaks in densities of >1000 ind. m⁻³ that occurred in late winter 1998–1999 at Stations 1 & 2 (Fig. 8A,B) but not at Station 3, where *P. inopinus* either did not occur or had densities <10 ind. m⁻³ from mid-November through early March. Life history stage composition at each sampling station (Fig. 10D–F) was similar to that for the combined data (Fig. 7B), with larger proportions of adults in winter and more nauplii and copepodids at other times. Station 3 (0 psu) tended to have lower proportions of adults and higher proportions of nauplii and copepodids in summer and autumn.

In the October 1998 distributional sampling, *Pseudodiaptomus inopinus* extended ~25 km upstream in the estuary to 0 psu but did not occur in the most upstream

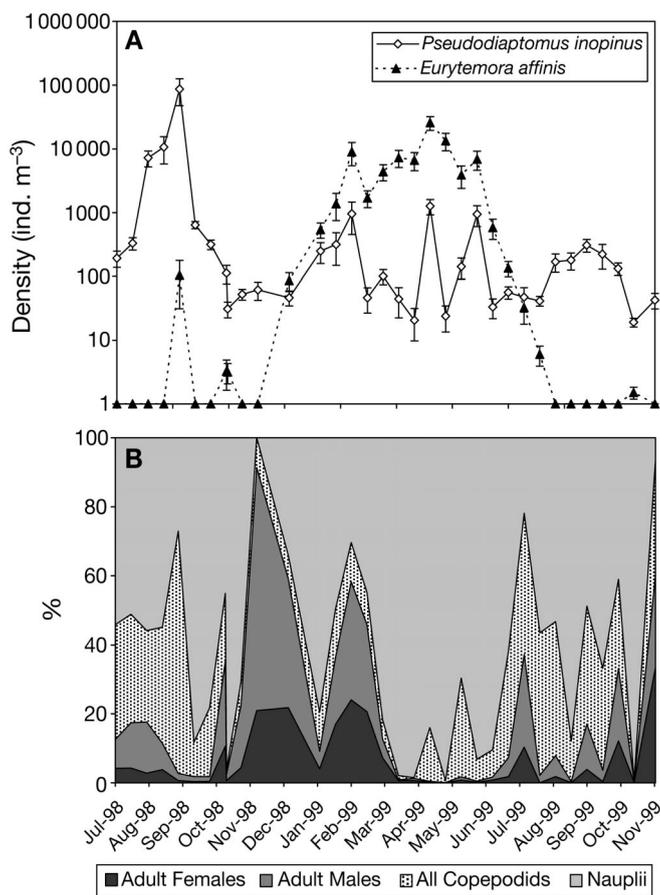


Fig. 7. *Eurytemora affinis* and *Pseudodiaptomus inopinus*. Total density (mean \pm SE) (A) and (B) life-history stage percent composition of *P. inopinus* from all stations combined ($N = 9$) in Chehalis River estuary 10 July 1998 to 3 November 1999. %: Percent composition by numbers

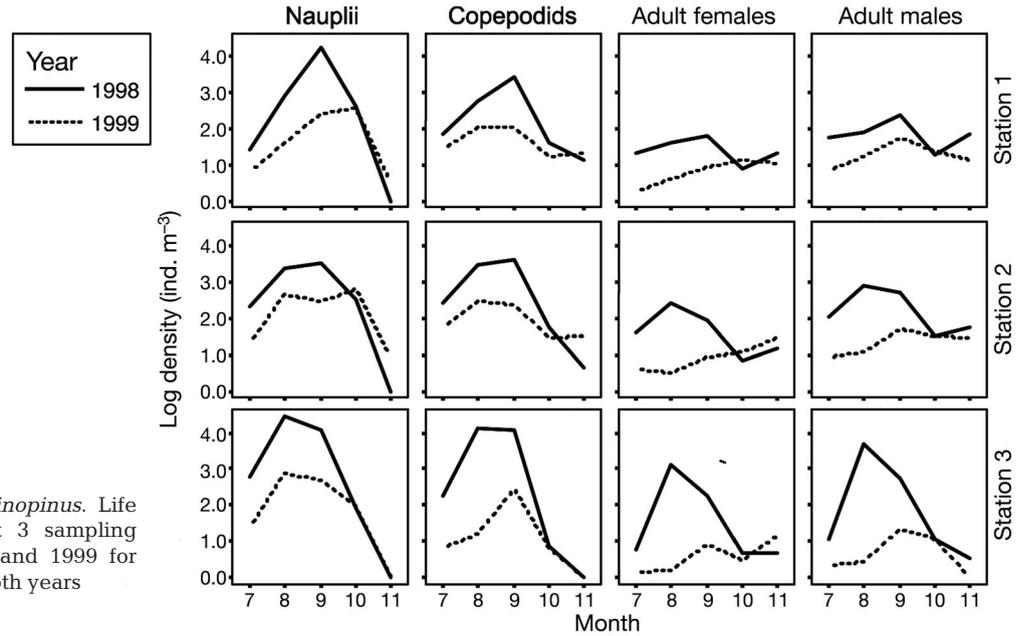


Fig. 8. *Pseudodiaptomus inopinus*. Life history stage densities at 3 sampling stations, comparing 1998 and 1999 for periods sampled in both years

station around river km 28 (Fig. 11). *P. inopinus* occurred only in samples from a region spanning approximately 10 river km, with highest abundances in a ~4 km reach encompassing salinities of 0 to ~10 psu. Similarly, in August and November 1999 *P. inopinus* was most abundant at 3 to 10 psu but did not occur at the most upstream stations. Other planktonic copepods were relatively rare in the estuary during the extended distribution sampling periods, except for 2 taxa, *Eurytemora americana* and *Acartia* spp., which were abundant at stations with salinities from ~9 to 21 psu, and thus overlapped little with *P. inopinus* in the estuary (Fig. 11).

Invertebrate predators

Adult *Neomysis mercedis* occurred throughout the year in the epibenthic sled samples (*N. mercedis* length and life history stage data are available from the corresponding author). Mean lengths were similar (~10 to 11.5 mm total length) from spring through autumn in both 1998 and 1999. From late January through late May 1999, adults were larger (>12 mm) with largest sizes occurring in February (>15 mm). Juveniles were mostly absent from samples from mid-August through late October in both years. Small juveniles (<6 mm) occurred in late July 1998 and from mid-

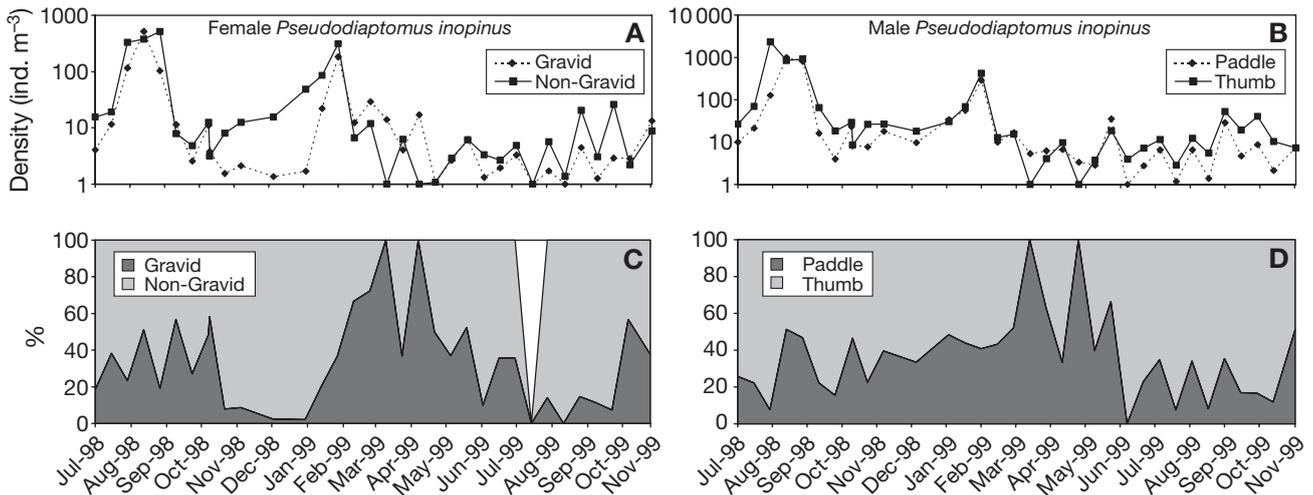


Fig. 9. *Pseudodiaptomus inopinus*. Total density (N = 9) (A,B) and percent composition (C,D) of gravid vs. non-gravid females and 2 fifth-leg morphotypes of males from Chehalis River estuary, Washington, 10 July 1998 to 3 November 1999. %: Percent composition by numbers

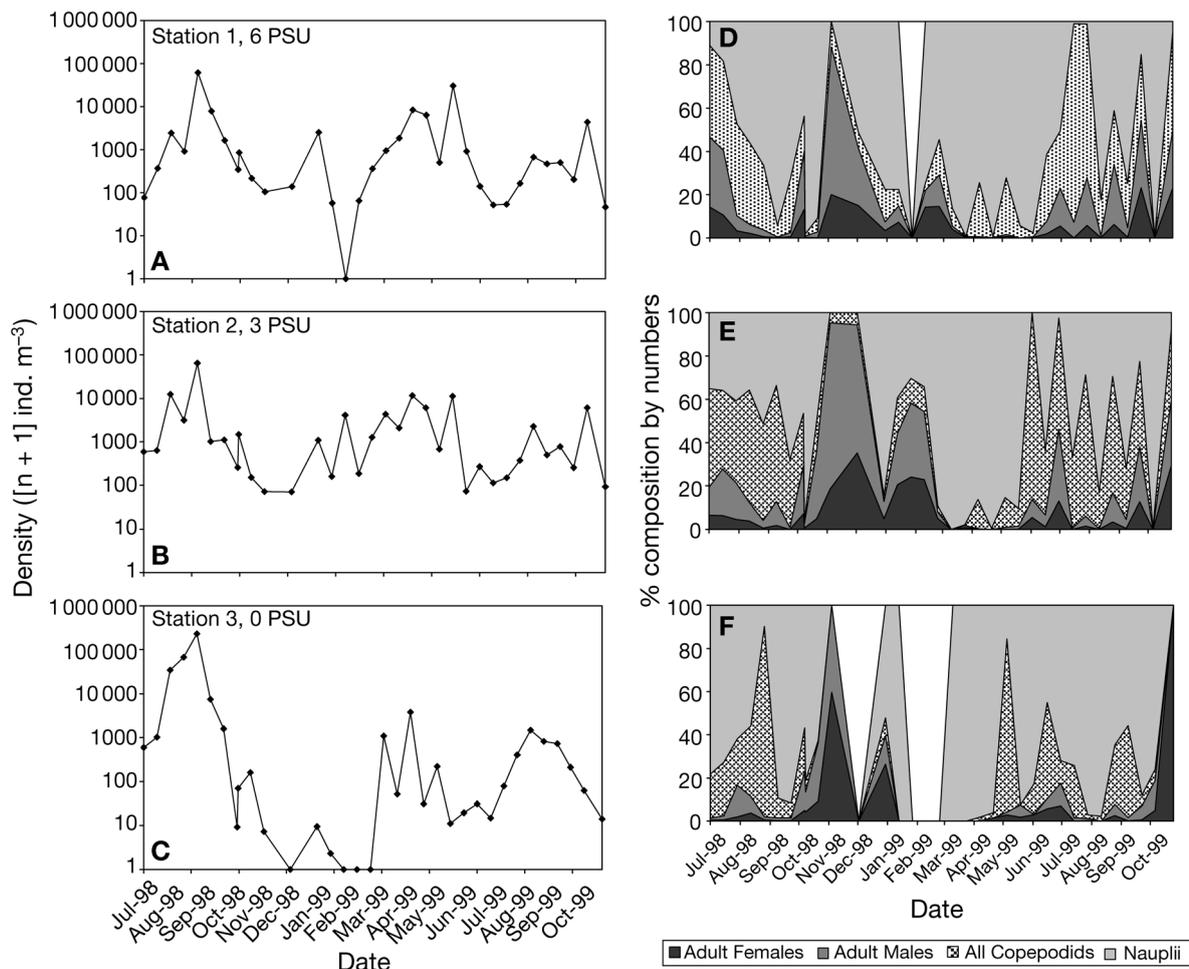


Fig. 10. *Pseudodiaptomus inopinus*. Total density (A–C) and life-history stage percent composition (D–F) from 3 salinity-based stations in Chehalis River estuary, 10 July 1998 to 3 November 1999

May to late June 1999. Larger juveniles (~6 to 8.5 mm) occurred mostly in the autumn and winter. Females dominated the life history stage composition of *N. mercedis* on most of the sampling dates. Gravid females dominated on the 7 August and 2 October 1998 sampling dates and from late June to mid-September in 1999. The proportion of gravid females was generally lowest from January through March 1999. Males were scarce from August to October 1998 and then were relatively abundant until mid-September 1999.

Prey occurred in nearly all *Neomysis mercedis* examined, but in juveniles it was almost always entirely unidentifiable. In adult *N. mercedis*, *Pseudodiaptomus inopinus* were abundant in diets from 24 July to 30 October 1998, comprising ~20 to 80% of the identifiable prey numbers on each sampling date during that period (Fig. 12). Other relatively abundant prey during this period were harpacticoid copepods (consisting mostly of the species *Coullana canadensis*, *Pseudobryda* sp., and *Mesochra rapiens*) and *Coro-*

phium spp. amphipods. From January to June 1999 *P. inopinus* comprised <5% of the diet composition, when mysid diets were dominated by harpacticoid copepods. This was also the only period in which the calanoid copepod *Eurytemora affinis* occurred in *N. mercedis* diets. From July to September 1999 *Corophium* spp. and harpacticoid copepods dominated prey numbers. *P. inopinus* were much less prominent in mysid diets than in the same time period in 1998, except for the 6 August sampling date, on which it comprised ~50% of prey numbers.

For *Crangon franciscorum* shrimp, only juveniles were analyzed for diet because few adults were captured and examination of a representative sample of their diets showed little identifiable material and no copepods. The pattern of *Pseudodiaptomus inopinus* occurrence in the diets of *C. franciscorum* juveniles was similar to that for *Neomysis mercedis*, with relatively high proportions occurring from 24 July to 30 October 1998 and low proportions in samples taken in 1999 (Fig. 13). Also, as with

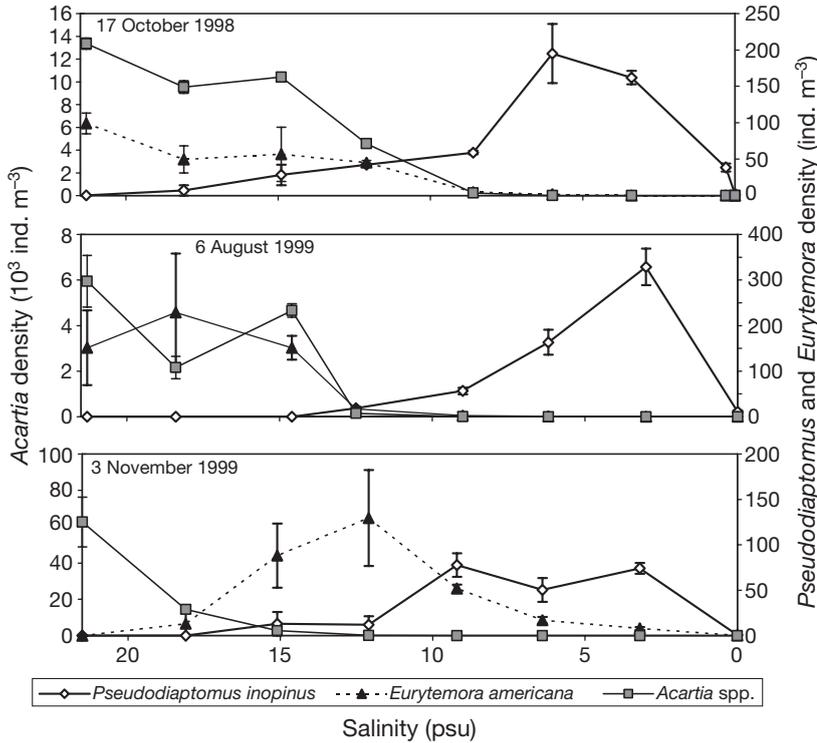


Fig. 11. *Pseudodiaptomus inopinus*, *Eurytemora americana* (right axis) and *Acartia* spp. (left axis). Densities (mean \pm SE) of combined adult and copepodid stages across the salinity gradient in Chehalis River estuary on 3 dates in 1998–1999

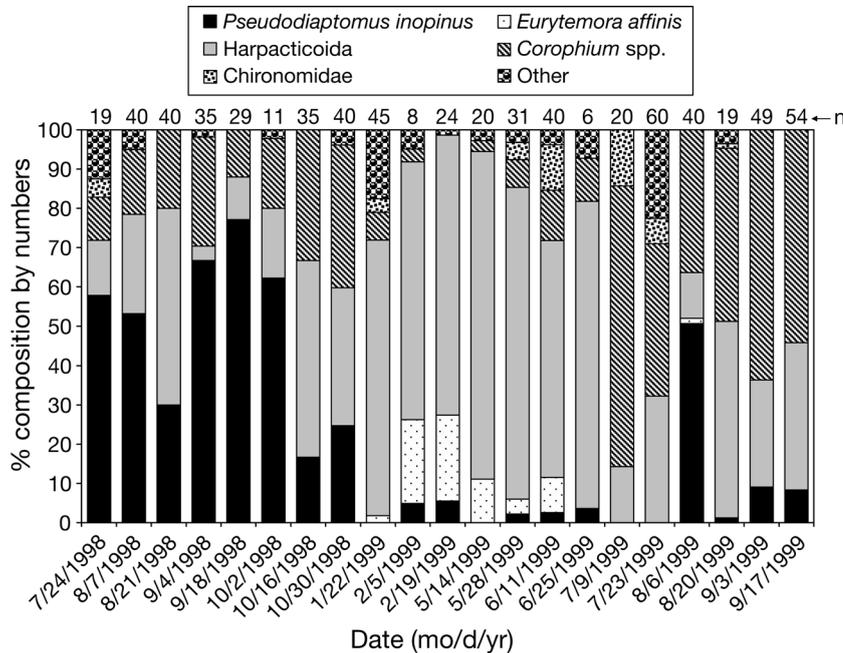


Fig. 12. *Neomysis mercedis*. Percent diet composition by numbers of identifiable prey in *N. mercedis* from Chehalis River estuary 1998–1999; n: number of individual diets examined on each date. Sample dates on which no *N. mercedis* were captured are not included

the mysids, there was one instance of relatively high diet composition of *P. inopinus* in 1999 (6 August; 33% of numerical diet composition). However, there were several differences between *Neomysis mercedis* and juvenile *C. franciscorum* diets. *Crangon franciscorum* fed more on Ostracoda, and *N. mercedis* consumed more Chironomidae (midge) larvae (Figs. 12 & 13). In 1999 prey numbers were dominated by harpacticoid copepods in juvenile *C. franciscorum* and by *Corophium* spp. in *N. mercedis*. Juvenile *C. franciscorum* also consumed *N. mercedis* on several dates.

In both species of invertebrate predators, *Pseudodiaptomus inopinus* in the diet were dominated by adults on most sampling dates (Fig. 14). Copepodid stages comprised 50% or more of the *P. inopinus* consumed on 24 September 1998 (both predator species) and 6 August 1999 (*Neomysis mercedis*). On most dates when both types of predator were sampled, *N. mercedis* consumed larger proportions of copepods and adult males and *Crangon franciscorum* juveniles fed more on adult female *P. inopinus*. Of the adult *P. inopinus* consumed in 1998, males predominated in *N. mercedis* diets. Conversely, *C. franciscorum* juveniles tended to feed more on female *P. inopinus*. Life history composition of *P. inopinus* in *N. mercedis* diets was more variable in 1999, with mostly females occurring in spring samples and copepods occurring on only the 6 August and 17 September sampling dates. *P. inopinus* occurred in the diets of juvenile *C. franciscorum* only on the 6 August sampling date.

Fish predators

Six species of known or hypothesized planktivorous fishes were relatively abundant in the beach seine samples: juvenile Chinook *Oncorhynchus tshawytscha* and chum salmon *O. keta*, threespine stickleback *Gasterosteus aculeatus*, peamouth chub *Mylocheilus caurinus*, juvenile starry flounder *Platichthys stellatus*, and American shad *Alosa sapidissima*. In terms of prey biomass, diets of Chinook salmon, threespine stickleback, and American shad were dominated by the mysid shrimp *Neomysis mercedis* (Fig. 15). In juvenile

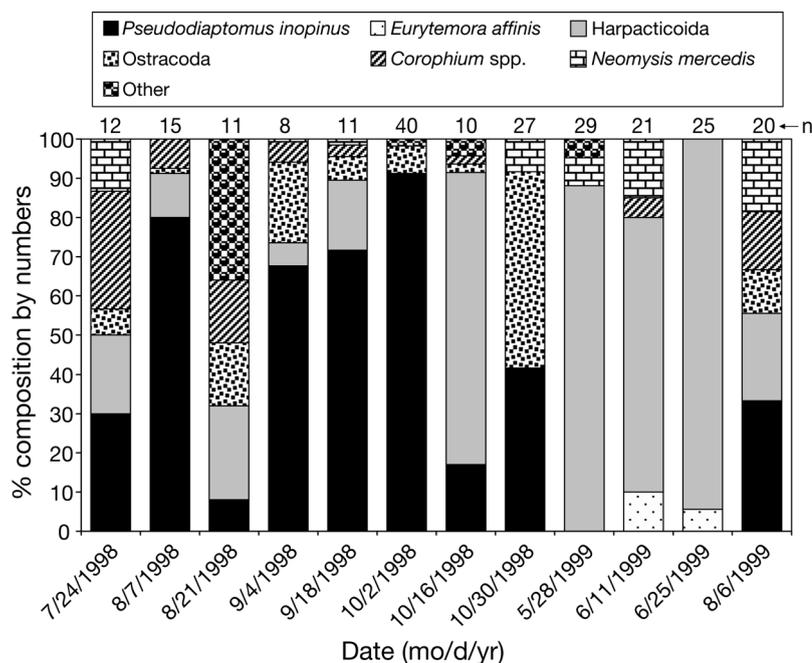


Fig. 13. *Crangon franciscorum*. Percent diet composition by numbers of identifiable prey in juvenile *C. franciscorum* from Chehalis River estuary 1998–1999; n: number of individual diets examined on each date. Sample dates on which no *C. franciscorum* were captured are not included

chum salmon and juvenile starry flounder, Chironomidae larvae, pupae, and emergent adults comprised most of the prey weight. Chironomidae and other insects were also relatively abundant in the diets of juvenile Chinook salmon and peamouth chub. The benthic gammarid amphipods *Corophium* spp. were the most abundant prey taxon in diets of peamouth chub and were also prominent in the diets of juvenile starry flounder.

Pseudodiaptomus inopinus were rare in the fish diets, never comprising more than 1% of prey biomass (Table 1). The highest numbers of *P. inopinus* occurred in American shad, and were also consumed in small numbers by threespine sticklebacks and juvenile starry flounders (Table 1).

DISCUSSION

Pseudodiaptomus inopinus is geographically widespread throughout Asia and occurs in a variety of fresh water and estuarine habitats (Mashiko 1951, Shen & Song 1979, Oka et al. 1991). In Asian estuaries it is part of a plankton assemblage that occurs mainly in fluvial-oligohaline reaches at salinities of 0 to 5 psu and is most abundant in autumn (Suh et al. 1991). We hypothesized that the Chehalis River late summer and early autumn low flow period would have peak densities of

P. inopinus because the estuary flushing rate was lowest at this time and the copepods could best maintain themselves and proliferate in the brackish-oligohaline region, as they do in their native habitats. However, relatively high abundance in plankton and predator diets occurred only in autumn 1998 and not in autumn 1999. Recruitment of copepodids and nauplii in spring/summer 1999 was not followed by a large increase in adults. This may have been due to predation by the main predators of *P. inopinus*: *Crangon franciscorum* and *Neomysis mercedis*. We cannot determine this because we did not measure predator densities, but we note that despite apparently good recruitment of *P. inopinus* juveniles, both of these predators had much lower proportions and total numbers of *P. inopinus* in diets in 1999 than in 1998, possibly indicating a general scarcity of the copepod due to other factors in 1999. We did not encounter any other invertebrate predators, but other fish predators might have been responsible for the decline of *P. inopinus* in 1999. However, most of the planktivorous fishes in the Chehalis River

estuary are found in the lower part of the estuary where *P. inopinus* does not occur, while those that do occur in the brackish-oligohaline region are transitory there (e.g. American shad, smelts) (Simenstad & Eggers 1981). The decreased numbers in autumn 1999 could not have been due to early flood events in the river, as such events did not occur. Nor could the decrease between 1998 and 1999 have been part of a permanent decline in *P. inopinus* in the Chehalis River estuary because densities exceeding 3000 total adults m^{-3} have since been found in September 2004 (J. R. Cordell unpubl. data). It is also possible that at the time this study was conducted, *P. inopinus* was a recent invader in the Chehalis River estuary and its population had not yet stabilized. In 1999, temperatures in the Chehalis River were colder by several degrees than in 1998 throughout the late summer and early autumn, and river flows were significantly higher in 1999 than in 1998. While we do not know the biological significance of these factors, or thresholds at which they would affect *P. inopinus* populations, they may have contributed to lowering densities of the copepods in 1999. Little is known of the range of temperatures at which *P. inopinus* occurs in its native habitats, but in at least one Asian estuary where it occurs (Chikugo River, Japan), temperatures are much warmer than in the Chehalis River estuary (22.5 to 27.8°C vs. 6.0 to 20.9°C) (Ueda et al. 2004 and this study). Therefore, it

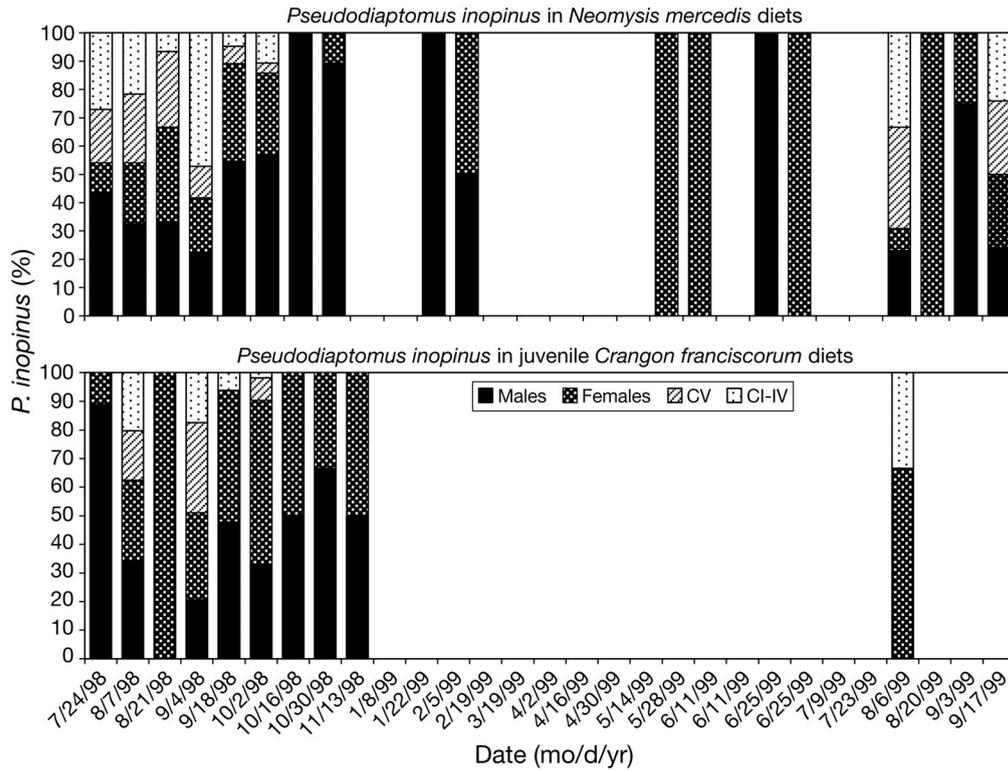


Fig. 14. Percent composition by numbers of life history stages of *Pseudodiaptomus inopinus* in diets of *Neomysis mercedis* and juvenile *Crangon franciscorum* from Chehalis River estuary 1998–1999. No data indicates dates on which no predators were found in samples. %: Percent composition by numbers; CV: copepod Stage V; CI–IV: copepod Stages I–IV

is possible that *P. inopinus* in the Chehalis River estuary experienced poor recruitment in 1999 because of the cool temperatures that year. Our study was too short to definitively answer these questions and multiple-year sampling of *P. inopinus* in its native and/or

invaded habitats would further clarify the degree of and reasons for interannual variation in this species.

Our data show that during flood periods, *Pseudodiaptomus inopinus* is largely absent from the Chehalis River estuary upstream of the river mouth. In Japan, a recent study by Ueda et al. (2004) concluded that this species repopulates estuaries by residing near the bottom in deep channels in the lower estuary during flood events, and this might also be the mode for repopulating the Chehalis River estuary.

Previous plankton surveys of northeast Pacific estuaries found that *Pseudodiaptomus inopinus* occurred mainly between salinities of 0 and 12 psu, with highest densities usually occurring around 0 to 6 psu (Cordell & Morrison 1996, J. R. Cordell unpubl. data). The present study confirms this distribution, and further suggests that it is most abundant in relatively short reaches of Northeast Pacific estuaries (in this study, ca. 4 km). *P. inopinus* is a strong vertical migrator, apparently using both light and water movement as cues (Suh et al. 1991, Bollens et al. 2002), so it seems likely that it actively maintains itself in this restricted area within the estuary. It appears to be beneficial for copepods to inhabit brackish-oligohaline regions of estuaries because these regions are often where the estuarine turbidity maximum (ETM) occurs, along with

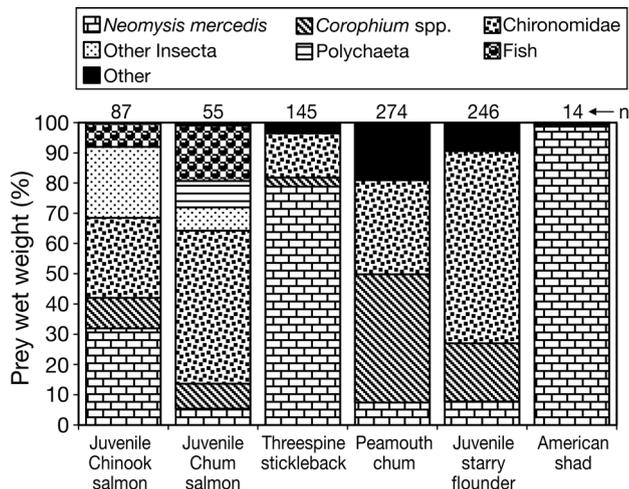


Fig. 15. Overall percent composition by weight of prey from species of potential or known planktivorous fish (beach seine-captured) from Chehalis River estuary 1998–1999; n: number of individual diets examined for each species

Table 1. *Pseudodiaptomus inopinus* in diets of fish captured in Chehalis River estuary. Fish species: no. of individuals in parentheses. *P. inopinus*: total eaten for each species of fish

Date	Fish species	<i>P. inopinus</i>
10 Jul 98	American shad (2)	29
10 Aug 98	Starry flounder (11)	2
16 Oct 98	Starry flounder (19)	55
21 Oct 98	Threespine stickleback (10)	8
30 Oct 98	Starry flounder (10)	10
30 Apr 99	Threespine stickleback (10)	1
26 Jul 99	Starry flounder (9)	5
26 Jul 99	American shad (4)	142
5 Aug 99	Starry flounder (10)	1
20 Aug 99	Starry flounder (10)	8

associated increases in suspended particulate matter, organic carbon, and organic nitrogen. For example, Islam et al. (2005) found that another brackish water copepod, *Sinocalanus sinensis*, occurred almost exclusively in the ETM region of the Chikugo estuary, Japan, where it appeared to consume elevated levels of organic material via a detritus-based food web. As in our study, these authors found that *Acartia* and several other copepod species in the estuary did not overlap with the low salinity species. Furthermore, they found that the food source for the copepods appeared to be different in the more saline parts of the estuary, consisting of phytoplankton rather than being detritus-based. Similar food web studies have not been conducted for *P. inopinus*, but it seems reasonable to expect that they also utilize detritus-based food sources in the ETM region of the Chehalis River estuary.

Pseudodiaptomus inopinus may have encountered little competition for resources in its invaded habitats, because there appear to be few native holoplanktonic taxa that co-occur with it in the brackish-oligohaline regions of northeast Pacific estuaries. Two species, the harpacticoid copepod *Coullana canadensis* and the calanoid copepod *Eurytemora affinis*, inhabit the ETM regions of US west coast estuaries (Morgan et al. 1997, Kimmerer et al. 1998). However, *C. canadensis* clearly prefers near-bottom depths and therefore probably does not compete extensively with planktonic copepods (Morgan et al. 1997). In estuaries elsewhere, *E. affinis* occurs mainly in the spring (Koepcke 2004, Lawrence et al. 2004, David et al. 2005) when *P. inopinus* would not be abundant. *E. affinis* formerly occurred throughout the year in the San Francisco estuary (Ambler et al. 1985), but appears to have been adversely affected there by the invasion of *Pseudodiaptomus forbesi* and the introduced bivalve *Potamocorbula amurensis* that feeds on *E. affinis* nauplii but not on *P. forbesi* nauplii (Kimmerer et al. 1994).

Orsi (1995) noted that *E. affinis* continues to be seasonally present in winter and spring when *P. forbesi* is scarce, both within and upstream of *Potamocorbula's* range. Similarly, our data show *E. affinis* was only abundant from January to May. A complicating factor is that *E. affinis* in the northeast Pacific appears to consist of at least 2 morphologically indistinct species: one is introduced from the Atlantic, occurring in San Francisco Bay and Grays Harbor, Washington, and the other is apparently endemic (Chehalis River estuary and other locations) (Lee 2000, Lee & Frost 2002). It is unknown whether *P. inopinus* interacts differently with different '*E. affinis*' sibling species, or if other abundant introduced filter feeders (e.g. the introduced Asian bivalve *Corbicula fluminea* in the Columbia River and other estuaries) benefit *P. inopinus* by preying on *E. affinis*. Clearly this warrants further investigation.

In the Chehalis River estuary, *Pseudodiaptomus inopinus* appears to have 2 reproductive peaks: one in late summer/early autumn, and the other in late winter/early spring. This is evidenced by peaks of both gravid females and adult males during these times. These results are very similar to those from a 1 yr study of an unidentified *Pseudodiaptomus* sp. closely related to *P. inopinus* in the Seomjin river estuary, Korea (Park et al. 2005). In our study, gravid female *P. inopinus* comprised the highest female proportions during periods of very low overall population abundance that spanned the end of the high-flow period in late winter/early spring. This may be evidence of a reproductive strategy in which the copepod repopulates the estuary by means of overwintering adult females that are either previously fertilized or ready for mating.

The presence of 2 very different fifth leg morphotypes of *Pseudodiaptomus inopinus* has been noted for some time, and the paddle-shaped type has been described as a distinct subspecies (*Pseudodiaptomus inopinus saccupodus*) (Shen & Tai 1962). The relative functions of the 2 types of male *P. inopinus* fifth legs are unknown, but may be related to reproduction. In the genus *Pseudodiaptomus*, the male grasps the female with the right side of the fifth leg and uses the left side to transfer the spermatophore to the female genital area (T. C. Walter pers. comm.). Mating experiments using unfertilized females, and the 2 male morphotypes would help us to understand their role in *P. inopinus* reproduction and potential impact on population dynamics.

Although other introduced *Pseudodiaptomus* species can be important direct food sources for estuarine fish (e.g. *P. forbesi* for delta smelt *Hypomesus transpacificus* in the San Francisco estuary; Nobriga 2002), in the Chehalis River estuary *P. inopinus* was not an important diet component for the fish that we sampled. How-

ever, it is important prey for *Neomysis mercedis* and thus fuels higher trophic levels through this invertebrate predator. The diet of at least 3 fishes (Chinook salmon, threespine stickleback, and American shad) was dominated by *N. mercedis*, which also occurred in juvenile *Crangon franciscorum* diets. *N. mercedis* is also a principal prey item for *C. franciscorum* in the San Francisco estuary (Siegfried 1982, Wahle 1985). In other estuaries and lakes *N. mercedis* is similarly trophically important, both competing with and providing food for other fish and invertebrate zooplanktivores (Wahle 1985, Chigbu et al. 1998, Feyrer et al. 2003, Hyatt et al. 2005). As a predator, *N. mercedis* is important in structuring zooplankton assemblages, and in some cases these effects probably exceed those of its fish competitors (Cooper et al. 1992, Chigbu 2004, Hyatt et al. 2005). *N. mercedis* has the potential for affecting *P. inopinus* populations in estuaries where the 2 species co-occur, but establishing that this is the case will require measuring predation rates and quantifying the population dynamics of *N. mercedis* and *P. inopinus* together. In estuaries, *N. mercedis* also appears to be an important predator on epibenthic meiofauna, consuming harpacticoid copepods, juvenile gammarid amphipods, and chironomid fly larvae (Johnston & Lasenby 1982, Simenstad & Cordell 1985, present study). There is some suggestion in the present study that *N. mercedis* at times obtained *P. inopinus* while foraging near the bottom, because *P. inopinus* often occurred in mysid diets along with benthic harpacticoid copepods and *Corophium* spp. amphipods.

Pseudodiaptomus inopinus may be an important new food source for *Neomysis mercedis* in the Chehalis River estuary. It often dominated the mysid diets during times when the *N. mercedis* population had high proportions of gravid females. It also had a high frequency of occurrence in *N. mercedis* diets during the late summer/early autumn period when the mysids produce generations that overwinter as large adults (Figs. 9 to 11; Johnston & Northcote 1989). Additional questions remain as to the food web interactions of *N. mercedis*, *P. inopinus*, *Crangon franciscorum* and other abundant taxa. For example, *P. inopinus* undergoes diel vertical migration in the Chehalis River estuary (Bollens et al. 2002) and it is not known whether *N. mercedis* preys on *P. inopinus* mainly on the bottom during the day or if predation also occurs at night in the water column. Our finding of generally higher percentages of adult males in *N. mercedis* diets as compared to *C. franciscorum* diets may be indicative of feeding on more planktonic individuals of *P. inopinus* by *N. mercedis*, because there are numerous examples of male copepods occurring higher in the water column than females (see literature review by Schabetsberger & Jersabek 2004).

Other questions concerning the food web are important but were not addressed in this study. First, we do not know if *Pseudodiaptomus inopinus* contributes to the diet of pelagic fish in the estuary because all of our fish samples were taken with a beach seine. Use of water column nets such as trawls and purse seines would provide more pelagic-oriented fish for diet analyses. Second, while *P. inopinus* appears to be important in the diets of *Neomysis mercedis* and *Crangon franciscorum* in the Chehalis River estuary, the extent to which it supplies the metabolic and nutritional needs of these predators in relation to native prey taxa is unknown. This could be addressed by the following studies: (1) feeding experiments using *P. inopinus* and native prey species to establish feeding response curves for different prey under different environmental conditions; (2) bioenergetic modelling, which would require measurements of consumption rates of the predators, energy content of the copepods and other prey taxa, and respiration and egestion of the predators (e.g. see Rudstam 1989); (3) establishing the fatty acid profile of *P. inopinus* to better understand its nutritional value to higher trophic levels—fatty acid profiles have only been established for a few calanoid copepods, and they can differ greatly based on copepod species and diets of the copepods themselves (Williams & Biesiot 2004). Third, studies of the food sources for *P. inopinus* (e.g. using stable carbon isotope analyses; Hanson & Tranvik 2003) would help to understand how this species is changing trophic pathways in its invaded habitats.

Although populations of *Pseudodiaptomus inopinus* have existed for more than 10 yr in the Chehalis River and other northeast Pacific estuaries (Cordell & Morrison 1996, J. R. Cordell, unpubl. data from 2000 & 2004) its long-term fate there remains to be seen. In other estuaries, introduced copepods that appeared to have been well established have apparently been displaced by new copepod invasions. For instance, in the San Francisco estuary, the previously abundant Asian cyclopoid *Limnoithona sinensis* disappeared after the introduction of its congener *L. tetraspina* (Orsi & Ohtsuka 1999). Likewise, in the Columbia River estuary and its tributaries, *P. inopinus* is now rare and has been replaced by 2 other Asian species, *P. forbesi* and *Sinocalanus doerrii* (Sytsma et al. 2004). *S. doerrii* also occurs in the Chehalis River estuary, but is not yet abundant there in comparison to *P. inopinus* (J. R. Cordell pers. obs.). In addition, new introductions of predators may affect populations of both native and introduced estuarine copepods. For example, several species of Asian mysids and the predatory copepod *Tortanus dextrilobatus* have recently been introduced to the San Francisco estuary (Modlin & Orsi 1997, Orsi & Ohtsuka 1999). *Tortanus dextrilobatus* has become

very abundant and appears capable of significantly affecting its copepod prey (Bollens et al. 2002, Hooff & Bollens 2004). Therefore, it appears that planktonic invasions in northeast Pacific estuaries are ongoing, and in some estuaries are evolving. Estuaries where most of these invasions occur are ecologically and hydrologically complex. Intensive long-term within-estuary studies and periodic broad-scale surveys of plankton assemblages in estuaries from this region are rare, but this type of information, along with more process-oriented studies of population dynamics, are needed in order to understand the status and impacts of invasive zooplankton species.

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