Research Article

Invasive copepods in the Lower Columbia River Estuary: Seasonal abundance, co-occurrence and potential competition with native copepods

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Editor's note:

This special issue of *Aquatic Invasions* includes papers from the 17th International Conference on Aquatic Invasive Species held in San Diego, California, USA, on August 29 to September 2, 2010. This conference has provided a venue for the exchange of information on various aspects of aquatic invasive species since its inception in 1990. The conference continues to provide an opportunity for dialog between academia, industry and environmental regulators within North America and from abroad.

Abstract

As part of a multi-year field study to investigate plankton dynamics in the Lower Columbia River Estuary (LCRE), we conducted monthly sampling of the mesozooplankton (> 73 μm) at a station near Astoria, Oregon. The planktonic copepod community was numerically dominated by three non-indigenous species (NIS), *Pseudodiaptomus forbesi*, *Limnoithona tetraspina*, and *Sinocalanus doerrii*, and two native species, *Eurytemora affinis* and *Diacyclops thomasi.* However, seasonal co-occurrence of non-indigenous and native copepods was highly variable between species-pairs. The native *E. affinis* and the non-indigenous *S. doerrii* showed the greatest temporal overlap (March-October), but other species-pairs also showed periods of considerable overlap during some seasons (e.g., *E. affinis* and *P. forbesi* in June-September). Spatial co-occurrence of native and non-indigenous species was also examined in temperature and salinity "space" (rather than geographic space): all six species-pairs (3 non-indigenous species × 2 native species) showed some degree of overlap, with the greatest (proportional) overlap occurring between the native *E. affinis* and the two non-indigenous species, *S. doerrii* and *P. forbesi*. This suggests the potential for competition to occur between native and non-native copepods in the LCRE, although with variation between seasons and species. Future studies are recommended that explicitly test for and distinguish between the relative importance of biological (e.g., competition and predation) and physico-chemical processes (e.g., freshwater runoff, eutrophication) in regulating the population dynamics of native and invasive copepods in the LCRE.

Key words: Columbia River Estuary; non-indigenous species; invasive copepods; competition; native species; plankton

Introduction

There have been many studies detailing the economic and ecological impacts of non-indigenous species (NIS) that invade terrestrial, marine and freshwater habitats. Though there are numerous cases of invasive planktonic animals, only a few have been studied in detail (Bollens et al. 2002). These plankton invaders can have profound ecological and economic impacts, the most notorious and well-studied being the ctenophore *Mnemiopsis leidyi* (Agassiz, 1865) in

the Black and Caspian Seas (Shiganova et al. 2004; Daskalov and Mamedov 2007; Roohi et al. 2008; Roohi et al. 2010).

Among the most common known planktonic invaders are crustaceans such as copepods and cladocerans, which have been introduced into estuaries and continental fresh waters throughout the world (Reid and Pinto-Coehlo 1994; Bollens et al. 2002). In North America, exotic planktonic crustaceans have been particularly successful, with eight planktonic copepod invaders documented in coastal rivers and their estuaries

(Cordell et al. 2008), and at least 10 other non-indigenous planktonic copepod and cladoceran species occurring in inland fresh waters (USGS 2009). Of these, most published studies have been conducted on the cladoceran *Bythotrephes longimanus* (Leydig, 1860)*,* which serves as a good example of the potential effects of a planktonic crustacean invader. *Bythotrephes* can have large effects on invaded plankton communities including negative effects on some of its competitors (Foster and Sprules 2009), declines in plankton species richness (Yan et al. 2002; Strecker et al. 2006), and reductions in total community biomass and abundance (Yan et al. 2001; Boudreau and Yan 2003; Strecker and Arnott 2005; Strecker et al. 2006; Strecker and Arnott 2008).

The ecology of non-indigenous copepods has been much less studied, but there are cases in which an introduced copepod has become so abundant that it dominates plankton abundance and has similarly large ecological effects (Bollens et al. 2002; Hooff and Bollens 2004; Bouley and Kimmerer 2006; Cordell et al. 2007; Cordell et al. 2008; Bollens et al. 2011b). In the lower Columbia River and its estuary, invasive copepods are now prominent in the zooplankton, including *Pseuodiaptomus inopinus* (Burckhardt, 1913), *Sinocalanus doerrii* (Brehm, 1909), *Limnoithona tetraspina* (Zhang and Li 1976), and *Pseudodiaptomus forbesi* (Poppe and Richard, 1890), with the latter species having spread almost 700 km upstream, well beyond the limits of brackish waters (Cordell et al. 2008; Cordell in press; Bollens et al. unpublished data). However, the seasonal dynamics of these copepod invaders, and their relationship to native copepods and environmental conditions such as salinity and temperature, have not been previously described.

We undertook a multi-year field study to investigate the plankton dynamics in the lower Columbia River estuary (LCRE), including monthly sampling at a station near Astoria, Oregon. Here we present 2 years (2005 and 2006) of data from triplicate vertical plankton hauls for mesozooplankton, as well as corresponding hydrography (temperature and salinity), which in estuaries is often associated with the habitat of planktonic species (Sotaert and Van Rijswijk 1993; Gewant and Bollens 2005; Graham and Bollens 2010; Bollens et al. 2011b). The specific objectives of this paper are to: i) describe the seasonal abundance patterns of both non-indigenous and native planktonic
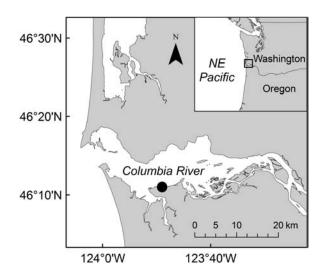

Figure 1. Map of the study site. Filled circle is the location of sampling.

copepods in the LCRE; ii) describe the physical (salinity-temperature) habitats of both non-indigenous and native copepods in the LCRE; and iii) explore possible competitive interactions between non-indigenous and native copepods in the LCRE.

Materials and methods

We sampled mesozooplankton, water temperature and salinity monthly between January 2005 and December 2006 on the south side of the lower Columbia River estuary (LCRE) from a dock in Astoria, Oregon (Figure 1). The dock (46°11'25"N; 123°49'28"W) is located approximately 20 km upstream of the mouth of the estuary and extends approximately 40 m from the shore. Water column depth during samplings varied between 4.0 and 6.5 m. On average, the estuary is 6–12m deep (Jay 1984) and the main channel is maintained at a depth of about 17m. Salinity and temperature profiles were taken using a YSI 85 profiler. Triplicate vertical tows were made from 0.5 m above the bottom to the surface using a 0.5-m mouth diameter, 73-µm mesh net to collect mesozooplankton. Two zooplankton samples (one each from October 24, 2005 and December 18, 2006) were damaged and were not analyzed. Volumes filtered were calculated using a flow meter positioned just inside the mouth of the plankton net. Samples were immediately preserved in 5% buffered formalin.

Mesozooplankton were identified and enumerated using a dissecting microscope at 25×. Copepods, including adults and copepodites, were identified to the species level using Edmondson (1959) and Thorp and Covich (2010). The cross-correlation coefficient at lag 0 was calculated, using R v. 2.13.1, to correlate abundances (individuals m^{-3}) of non-indigenous copepod species to abundances of native copepod species. To correct for autocorrelation, the first (and, in one instance, second order) differences of log-transformed abundances were used in the correlations. In addition, we overlaid each species presence/absence in temperature-salinity space to qualitatively estimate the degree of overlap between the "habitat" distributions of non-indigenous and native copepods.

Results

Water column average temperature and salinity varied seasonally in a predictable and expected pattern, with temperature reaching a minimum (5°C) in late winter and peaking (21°C) in late summer, and salinity reaching a minimum (0) in late spring and maximum values (9–12) in late autumn (Figure 2A).

Three species of non-indigenous planktonic copepods were abundant in our samples: *Pseudodiaptomus forbesi*, *Limnoithona tetraspina*, and *Sinocalanus doerrii* (Figure 2B). *P. forbesi* was broadly abundant between June and December, and peaked in October and November. *L. tetraspina* had a similar yet narrower seasonal abundance pattern (August through October), but was two orders of magnitude less abundant than *P. forbesi*. *S. doerrii* had a much more variable seasonal abundance pattern, with minor peaks occurring in spring (March-April) as well as late summer-early autumn (August-September).

Two species of native planktonic copepods were abundant in our samples – *Eurytemora affinis* (Poppe, 1880) and *Diacyclops thomasi* (Forbes, 1882) (Figure 2C). *E. affinis* reached peak abundance in spring/summer (May–August), but was present at lower abundances throughout much of the rest of the year. *D. thomasi* had a somewhat more restricted seasonal abundance pattern, peaking in late spring/early summer (April–June) of each year.

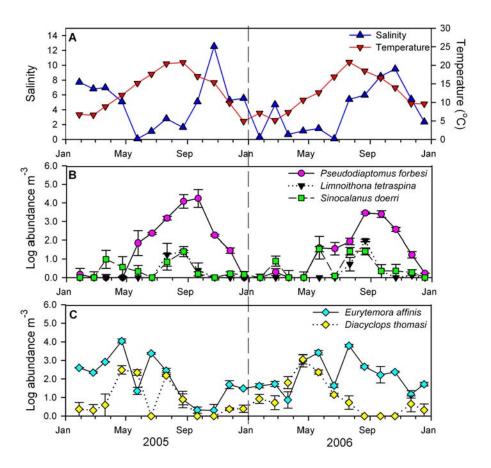Non-indigenous and native planktonic copepod species overlapped in their seasonal abundance patterns to differing degrees (Figure 2). Two species-pairs showed positive correlations in their abundances, whereas 4 other species-pairs showed negative correlations (Table 1). The native *Eurytemora affinis* and the non-indigenous *Sinocalanus doerrii* showed the strongest positive correlation, and thus their patterns of abundance were the most in phase. The abundances of other species-pairs did not increase together, but still showed periods of considerable overlap (e.g., *E. affinis* and *P. forbesi* in June-September; Figure 2).

Non-indigenous and native planktonic copepod species also differed in their distributions within temperature-salinity space (Figure 3). (Assessment of their distribution in geographic [horizontal and vertical] space was not possible given our sampling at only one station.) Although all six species-pairs (3 non-indigenous species × 2 native species) showed some degree of overlap, the greatest (proportional) overlap was between the native *E. affinis* and the two non-indigenous species, *S. doerrii* and *P. forbesi*. The least (proportional) overlap in temperature-salinity space was between the native *D. thomasi* and the non-indigenous *L. tetraspina*. However, it should be noted that these comparisons are based on water column averages of copepod abundance, temperature and salinity, which might obscure finer-scale vertical associations.

Discussion

We found two native and three non-indigenous planktonic copepod species to be abundant and to co-occur in the LCRE. *Diacyclops thomasi* is a freshwater cyclopoid that is widespread in Canada and the conterminous United States, usually occurring in large lakes and reservoirs but also in smaller water bodies (Reid and Williamson 2010). *D. thomasi* also occurs far upstream in the Columbia River (e.g., Prahl 1998; Rollwagen-Bollens et al. unpublished data; Bollens et al. unpublished data) and is likely being advected into the estuary, where it may become stressed by exposure to salinity. On the other hand, *D. thomasi* has been shown to be euryhaline in inland lakes (Meyer and Effler 1980; Hammer 1993) and may have reproducing sub-populations in the LCRE distinct from those in the reservoirs. *Eurytemora affinis* is a euryhaline species complex that is widely distributed in the coastal areas of the northern

Figure 2. A) Temperature and salinity, **B**) abundance (individuals per m³) of three species of non-indigenous copepods, and **C**) abundance (individuals per m³) of two species of native copepods in the lower Columbia River estuary, January 2005 through December 2006.

hemisphere (Lee 1999; Lee and Frost 2002). The *E. affinis* clade that occurs in the LCRE is considered native because it is part of a North Pacific clade that is genetically distinct from other clades in Japan, Europe, and eastern North America (Lee 2000; Lee and Frost 2002).

The three non-indigenous copepods are native to Asia. *Pseudodiaptomus forbesi* was introduced to the San Francisco Estuary (SFE) in the 1980s (Orsi and Walter 1991) and is now broadly abundant in the Columbia River, extending from the lower estuary to more than 600 kilometers upstream and into the Snake River, the main tributary (Cordell et al. 2008; Cordell in press). *P. forbesi* dominates the mesozooplankton in late summer in some of the upstream reservoirs, reaching densities up to 25,000 m⁻³ (Cordell In Press). In our study of the LCRE, *P. forbesi* peak abundances also occurred in late summer, despite relatively high salinities (4-12). *Limnoithona tetraspina* was first collected in the SFE in 1993

(Orsi and Ohtsuka 1999) and has since become the most abundant copepod in the low salinity parts of that estuary (Bouley and Kimmerer 2006; Bollens et al. 2011b). *L. tetraspina* was first observed in the LCRE in 2003 (Sytsma et al. 2004), where it now extends at least 75 km upstream (Cordell et al. 2008). *Sinocalanus doerrii* is a planktonic copepod native to the rivers of China and was first recorded in the SFE in 1978 (Orsi et al. 1983) and in the LCRE in 2002 (Sytsma et al. 2004).

P. forbesi, *S. doerrii*, and *L. tetraspina* co-occur in their native habitat (e.g., in the Yangtze River; Chen and Liu 2009; Zhou et al. 2009) and may have co-evolved so as to limit direct competition with each other. In the invaded habitat of the LCRE, however, they clearly have not co-evolved with the native copepods, *E. affinis* and *D. thomasi*, and for this reason alone one might expect potential competition between copepods to be high. Overall, we found

Table 1. Cross-correlation coefficients of the first differences of log abundances of non-indigenous (column headers) versus native (row headers) planktonic copepods (n = 23). Positive values indicate species abundances increase in phase and thus high potential for competition; negative values indicate seasonal separation and thus a lower likelihood of competition (although these species may still overlap considerably in time and space [Figure 2]).

	Sinocalanus doerrii	*Pseudodiaptomus forbesi*	*Limnoithona tetraspina*
Eurytemora affinis	0.319	-0.252	-0.014
Diacyclops thomasi	0.060	-0.317†	-0.088

†Second order differences correlated.

these two native and three non-indigenous planktonic copepods to co-occur to varying degrees in the LCRE, suggesting very different potential for competition, depending on the species-pair.
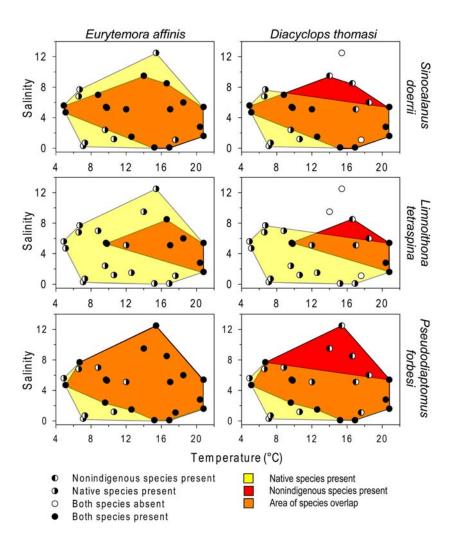
One particularly important aspect of competition concerns food resources. Almost nothing is known about the diets and feeding dynamics of copepods in the LCRE, although studies from other locations are relevant. Cyclopoid copepods generally, and *D. thomasi* (native) and *L. tetraspina* (NIS) specifically, are known to be omnivorous and/or predatory in other habitats, feeding on protozoa (particularly aloricate ciliates and flagellates), juvenile copepods, rotifers, and even larval fish (LeBlanc et al. 1997; Hanson and Hairston 1998; Bouley and Kimmerer 2006; Gifford et al. 2007; Rollwagen-Bollens et al. unpublished data). This potential for *D. thomasi* and *L. tetraspina* to compete for food resources would seem to be significant. However, this is mitigated to a great extent in the LCRE by the fact that these two species have somewhat different seasonal abundance patterns, with *D. thomasi* dominant in spring, and *L. tetraspina* abundant in summer (Figure 2, Table 1).

The other three species of copepods in our study – *E. affinis* (native), *P. forbesi* (NIS) and *S. doerri* (NIS) – are all calanoids, and are generally thought to be more herbivorous, although protozoans are also sometimes consumed (Orsi 1995; Merrell and Stoecker 1998; Bouley and Kimmerer 2006). These three species would therefore seem to be likely competitors for food. Indeed, these three species showed the greatest overlap in the LCRE in both seasonal abundance (Figure 2) and distribution in temperature-salinity space (Figure 3). Thus the potential for competition for food between these three calanoid species in the LCRE would seem to be great. Another interesting aspect of potential competition concerns the differential ability of certain species of copepods to consume harmful algae. For instance, Ger et al. (2010) found *P. forbesi* in the SFE was better able than *E. affinis* to tolerate consuming the nuisance cyanobacterium *Microcystis*, which might represent an advantage for the invasive over the native copepod.

Predation is another important process affecting seasonal abundance patterns in zooplankton (Landry 1976; Steele and Frost 1977; Verity and Smetacek 1996; Boero et al. 2008). Estuarine copepods are preyed upon by a wide range of both invertebrate (e.g., Hooff and Bollens 2004; Cordell et al. 2007) and vertebrate predators (e.g., Bollens and Frost 1989; Cohen and Bollens 2008; Bollens et al. 2010), and the same is likely to be the case for the five LCRE copepod species in our study. Predation by these and other predators likely contributed to the late summer and autumn declines in population numbers seen for most LCRE copepods in our study (Figure 2). However, little is known about species-specific predator-copepod dynamics in the LCRE, although studies from other estuaries provide some insights.

One feeding study of juvenile striped bass (*Morone saxatilis*) in the SFE found that of four native and non-indigenous copepods used as prey, *S. doerrii* were consumed the least, presumably due to its pronounced escape response (Meng and Orsi 1991). Also in the SFE, the clam *Corbula amurensis* was found to consume *E. affinis* larvae, whereas *P. forbesi* larvae were better able to avoid predation by the clam (Kimmerer et al. 1994; Kimmerer and Orsi 1996). A diet analysis of planktivorous juvenile delta smelt (*Hypomesus transpacificus)* in the SFE found that *L. tetraspina* rarely comprised more than 10% of the fish diets while comprising up to 80% of the plankton numbers during the same time period (Bouley and Kimmerer 2006). This may be due to the small size of *L. tetraspina* relative to co-occurring calanoid copepods, which might make it too small for visual predators to consume efficiently (Gould and Kimmerer 2010).

Figure 3. Occurrence of planktonic copepods in relation to salinity and temperature in the lower Columbia River estuary, January 2005 through December 2006.

Protozoan-metazoan linkages are important to the pelagic food web in estuaries (e.g., Rollwagen-Bollens and Penry 2003; Rollwagen-Bollens et al. 2006; Gifford et al. 2007), and may ultimately determine the amount of material and energy available to higher trophic levels (e.g., Rollwagen-Bollens et al. 2011). Because *L. tetraspina* is both omnivorous and extremely abundant in the SFE, it is possible that this has contributed to declines in fish abundances in the low salinity zone of the estuary, i.e., by consuming substantial amounts of lower level productivity while not being of large enough size individually to be a desirable prey type for visually orienting planktivorous fish (Gould and Kimmerer 2010). But again, the role of predation in modulating native and NIS copepod population dynamics in the LCRE is currently unknown, and warrants further study.

The absence of a fourth NIS copepod, the calanoid *Pseudodiaptomus inopinus*, in our study of the LCRE is noteworthy. *P. inopinus* was first seen in the estuary in 1990 (Cordell et al. 1992), and has become very abundant in brackish and tidal fresh waters of a number of other estuaries along the Pacific coast of the USA (Cordell and Morrison 1996; Cordell et al. 2007). However, *P. inopinus* has recently become rare in the LCRE (Sytsma et al. 2004; Cordell et al. 2008), although the reasons for this are unknown. Again, the importance of both biological and physico-chemical processes in modulating the population dynamics and persistence of this copepod, as well as other NIS and native copepods in the LCRE, needs to be investigated.

Our sampling of planktonic copepods in the LCRE was necessarily limited in time and space – chief among these limitations was the absence

of any vertically stratified sampling. One of the major forms of habitat partitioning for planktonic copepods is differing vertical distribution, which can vary considerably between species, even for closely related, similarly sized, co-occurring species (e.g., Ambler and Miller 1987; Bollens et al. 1993; Mackas et al. 1993). Unfortunately, little is known about the vertical distribution of the copepod taxa in the LCRE. Morgan et al. (1997) found *E. affinis* densities were greater in the water column during flood tide than ebb tide, suggestive of vertical migration on a tidal cycle in the LCRE. *Pseudodiaptomus inopinus,* an NIS copepod closely related to *P. forbesi,* was fairly closely associated with the river bottom during the day and migrated to mid-depths during the night in the nearby Chehalis River estuary (approximately 100 km north of the LCRE) (Bollens et al. 2002). In addition, a few studies in other systems have reported on vertical distributions of *E. affinis* (Hough and Naylor 1991; Kelso et al. 2003), *P. forbesi* (Kimmerer et al. 1998; Bollens et al. 2011b), *S. doerrii* (Orsi et al. 1983) and *D. thomasi* (Wells 1960; Carter 1969; Wilson and Roff 1973). But as for direct comparisons of vertical distributions of native vs. NIS copepods in the LCRE, this is unknown and warrants investigation. Indeed, the degree of competitive interaction between NIS and native copepods could depend critically on the degree of their vertical overlap.

In summary, we found three non-indigenous (*P. forbesi*, *L. tetraspina* and *S. doerrii*) and two native planktonic copepods (*E. affinis* and *D. thomasi*) to co-occur and overlap to varying degrees in their distributions in the LCRE, suggesting strong potential for competition. We recommend that future studies explicitly test for and distinguish between the relative importance of biological (e.g., competition and predation) and physico-chemical processes (e.g., freshwater runoff, eutrophication) in regulating the dynamics of native and non-indigenous copepods in the LCRE and elsewhere. A combination of field, experimental and modeling approaches might prove most fruitful, as has recently been recommended in a somewhat different context by Bollens et al. (2011a). Whatever the means, understanding and eventually predicting the ecological consequences of copepod invasions will be critical to protecting and conserving sensitive aquatic ecosystems such as the LCRE and other estuaries.

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