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Zooplankton invasions: a brief review, plus two case studies from the northeast Pacific Ocean

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Abstract

Invasions of aquatic habitats by non-indigenous species (NIS), including zooplankton, are occurring at an alarming rate and are causing global concern. Although hundreds of such invasions have now been documented, surprisingly little is known about the basic biology and ecology of these invaders in their new habitats. Here we provide an overview of the published literature on NIS zooplankton, separated by life history (holoplankton vs. meroplankton), habitat (marine, estuarine, freshwater), and biological level of organization or topic (e.g. distribution and range extension, physiology, behavior, feeding, community impacts, ecosystem dynamics, etc). Amongst the many findings generated by our literature search, perhaps the most striking is the paucity of studies on community and ecosystem level impacts of NIS zooplankton, especially in marine and estuarine systems. We also present some results from two ongoing studies of invasive zooplankton in the northeast Pacific Ocean – *Pseudodiaptomus inopinus* in Washington and Oregon coastal estuaries, and *Tortanus dextrilobatus* in San Francisco Bay. Both of these Asian copepods have recently expanded their range and can at times be extremely abundant (10^3 m^{-3}). We also examine some aspects of the trophic (predator–prey) ecology of these two invasive copepods, and find that they are likely to be important in the flow of material and energy in the systems in which they now pervade, although their impacts at the ecosystem level remain to be quantified. Finally, the findings of both our literature search and our two case studies of invasive zooplankton lead us to make several recommendations for future research.

Introduction

The introduction and successful establishment of non-indigenous species (NIS) in aquatic and terrestrial habitats has become a major global concern. Indeed, this phenomenon has spawned several books (e.g. Elton, 1958; Mooney & Drake, 1986; Williamson, 1996), governmental reports (e.g. OTA, 1993; Elston, 1997), and a new professional journal ("Biological Invasions"; Kluwer Academic Publishers), highlighting the importance of invasion biology to both basic scientific research and applied policy and resource management issues. The occurrence of aquatic (freshwater, estuarine and marine) NIS taxa, while difficult to quantify exactly, is now suspected to total in the hundreds (e.g. Carlton & Geller, 1991; Carlton & Geller, 1993; Ruiz et al., 1997; Cohen & Carlton, 1998).

With respect to causes, several vectors or mechanisms of transport of aquatic NIS have been identified, including release of ballast water of ships, and accidental or intentional release by aquaculture, fisheries or pet industries (e.g. Ruiz et al., 1997; Elston, 1997). Yet the consequences, or ecological impacts, of NIS are not always well understood (Parker et al., 1999), especially in planktonic systems. Indeed, the extension of research on NIS from documenting occurrences to understanding ecological consequences is a major challenge for all of invasion biology, and certainly applies to zooplankton biology as well.

Thus, the objectives of this paper are (i) to review the current state of research on NIS zooplankton, and (ii) to include preliminary results from two ongoing studies of invasive zooplankton in the northeast Pacific Ocean – the Asian copepods *Pseudodiaptomus inopinus* in Washington and Oregon coastal estuaries, and *Tortanus dextrilobatus* in San Francisco Bay Estuary. Our literature review is intended to provide a broad overview of what topics within the biology and ecology of NIS zooplankton have received significant attention to date, and which others, by contrast, have been relatively under-studied and thus may warrant more attention in the future. Our two case studies are used as examples from our ongoing research projects of how to go beyond documenting occurrences of NIS zooplankton, and to try to elucidate some of the underlying biology and ecology of these organisms. We also include some discussion, admittedly speculative, of the impact these zooplankton invaders might have on native communities and ecosystems. Finally, we offer some summary comments, based on both the literature review and our two case studies, including some recommendations for future research.

Background and literature review

The growing number of published reports over the past decades concerned with the biology or ecology of non-indigenous species (NIS) of zooplankton has been remarkable, although we are aware of no review of the literature on this topic. We therefore felt that it would be timely to provide such a review. Our objective is not to be exhaustive in our literature search and to summarize each paper's findings, but rather to provide an overview of the extant literature regarding NIS zooplankton, and to organize it in such a way as to illustrate some general trends and make recommendations for future research.

Taking a similar approach to that of Parker et al. (1999), we compiled the results of a literature review on non-indigenous zooplankton from six electronic abstract services in aquatic sciences: Aquatic Science and Fisheries Abstracts (1978–2001), Oceanic Abstracts (1981–2001), Biological Sciences (1982–2001), Biosis (1985–2001), Zoological Record (1993–2001), and Current Contents. The term 'non-indigenous' is interpreted herein to encompass the breadth of literature which reports on species with reproducing populations outside their known native distribution, including those that have been described as 'introduced', 'invasive', 'exotic', or 'alien' (see Davis & Thompson, 2000 for a useful nomenclature scheme to distinguish between these terms, but also Daehler, 2001 for a critique). Furthermore, in the case of non-indigenous meroplanktonic organisms, only those references that explicitly studied the planktonic stage(s) have been included. For instance, the vast majority of literature on Zebra Mussels (*Dreissena* spp.) in the Great Lakes, and the Asian clam *Potamocorbula amurensis* in San Francisco Bay, is concerned with the benthic stages of these organisms, and thus does not fall within the confines of our literature review of zooplankton.

In order to maintain consistent methodology, and to avoid any regional bias, only references reported in these databases have been included in our review (Table 1). This includes both peer reviewed and 'gray' literature, but excludes abstracts of conference presentations. We are aware of several peer reviewed (e.g. Carlton, 1985) and gray literature (e.g. Cohen and Carlton, 1995; Orsi, 1995; Avent et al., 2000) articles which meet our criteria but were nonetheless not found in these databases, and so have been excluded from Table 1.

Carlton (1985) provided a comprehensive review of the history of ballast water introductions of aquatic invaders, including zooplankton. Given that our review of NIS zooplankton is focused on the past 25 years (i.e. the period covered by electronic databases), Carlton (1985) should be consulted for additional (but far less numerous) references to the historical literature (e.g. Rees & Cattley, 1949; Calder & Burrell, 1969; Grindley & Grice, 1969; Lachner et al., 1970; Alvarino, 1975).

We separated our search results according to zooplankton life history (i.e. holoplankton vs. meroplakton), habitat (marine, estuarine, freshwater), and biological organization or topic (i.e. distribution and range extension, dispersal, physiology, behavior, other population biology, feeding, community impacts, ecosystem dynamics, and general/review). The 'general/review' category was included to capture the variety of papers that did not study a specific non-indigenous zooplankton species, but which were nonetheless relevant to the scope of our study. Placement of any given paper within a given cell in our table is of course subject to interpretation; certainly other investigators might generate a different table, either in format or even content.

Table 1. Results of a literature search of six electronic databases for published studies on non-indigenous species (NIS) of zooplankton. Numbers provided under 'totals' (last row and last column) are total number of publications and total number of taxa, respectively, for any given category. All other numbers refer to specific citations, listed below the table

Non- Indigenous Zooplankton	Holoplankton			Meroplankton			Totals
	Marine	Estuarine	Freshwater	Marine	Estuarine	Freshwater	(# citations / *taxa*)
Range Extension/ Distribution	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 43, 136, 182, 217, 219, 238, 242	1, 16, 18, 19, 21, 22, 23, 24, 25, 32, 66, 68, 139, 150, 152, 153, 155, 158, 159, 190, 196, 229, 230, 234, 241, 248, 250	28, 29, 38, 44, 47, 49, 51, 52, 59, 63, 65, 69, 71, 86, 89, 100, 104, 117, 119, 129, 131, 140, 141, 142, 144, 146, 148, 154, 156, 179, 180, 183, 184, 194, 198, 200, 204, 208, 209, 211, 212, 219, 222, 224, 228, 235, 245, 246, 251,	1, 31, 60, 191, 247	1, 37, 54	30, 39, 90, 151, 192, 240	109 / *61*
Dispersal	20, 42, 54, 58, 82, 125, 147	17, 20, 42, 50, 54, 68, 82, 122, 125, 147, 168	28, 69, 92, 93, 108, 160, 180, 204, 223, 237, 244	20, 42, 54, 58, 125, 191, 227, 247	20, 37, 42, 50, 54, 125, 252	33, 34, 36, 83, 84, 90, 151, 192, 225, 226	40 / *20*
Physiology	118, 123	50, 69	45, 72, 73, 97, 98, 105, 109, 113, 114, 117, 137, 204, 209, 221	31	50, 252	163, 193, 240	24 / *9*
Behavior		56, 65	59, 119, 195, 200				6 / *6*
Other Population Biology (e.g. demographics, life histories)	2, 9, 14, 26, 62, 120, 126, 136	21, 68, 69, 250	35, 55, 65, 70, 72, 78, 81, 89, 95, 98, 115, 116, 117, 137, 156, 162, 166, 179, 183, 185, 188, 195, 207, 224, 235, 246, 251	31, 60, 199, 247	252	30, 39, 40, 41, 151, 173, 186, 225, 226	53 / *23*
Feeding (predator/prey)	4, 9, 130, 132, 133, 134, 135, 218	27, 153, 169	45, 51, 59, 64, 78, 79, 85, 91, 94, 96, 99, 102, 103, 106, 107, 109, 110, 111, 112, 117, 143, 160, 165, 167, 170, 171, 172, 189, 194, 195, 197, 210, 212, 220			57, 175	47 / *17*
Community Impacts	2, 62, 120, 126, 127, 128, 138, 205, 216, 243	236	17, 46, 51, 52, 64, 74, 75, 76, 77, 78, 80, 87, 88, 94, 143, 157, 161, 176, 181, 189, 197, 201, 202, 209, 210, 214, 215, 220, 231, 244, 245, 249				44 / *12*
Ecosystem Dynamics	26, 121, 138, 145, 187, 232, 233		48, 53, 164				10 / *5*
General / Review	71, 124, 149, 203	67, 70, 124, 149, 206	69, 70, 101, 177, 213	61, 124, 149	61, 67, 124, 149	174, 178, 239	15 / *na*
Totals (# citations / # *taxa*)	55 / *14*	47 / *18*	134 / *27*	15 / *4*	12 / *1*	24 / *4*	252 / *63*

Table 1. (continued)

1, Reise et al. (1999); **2**, Volovik et al. (1996); **3**, Sander & Moore (1979); **4**, Kurashova et al. (1992); **5**, Hirakawa (1986); **6**, Malyshev & Arkhipov (1992); **7**, Mutlu (1999); **8**, Romanova et al. (1999); **9**, Shiganova et al. (2000); **10**, Studenikina et al. 1992; **11**, Vinogradov et al. (1989); **12**, Hirakawa (1988); **13**, Fleminger & Hendrix-Kramer (1988); **14**, Grabe (1989); **15**, Larson & Arneson (1990); **16**, Suarez-Morales et al. (1999); **17**, Threlkeld et al. (1980); **18**, Cordell et al. (1992); **19**, Orsi et al. (1983); **20**, Carlton & Geller (1993); **21**, Bakker & Rijsjik (1989); **22**, Ferrari & Orsi (1984); **23**, Orsi & Walter (1991); **24**, Cordell et al. (1992); **25**, Cordell & Morrison (1996); **26**, Volovik et al. (1995); **27**, Kimmerer et al. (1994); **28**, Havel & Hebert (1993); **29**, Reid & Pinto-Coelho (1994); **30**, Martel et al. (1994); **31**, Epifanio et al. (1998); **32**, Ambler et al. (1985); **33**, Johnson & Carlton (1996); **34**, Neary & Leach (1992); **35**, Work & Gophen (1999); **36**, Carlton (1992); **37**, Carlton et al. (1990); **38**, Ueda & Ohtsuka (1998); **39**, Grigorovich & Pashkova (1997); **40**, Brady et al. (1995); **41**, Nichols & Black (1994); **42**, Lavoie et al. (1999); **43**, Taniguchi (1974); **44**, Jack & Thorpe (1995); **45**, Lehman & Branstrator (1995); **46**, Branstrator (1995); **47**, Wolf et al. (1994); **48**, Lehman & Caceres (1993); **49**, Duchovnay et al. (1992); **50**, Smith et al. (1999); **51**, Ketelaars et al. (1999); **52**, Rieman & Falter (1981); **53**, Havens & East (1997); **54**, Chu et al. (1997); **55**, Burkhardt (1994); **56**, Simenstadt et al. (1994); **57**, MacIsaac & Sprules (1992); **58**, Gollasch et al. (2000); **59**, Spadinger & Maier (1999); **60**, McDermott (1998); **61**, Carlton (1999); **62**, Shiganova (1998); **63**, Dumont & Martens (1996); **64**, Maier (1996); **65**, Kimmerer et al. (1998); **66**, Modlin & Orsi (2000); **67**, Cohen & Carlton (1998); **68**, Lee (2000); **69**, Lee (1999); **70**, Lee & Bell (1999); **71**, Saunders (1993); **72**, Ketzner & Bradley (1982); **73**, Bradley (1978); **74**, Goldman et al. (1979); **75**, Langeland (1981); **76**, Morgan et al. (1981); **77**, Vanni (1986); **78**, Stewart (1989); **79**, Bur & Klarer (1991); **80**, Lehman (1991); **81**, Weider (1991); **82**, Williams (1977); **83**, Martel (1992); **84**, Martel (1993); **85**, Juergens et al. (1994); **86**, Havel et al. (1995); **87**, Kolar et. al. (1997); **88**, Yan & Pawson (1997); **89**, East et al. (1999); **90**, Kraft & Johnson (2000); **91**, Coulas et al. (1998); **92**, Jarnagin et al. (2000); **93**, Jarnagin (1999); **94**, Wahlstrom & Westman (1999); **95**, Yan & Pawson (1998); **96**, Schultz & Yurista (1998); **97**, Lehman et al. (1997); **98,** Garton et al. (1990); **99**, Keilty (1990); **100**, Makarewicz & Jones (1990); **101**, Sprules et al. (1990); **102**, Schneeberger (1991); **103**, Mills et al. (1992); **104**, Yan et al. (1992); **105**, Yurista (1992); **106**, Lehman (1993); **107**, Vanderpoloeg et al. (1993); **108**, Berg & Garton (1994); **109**, Burkhardt & Lehman (1994); **110**, Barnhisel & Harvey (1995); **111**, Schulz & Yurista (1995); **112**, Yurista & Schulz (1995); **113**, Lehman & Branstrator (1996); **114**, Yurista & Schulz (1996); **115**, Bilkovic & Lehman (1997); **116**, Yurista (1997); **117**, Work & Gophen (1995); **118**, Borodkin & Korzhikhova (1991); **119**, Davidson & Kelso (1997); **120**, Kovalev & Piontkovski (1998); **121**, Lebedeva & Shushkina (1994); **122**, Pierce et al. (1997); **123**, Minkina & Pavlova (1995); **124**, Carlton (1996); **125**, Carlton & Geller (1991); **126**, Khoroshilov & Lukasheva (1999); **127**, Shushkina & Musaeva (1990); **128**, Shushkina & Vinogradov (1991); **129**, Stoeckel et al. (1996); **130**, Stoeker et al. (1987); **131**, Hiskey (1996); **132**, Tshiken- Lukanina et al. (1991); **133**, Tshiken- Lukanina et al. (1993); **134**, Tshiken- Lukanina et al. (1999); **135**, Vinogradov et al. (1995); **136**, Zaika & Sergeyeva (1990); **137**, Work & Gophen (1999); **138**, Zaitsev (1992); **139**, Bryan & Grant (1974); **140**, Amoros (1980); **141**, Becket & Turanchik (1980); **142**, Pennington & Fletcher (1980); **143**, Dodson & Cooper (1983); **144**, Ferreira (1985); **145**, Grishyn et al. (1994); **146**, Bailly et al. (1987); **147**, Ruiz et. al. (2000); **148**, Rayner (1988); **149**, Ruiz et al. (1997); **150**, Hoffmeyer (1990); **151**, Stoeckel et al. (1997); **152**, Salemaa & Hietalhati (1993); **153**, Ojaveer & Lumberg (1995); **154**, Guenduez (1988); **155**, Krylov et al. (1999); **156**, MacIsaac et al. (1999); **157**, Saunders et al. (1999); **158**, Bielecka et al. (2000); **159**, Gorokhova et al. (2000); **160**, Neill (1978); **161**, Kerfoot (1980); **162**, Morgan (1980); **163**, Wright et al. (1996); **164**, Hanson (1982); **165**, Garnaas (1986); **166**, Vanni (1987); **167**, Barnhisel (1991); **168**, Williams et al. (1988); **169**, Meng & Orsi (1991); **170**, Naesje (1995); **171**, Tohtz (1993); **172**, Hammar (1988); **173**, Frischer et al. (1995); **174**, Johnson (1995); **175**, Liebig & Vanderploeg (1995); **176**, Vogel & Li (2000); **177**, Hokstad & Skurdel (1996); **178**, Johnson & Padilla (1996); **179**, Morgan (1981); **180,** Dzialowski et al. (2000); **181**, Vanni (1988); **182**, Uitto et al. (1999); **183**, Demelo & Hebert (1994); **184**, Duffy et al. (2000); **185**, Hairston et al. (1999); **186**, Ackerman et al. (1994); **187**, Berdnikov et al. (1999); **188**, Berg & Garton (1988); **189**, Black & Hairston (1988); **190**, Bowman & Orsi (1992); **191**, Byrne et al. (1997); **192**, Cataldo & Boltovskoy (2000); **193**, Chalker-Scott et al. (1992); **194**, Charlebois et al. (2001); **195**, Chess (1988); **196**, Cordell (1998); **197**, Dumitru et al. (2001); **198**, Elmore & Bunting (1979); **199**, Evans et al. (1998); **200**, Gasol et al. (1995); **201**, Gilbert (1989); **202**, Goldman (1981); **203**, Greve (1994); **204**, Grigorovich et al. (1998); **205**, Gubanova et al. (2001); **206**, Hairston & Bohonak (1998); **207**, Hall & Yan (1997); **208**, Harper (1984); **209**, Havens et al. (2000); **210**, Hoffman et al. (2001); **211**, Hudson et al. (1998); **212**, Jensen et al. (2001); **213**, Jeppesen et al. (2001); **214**, Johnson & Havel (2001); **215**, Ketelaars & Breemen (1994); **216**, Kideys (1994); **217**, Kovalev et al. (1996); **218**, Krsinic & Njire (2001); **219**, Langeland (1974); **220**, Langeland (1988); **221**, Lennon et al. (2001); **222**, Mabee (2001); **223**, MacIsaac et al. (2000); **224**, Makarewicz et al. (2001); **225**, Martel et al. (1995); **226**, Martel et al. (2001); **227**, McQuaid & Phillips (2000); **228**, Muzinic (2000); **229**, Naumenko (2000); **230**, Naumenko & Polunina (2000); **231**, Nero & Sprules (1986); **232**, Oguz et al. (1998); **233**, Oguz et al. (2001); **234**, Ohtsuka & Ueda (1999); **235**, Ojaveer et al. (2001); **236**, Ojaveer et al. (1999); **237**, Pajunen (1986); **238**, Palma (1994); **239**, Ram & McMahon (1996); **2420**, Reed et al. (1998); **241**, Rees & Gershwin (2000); **242**, Shiganova et al. (1995); **243**, Shiganova & Bulgakova (2000); **244**, Shurin (2000); **245**, Shushkina et al. (1990); **246**, Stella (1989); **247**, Strasser (1989); **248**, Telesh et al. (2000); **249**, Threlked (1981); **250**, Bulnheim (1985); **251**, Taylor & Hebert (1993); **252**, Nicolini & Penry (2001).

Literature review results

The past 20 years have seen a dramatic increase in the number of documented occurrences of NIS zooplankton (Table 2), as well as a rapidly growing literature on their biology and ecology (Table 1). Our literature review yields several interesting findings, both with respect to what has previously been studied, as well as gaps in our understanding of important processes. First, with respect to holoplankton, there have been substantially more studies in freshwater (n=134) *versus* marine and estuarine environments (n= 55 and 47, respectively), despite the fact that there are a greater number of non-indigenous species (NIS) reported for estuarine and marine environments (32 taxa combined) compared to freshwater (27 taxa) (Table 1).

Table 2. Taxa identified from Table 1 (see Table 1 for citation references)

NIS Taxa	Location of Study	Citations
Holoplankton – Marine		
Acartia omorii	Southern Chile	12
Beroe ovata	Black Sea, Sea of Azov, Ukraine	8, 9, 243
Carybdea marsupialis	California coast	15
Centropages abdominalis	Southern Chile	5
Euphausia sibogae	Eastern Indian Ocean	43
Mnemiopsis leidyi	Black Sea, Marmara Sea, Sea of Azov	2, 6, 7, 9, 10, 11, 62, 118, 120, 121,123, 127, 128, 130, 132, 133, 134, 135, 138, 145, 205, 232, 242, 243, 245,
Mnemiopsis mccradyi	Black Sea	217
Muggiaea atlantica	German Bight, Southeast Pacific, Adriatic Sea	203, 218, 238
Oithona davisae	Southern Chile	12
Oithona oculata	Barbados	3
Phyllorhiza punctata	California coast	15
Podon intermedius	Caspian Sea	4
Pseudodiaptomus marinus	Southern Chile	13
Rhopalophthalmus tattersallae	Arabian Gulf	14
Holoplankton – Estuarine		
Mesocyclops ogunnus	Cayman Islands, Brazilian coast	16, 29
Acanthomysis hwanhaiensis	San Francisco Estuary	66
Acartia tonsa	Baltic Sea	229
Cercopagis pengoi	Baltic Sea, Gulf of Finland	153, 155, 158, 159, 182, 230, 236, 248
Deltamysis holmquistae	San Francisco Estuary	190
Eurytemora affinis	North America, Europe, Asia	68, 69
Gammarus tigrinus	Europe	250
Hemimysis anomala	Netherlands, Baltic Sea	152, 215
Limnothoina sinensis	San Francisco Estuary	22
Moerisia sp.	San Francisco Estuary	241
Neomysis americana	South American Coast	150
Oithona davisae	San Francisco Estuary	22, 32
Podon intermedius	Chesepeake Bay	139
Pseudodiaptomus forbesi	San Francisco Estuary	23, 65, 169
Pseudodiaptomus inopinus	Northeast Pacific	18, 24, 25, 56, 196
Pseudodiaptomus marinus	San Francisco Estuary	23
Sinocalanus doerrii	San Francisco Estuary	19, 32, 65
Temora longicornis	Netherlands	21

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The reason for this greater research effort on NIS in freshwater *versus* marine and estuarine systems is unclear. Part of it may be due to the greater awareness and funding surrounding issues related to the zebra mussel invasion of the Great Lakes, which has had a considerable economic impact and much media attention. Alternatively, this could be the result of a cultural difference in the training and focus (on average) of limnologists *versus* oceanographers, with the former being more inclined to investigate purely biological interactions, and the latter more inclined to look at physical mechanisms underlying biological dynamics. Whatever the cause, we argue that both groups should pay greater attention to the impacts of NIS zooplankton, but especially the marine and estuarine ecologists, who seem to have lagged behind.

Table 2. contd.

Holoplankton – Freshwater		
Alona weinecki	Easter Island	63
Boeckella triarticulata	Northern Italy	246
Bosmina coregoni	North America	183
Brachionus forficula	North America	222
Bythotrephes cederstroemi	North America, Europe	45, 46, 48, 55, 79, 80, 81, 91, 92, 93, 95, 96,97, 98, 99, 100, 101, 102, 103, 104, 105,106, 108, 111, 112, 114, 115, 116, 167, 188, 207, 210
Bythotrephes longimanus	North America, Europe	94, 108, 197, 204, 215, 223
Cercopagis pengoi	Great Lakes	156, 193, 224, 235
Chaoborus americanus	Central North America	181, 189
Craspedacusta sowerbyi	Western Europe, Eastern North America, Africa	59, 141, 142, 143, 144, 146, 148,
Cyclops scutifer	Norway	219
Daphnia ambigua	Europe	64, 71, 140
Daphnia cristata	Norway	75
Daphnia curvirostris	Eastern North America	184
Daphnia galeata	Great Lakes	251
Daphnia lumholtzi	Eastern North America	28, 35, 44, 53, 86, 87, 89, 117, 119, 129, 131, 137, 180, 209, 214, 221, 228
Daphnia pulex	Spain, Kenya, Honduras, British Columbia	77, 78, 85, 160, 166, 200, 201, 208, 237
Eurytemora affinis	North America, Europe, Asia	68, 71, 72, 73, 220,
Hemimysis anomala	Netherlands, Baltic Sea	51, 152
Limnosida frontosa	Norway	212
Mesocyclops leuckarti	Tennessee, Norway	198, 219
Mesocyclops ogunnus	Brazil	29
Mesocyclops oithonoides	Norway	219
Mysis relicta	Norway, Sweden, Western United States, Central Canada	17, 47, 52, 74, 75, 76, 161, 162, 164, 165, 170, 172, 176, 177, 179, 195, 202, 220, 231, 249
Sarscypridopsis sp	Easter Island	63
Sinodiaptomus sarsi	Turkey	154
Sinodiaptomus valkanovi	Bulgaria, North America	38
Thermocyclops crassus	Great Lakes	49
Meroplankton – Marine		
Asterias amurensis	Tasmania	191, 199
Hemigrapsus sanguineus	Northwest Atlantic	31, 60
Mya arenaria	North Sea	247
Mytilus galloprovencialis	South Africa229	
Meroplankton – Estuarine		
Potamocorbula amurensis	San Francisco Estuary	37, 252
Meroplankton – Freshwater		
Corbicula fluminea	North America	41
Dreissena bugensis	North America	41, 163, 226
Dreissena polymorpha	North America	30, 33,34, 36, 40, 41, 83, 84, 90, 151, 163, 173, 175, 186, 193, 194, 223, 225, 239, 240
Limnoperna fortunei	Argentina	192

With respect to meroplankton, our review shows a striking paucity of studies of the planktonic stages of these organisms in all environments, be it marine, estuarine or freshwater (Table 1). Although arguably a more difficult life history stage to study than the larger, often more sedentary (in the case of bivalves, for instance) adult stages, the meroplanktonic stages are often the key to understanding dispersal, and thus the control and management of these species. This would appear to be an area of research that provides considerable opportunity for future work.

A fair amount of research has been done identifying ballast water transfer as a vector of dispersal (e.g. most of the 40 references appearing in Table 1), but vastly less has been done with regard to the physiology, behavior, or predator–prey dynamics of NIS zooplankton. Yet it is exactly these aspects of an organism's biology and ecology that will largely determine its success in the new habitat, irrespective of arrival mechanism. In short, there is a tremendous amount of basic biology and ecology of NIS zooplankton that should be explored.

Particularly noteworthy is that there are a limited number of studies that address community and ecosystem level impacts of NIS zooplankton. This is true of both holoplankton and meroplankton, across all three habitat types, but especially so for estuarine holoplankton (only one published report) and for all meroplankton (no published reports). Note also that of the 17 citations of marine holoplankton in these categories, all are concerned with gelatinous zooplankton (e.g. the ctenophore *Mnemiopsis* spp.) in the Black and Azov Seas. Yet the total number of taxa successfully introduced is suspected to be in the hundreds (e.g. Carlton & Geller, 1991; Carlton & Geller, 1993; Ruiz et al., 1997; Cohen & Carlton, 1998, Table 1). The paucity of published reports of community and ecosystem level impacts could be due either to the limited occurrence of such impacts (i.e. they have been thoroughly searched for, but found to occur only rarely), or alternatively, to the limited number of attempts to discern such impacts. We strongly suspect the latter, and recommend that more research be undertaken in this area.

Finally, we point to two heretofore under-utilized techniques for studying NIS zooplankton ecology, namely molecular genetic techniques and paleo-ecological techniques. Genetics has been applied far more commonly to adult, benthic populations (e.g. Geller et al., 1994, 1997), and only fairly recently to holoplanktonic populations in freshwater (e.g. Havel & Hebert, 1993; Lee, 1999, Lee, 2000; Lee & Bell, 1999). The longer-term, historical context of invasions in aquatic environments has recently been addressed by Hairston et al. (1999) and Duffy et al. (2000) using paleo-ecological techniques to explore dynamics of past introductions (although it should be noted that this approach works only for organisms whose body parts are readily preserved). Both of these techniques promise to provide important new insights.

Two case studies

First a brief comment on nomenclature: as will be evidenced below, we feel justified in using the term 'invasive', rather than 'non-indigenous', to describe *Pseudodiaptomus inopinus* in Pacific Northwest estuaries and *Tortanus dextrilobatus* in San Francisco Bay, as these copepods are both novel *and* they have had a great impact on their new environment (*sensu* Davis & Thompson, 2000).

Case study I: Pseudodiaptomus inopinus in Pacific Northwest estuaries

The Asian copepod *Pseudodiaptomus inopinus* was first reported from the Northeast Pacific by Cordell et al. (1992), who documented its introduction to and establishment in the Columbia River estuary. Cordell & Morrison (1996) subsequently reported that this species had invaded at least seven other estuaries in the Pacific Northwest. Here we report preliminary results of a multi-year study to determine: (i) the broad-scale geographic distribution of *P. inopinus* in the estuaries of the Pacific Northwest United States and Western Canada; (ii) the vertical distribution and migration behavior of *P. inopinus*, and (iii) which predators are consuming *P. inopinus* in its newly invaded habitat, and whether or not they prefer *P. inopinus* to native copepods.

Materials and methods

Broad-scale geographic distribution of *Pseudodiaptomus inopinus* was determined on a survey in autumn of 1996, in which 21 river estuaries were sampled, ranging from southern British Columbia to central California. These river estuaries, from north to south, were the Squamish, Nanaimo, Fraser, San Juan, Snohomish, Dungeness, Duwamish, Puyallup, Willapa, Naselle, Tillamook, Yaquina, Siuslaw, Coos, Coquille, Rogue, Chetco, Klamath, Eel, Noyo, and Russian. Zooplankton were collected during the day by vertical hauls of a 0.5 m diameter, 250 μm mesh plankton net (chosen to target copepodid stages of *P. inopinus*), hauled from near bottom to the surface. In each river, up to 5 mid-channel samples were collected at bottom salinities of 0, 1.5, 3, 5, and 9–15 psu (i.e. as far downstream as practical), as measured with a YSI model 33 salinity probe. In rivers with shorter transition zones, fewer than five, but never less than two, samples were collected. Zooplankton samples were fixed in formaldehyde (5–10%) and returned to the laboratory for microscopic identification and enumeration of organisms.

The Chehalis River estuary in western Washington, U.S.A., a known site of invasion of *Pseudodiaptomus inopinus* (Cordell & Morrison, 1996), was chosen for more intensive studies during 1998–2000. To investigate vertical distribution and possible migration of *P. inopinus* in the Chehalis River estuary, we sampled zooplankton on 28–30 July, 1999 with a submersible pump system (3.6 cm diameter hose; 4.0 l s^{-1} pump rate), in which water (mean sample volume = 1150 l) was passed through a 73 μm mesh (chosen to ensure sampling of all copepodid stage*s*). Preliminary sampling indicated that *P. inopinus* was abundant around the 6 psu bottom salinity, which moved up/downstream with the tides. Because we wished to repeatedly sample the same 'population' of zooplankton over time (i.e. those in and around the 6 psu bottom salinity), the vessel was allowed to drift with the tides, with only modest repositioning necessary to stay in the main channel. This up/downstream movement, however, resulted in a variable bottom depth (range from 3.5 to 12.8 m). We therefore had to sample at relative, rather than absolute depths, which we chose as 0.25 m above the bottom, 0.25 m from the surface, and a depth equidistant between the bottom and surface. Salinity and temperature were measured at each depth with a YSI Model 33 salinity/conductivity/temperature meter, the probe of which was attached to the pump intake hose. Zooplankton samples were collected every 2 h over a 55-h period (0600 on 28 July, 1999 to 1500 on 30 July, 1999). Samples were fixed in formaldehyde (5–10%) and returned to the laboratory for microscopic identification and enumeration of organisms. All *P. inopinus* copepodids retained on a 230 μm sieve (CI–CVI) were counted, although only data on adult females are reported here. A weighted mean depth was calculated for each vertical series of samples (Bollens & Frost, 1989), in which we assigned a value of 3 to the near-bottom sample, 2 to the mid-water sample and 1 to the surface.

Additional field sampling for diet studies of both invertebrate and vertebrate predators were made in the Chehalis River from July, 1998 to November, 1999. Fishes were collected at a station near the upstream summer salinity intrusion extreme by daytime deployment of a 30-m beach seine set by a small boat and pulled in to shore. Invertebrate predators were sampled by daytime deployment of an epibenthic sled (0.25 $\times$ 0.75 m opening, 720 μm mesh net) in the central channel of the river (mean depth ca. 5 m). Predators were preserved in formaldehyde, and subsequently taken back to the laboratory for identification and microscopic analysis of stomach contents.

Predation experiments were undertaken during August 3–10, 1999, and May 9–16, 2000, using predators and prey collected from the Chehalis River. Vertebrate predators were collected by daytime beach seining (see above) or fyke net (0.5 cm mesh; 15 m wings). Fishes collected included juvenile starry flounder, *Platichthys stellatus* (4–7 cm), shiner perch, *Hyperprosopon aggregata* (2.5–4 cm), several different gobies (family Gobiidae), juvenile *Oncorhynchus tshawytscha* (5 cm), and young-of-the-year three-spined sticklebacks, *Gasterosteus aculeatus* (2–3 cm). Invertebrate predators, including the shrimp *Crangon franciscorum* and the mysid *Neomysis mercedis*, were collected with an epibenthic sled (720 μm mesh) in the central channel of the river. Zooplankton prey, including the invasive copepod *Pseudodiaptomus inopinus* and the 'native' copepod *Acartia* (*Acartiura*) sp., were collected using either a 0.5 m, 153 μm mesh plankton net or a epibenthic sled with a 100 μm mesh net. (Although we can not be certain that the specimens of *Acartia* (*Acartiura*) sp. we collected were native, and not introduced, the range of this copepod subgenus includes the northeast Pacific (Bradford, 1976 and references therein**)**, and thus we think it highly likely that the specimens collected in our study were native.) Predators and prey were brought back to the lab in Westport, WA and transferred into aerated, room temperature aquaria. Most specimens were collected at approximately 6 psu, but others were gradually acclimated to changing salinity over the course of 2 days, until they reached 6 psu. After acclimation, all predators used in the experiments appeared healthy and normal. All predators were starved 24 h before the experiments.

We used an experimental protocol modified from that of Bollens & Frost (1991), Bollens et al. (1993), and Avent et al. (2001). In brief, four 38-l glass aquaria were wrapped on all sides and bottom with black plastic to eliminate light from those directions and prevent the fish from becoming frightened before and during the experiments. The aquaria were filled with 35 l of 6 psu water (collected from the estuary) and placed outdoors without aeration. For each experiment, 50 adult female *Pseudodiaptomus inopinus* and 50 adult female *Acartia* sp. were sorted and placed into a 'copepod' aquarium. Immediately prior to the start of each fish predation experiment, two starved fish were placed in an aquarium containing a mixture of live zooplankton, and allowed to initiate feeding, at which point they were immediately removed and placed into the 'copepod' aquarium (our previous experience – see references above – has shown this inducement to feeding to be necessary). After approximately 50 strikes were observed, the fish were removed from the aquarium, rinsed and put into a bath of MS-222 solution and then fixed with 5% buffered Formalin. In the case of experiments with invertebrate predators, each experiment was run for 24 h. At the end of each experiment, remaining copepods were rinsed from the aquarium and counted; missing copepods were assumed to have been eaten by the predators. Binomial statistical tests (numbers of each of the two copepod species eaten) were performed using SPSS for Windows, Ver. 10.0.5.

Results and discussion

Pseudodiaptomus inopinus were found in a total of 11 of 31 river estuaries sampled during two broad-scale surveys of Autumn 1991 and 1992 (Cordell & Morrison, 1996) and our survey of Autumn 1996 (Fig. 1). The occurrence of *P. inopinus* was limited to Oregon and southern Washington, and was absent from northern California and southern British Columbia. This probably represents little or no increase in range from that of 1991/1992, as reported by Cordell & Morrison (1996). Specifically, our 1996 sampling showed *P. inopinus* to be present in the Naselle, Siuslaw, and Coquille rivers**,** in addition to the previous occurrences observed by Cordell & Morrison (1996). This copepod is thought to have been introduced from Asia via ballast water between 1980 and 1990 (Cordell et al., 1992), and to have rapidly expanded its range shortly thereafter (Cordell & Morrison, 1996). Based on our more recent observations, however, the copepod's range extension seems to have dramatically slowed or stopped all together. Our data from the seven estuaries in which *P. inopinus* was present in 1996

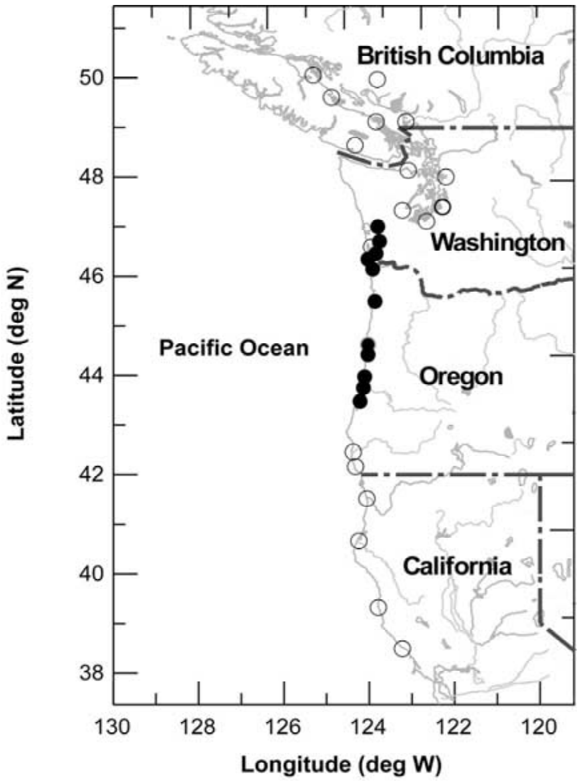

Figure 1. Distribution of the Asian copepod *Pseudodiaptomus inopinus* in river estuaries in the Pacific Northwest, United States and British Columbia, Canada (open circles = absent; closed circles = present). This is a composite map based on two broad-scale surveys: Autumn 1991 and 1992, as reported by Cordell & Morrison (1996), and Autumn 1996 (this study). Rivers from North to South (bold = *P. inopinus* present) are Campbell, Courtenay, Squamish, Nanaimo, Fraser, San Juan, Skagit, Snohomish, Dungeness, Duwamish, Puyallup, Nisqually, Skokomish, **Chehalis**, **Willapa**, Palix, **Naselle**, **Columbia**, **Youngs**, **Tillamook**, **Yaquina**, **Siuslaw**, **Umpqua**, **Coos**, **Coquille**, Rogue, Chetco, Klamath, Eel, Noyo, and Russian.

(Fig. 2; more recent samples are still being analyzed) show this copepod to be confined predominantly to the lower salinity (< 10 psu) reaches of estuaries, with peak abundances occurring in the 2–5 psu range.

Results from our feeding selectivity experiments indicate that *P. inopinus* is consumed by a wide range of predators about as readily as is the native and similarly sized copepod *Acartia* (*Acartiura*) sp. (Table 3). Exceptions to this are one experiment with shiner perch and one with starry flounder, each showing a feeding preference for *P. inopinus*; while in one other experiment, mysids showed a preference for *Acartia* (*Acartiura*) sp. These results imply that the recently introduced copepod is an acceptable prey type for native predators. Our field studies of pred-

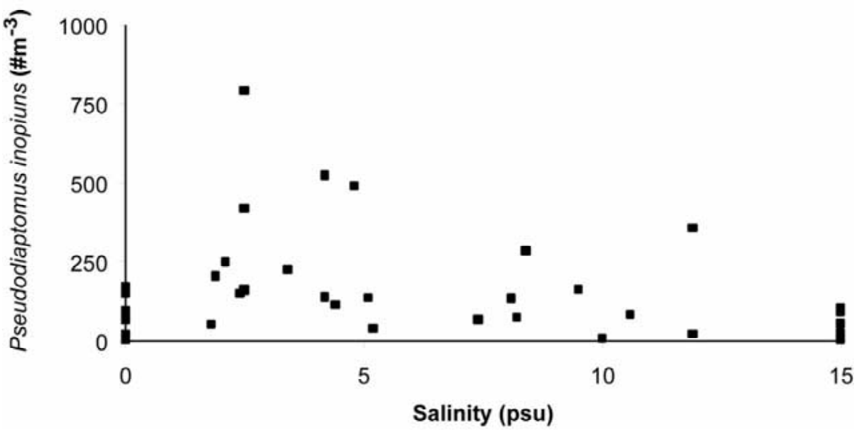

Figure 2. Abundance of the copepod *Pseudodiaptomus inopinus* in relation to salinity in seven Pacific Northwest river estuaries (Chehalis, Willapa, Columbia, Youngs, Yaquina, Umpqua, and Coos) sampled in Autumn, 1996.

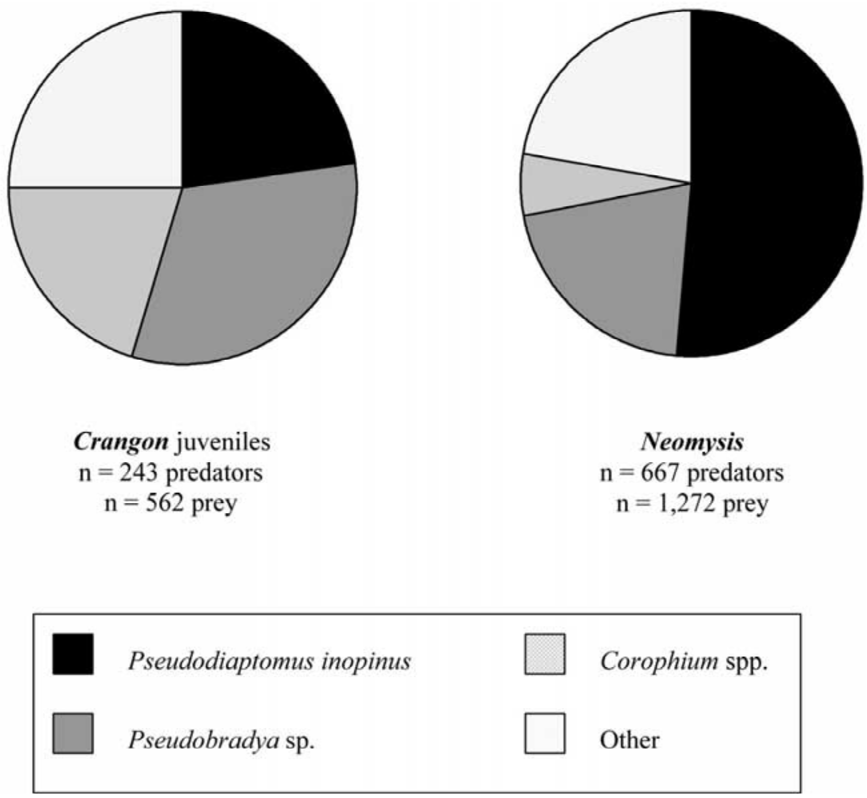

Figure 3. Diet (percent by number) of the invertebrate predators, *Neomysis mercedis* and *Crangon franciscorum* juveniles, collected from the Chehalis River, WA, between July, 1998 and November, 1999.

ator diets corroborate this, and suggest that *P. inopinus* may be a dominant component of the diet of the invertebrate predators *Neomysis mercedis* and *Crangon franciscorum* (Fig. 3).

As with any planktonic animal, the extent to which *P. inopinus* comes into contact with and is consumed by different predator types will depend in part on its vertical distribution and migration. We have found *P. inopinus* in the Chehalis River to be a strong diel vertical migrator, being associated very closely with the bottom during the day, and leaving the bottom and entering the water column only at night (Fig. 4).

Table 3. Results of feeding selectivity experiments in which various fish and invertebrate predators were simultaneously offered adult females of the invasive copepod *Pseudodiaptomus inopinus* and the native copepod *Acartia* (*Acartiura*) sp. as prey

Predator	Prey		Binomial Test
	Pseudodiaptomas inopinus	*Acartia* (*Acariura*) sp.	*p*-value
Shiner Perch	22	9	<0.05*
Shiner Perch	11	9	>0.05
Shiner Perch	29	31	>0.05
Threespine Stickleback	44	34	>0.05
Threespine Stickleback	28	19	>0.05
Gobidae	11	10	>0.05
Starry Flounder	29	12	<0.05*
Starry Flounder	16	20	>0.05
Crangon franciscorum	6	11	>0.05
Crangon franciscorum	1	2	>0.05
Neomysis mercedis	8	11	>0.05
Neomysis mercedis	6	22	<0.005**

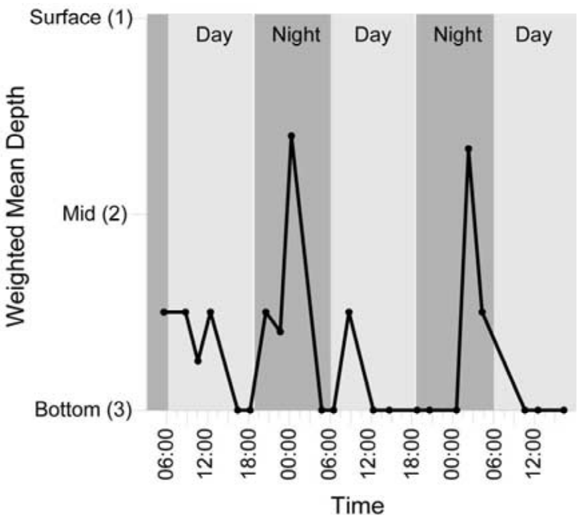

Figure 4. Vertical distribution of adult female *Pseudodiaptomus inopinus* in the Chehalis River, WA, July 28–30, 1999. Samples were collected every 2 h over 55 h (note day and night designated by shading), and weighted mean depth was calculated as the mean of three samples collected at 0.25 m below the surface, at mid-depth, and at 0.25 m above the bottom.

This strong association with the bottom by the genus *Pseudodiaptomus*, especially during the daytime, has been reported before, leading to its being described as a 'demersal' copepod (e.g. Fancett & Kimmerer, 1985). Such a distribution would result in substantial spatial overlap with *Neomysis mercedis* and *Crangon franciscorum*, both of which are epibenthic (demersal) during the daytime and migrate into the water column at night (Bollens et al., unpublished data).

Vertical distribution will affect contact and predation rates with fishes as well. We did not, however, find many fishes in the Chehalis River to contain *P. inopinus* in their diet, although these results may be biased by the fact that our fish sampling was conducted in the shoals (where beach seining was possible), whereas *P. inopinus* is more common in the deeper channels of the river. Yet there may be an indirect predatory impact of the fishes, particularly the demersal species. *Neomysis mercedis*, which is perhaps the dominant predator of *P. inopinus* (Fig. 3), is itself a major component of the diet of several demersal or bottom feeding fishes (e.g. prickly sculpin and starry flounder), but is less prevalent or absent from the diet of the pelagic zooplanktivores (e.g. surf smelt) in the Chehalis River (Fig. 5). However, the magnitude of predation mortality inflicted on *P. inopinus* at the population level, by either invertebrate or vertebrate predators, remains to be quantified.

In terms of community impacts, our data show dramatic differences in the total mesozooplankton community composition in those rivers without *P. inopinus* (top of Fig. 6) *versus* those river estuaries with *P. inopinus* (bottom of Fig. 6). In short, when *P. inopinus* occurred, other estuarine copepods were largely absent (*Eurytemora affinis*) or reduced in relative abundance (*Acartia* spp.). The result was that *P. inopinus* totally dominated the mesozooplankton assemblage in the low salinity zones of these estuaries. Whether this is due to competition for limiting resources (e.g. phytoplankton food), predation, or some other coincidental factor(s) remains to be determined.

These observations on the distribution, behavior and some trophic interactions of *P. inopinus* lead us to speculate that the invasion of this Asian copepod may have led to dramatic food web and even ecosystem changes in these estuaries. Exactly how the flow of energy and material might have changed as a result of *P. inopinus* replacing or reducing preexisting estuarine zooplankton populations remains to be determined, and we point to the relative magnitudes of benthic energy flow (e.g. via mysids and benthic feeding fishes) *versus* pelagic energy flow (e.g. via fully planktonic copepods and zooplanktivorous fishes) as an area particularly ripe for future study. Such changes in energy flow could have important implications for the production of commercially and recreationally important salmonids, the juvenile stages of which feed in the lower reaches of river estuaries during their out-migration to the sea. These ideas should be tested either experimentally, through large-

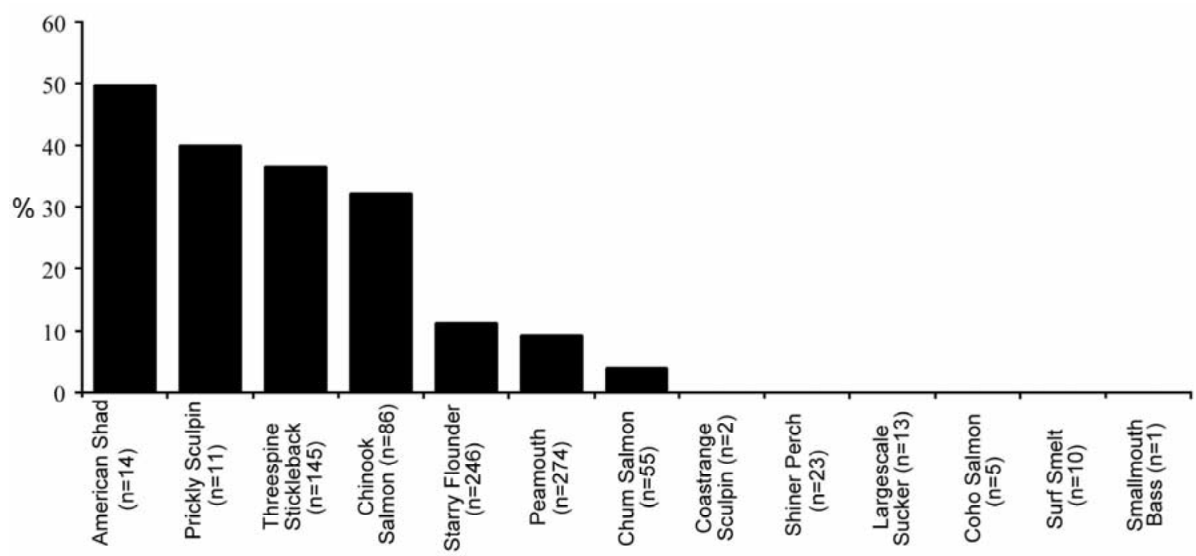

Figure 5. Percent contribution (by weight) of *Neomysis mercedis* in the diets of several species of fish collected in the Chehalis River, WA, between July 1998 and November 1999. *n* = number of fish stomachs examined.

scale manipulations (e.g. enclosures or limnocorrals), or more realistically, by a combination of simulation modeling and comparative field studies of food web dynamics in both invaded (*P. inopinus* present) *versus* non-invaded (*P. inopinus* absent) river estuaries.

Case study 2: Tortanus dextrilobatus in San Francisco Bay Estuary

The Asian copepod *Tortanus dextrilobatus* was first observed in the San Francisco Bay Estuary by Orsi (1995), and subsequently by Bollens et al. (1999), Kimmerer et al. (1999), Avent et al. (2000), and Purkerson et al. (Submitted). Yet nothing about this copepod's general biology or ecology in this new habitat has appeared in the literature. Here we report on results of a combined field and laboratory study with the objectives of determining: (i) the distribution and abundance of *T. dextrilobatus* relative to other introduced and native zooplankton in the San Francisco Bay Estuary; and (ii) the feeding selectivity of the carnivorous *T. dextrilobatus* on NIS *versus* native copepods in its newly invaded habitat.

Materials and methods

Field collections were made aboard the United States Geological Survey's Research Vessel *Polaris*. Zooplankton samples were collected bi-monthly for 3 years (beginning January, 1997 through November, 1999) at six stations spanning the various subembayments of San Francisco Bay: two in San Pablo Bay (stations 12 and 13), two in Central Bay (17 and 21) and two in South Bay (stations 24 and 30) (Fig. 7). At each station a 0.50 m diameter, 73 μm mesh plankton net (chosen to sample a broad size range of zooplankton) was gently hauled (10 m min^{-1}) vertically from near bottom to the surface, and the contents rinsed into a jar and fixed with 5–10% formaldehyde-seawater solution. Samples were returned to the laboratory for microscopic identification and enumeration of various size fractions of the zooplankton. For the purposes of this paper, we report only on the $>$500 μm size fraction.

We also ran several feeding selectivity experiments, using *T. dextrilobatus* as predators and both native and non-indigenous copepods as prey. Live zooplankton were collected in the Carquinez Strait region of San Francisco Bay using oblique and vertical hauls of a 153 μm mesh, 0.5 m diameter plankton net (chosen to target copepodid stages of potential copepod prey), transported to the laboratory (Romberg Tiburon Center for Environmental Studies), and stored in a temperature controlled room set to that of the ambient water column at the collection site (10–15 °C). Two adult female *T. dextrilobatus* were subsequently sorted and placed into each 1-l jar containing filtered seawater of the same salinity as the collection site (10–12 psu). Predators were starved for at least 2 h prior to the onset of each experiment. Nine individuals of each prey type were then sorted from the bulk, 'live'

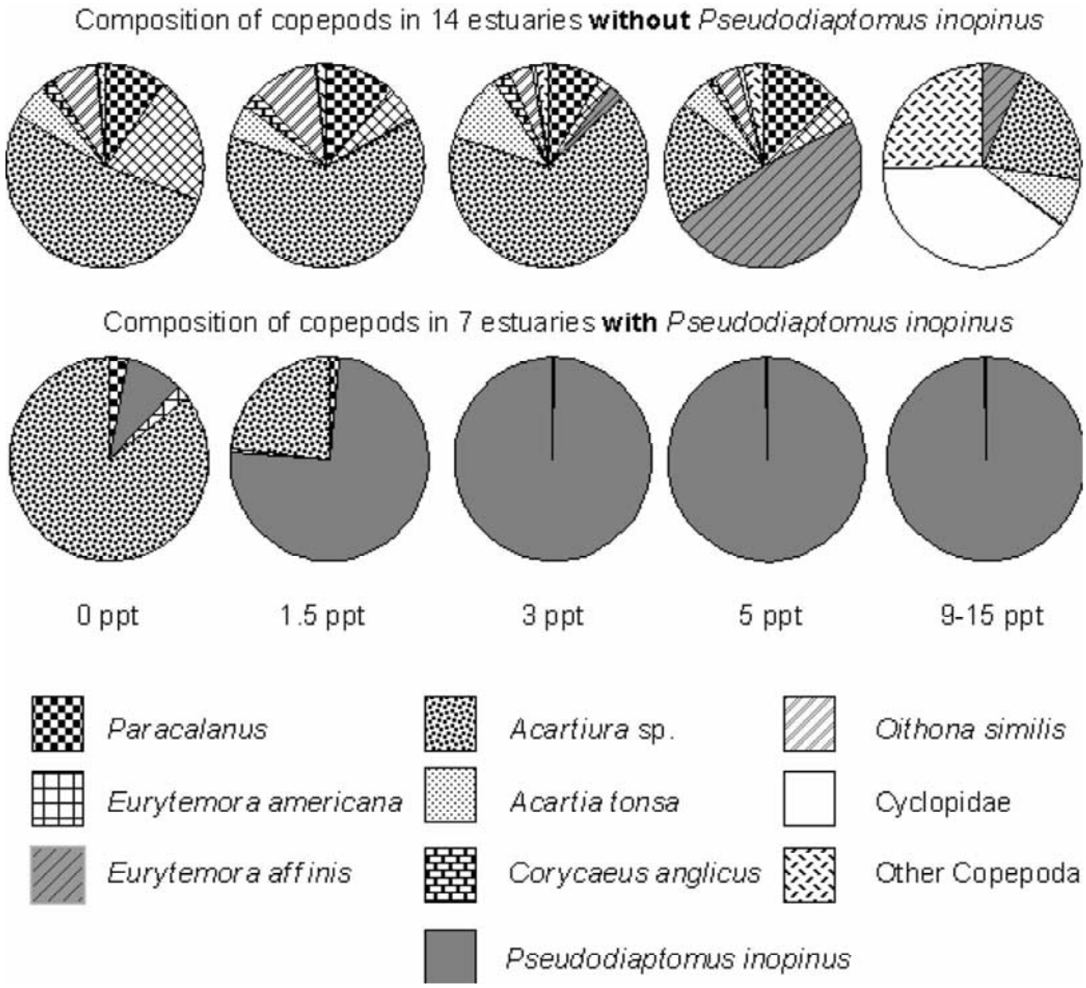

Figure 6. Percent numerical composition of copepods across the 0–10 psu salinity gradient, averaged among 14 west coast estuaries in which *Pseudodiaptomus inopinus* is absent (top), and 7 west coast estuaries in which *P. inopinus* is present (bottom). Data based on the 21 river estuaries sampled in 1990 and 1991 (other data not yet available).

zooplankton sample and transferred into the 1-l jars containing *T. dextrilobatus*. Each treatment consisted of four replicate jars and one control (no predators) jar. Jars were placed on a rotating plankton wheel (1 rpm) in a dark, temperature controlled room. After 24 h, samples were filtered through a 25 μm sieve, fixed with formaldehyde (5–10% solution), and later counted under a dissecting microscope. Prey organisms found to be 'missing' (i.e. number in control jar minus number in treatment jar) were assumed eaten by the predator.

Results and discussion

Our field sampling shows *T. dextrilobatus* to be both widespread and, at times, extremely abundant in San Francisco Bay (Fig. 8). *Tortanus dextrilobatus* is generally present in San Pablo Bay and South Bay, and less often in Central Bay, with peak abundances occurring in late spring and summer. The observation that this copepod reaches densities of $>10^3$ m^{-3}is particularly noteworthy in that it is thought to be an obligate carnivore as an adult.

Our feeding selection experiments showed that adult female *T. dextrilobatus* did not consistently distinguish between native and non-indigenous prey: in one experiment it preferred the native *Acartia* (*Acartiura*) sp. to the NIS copepod *Oithona davisae* (24 vs. 9, p <0.05, binomial test), while in another experiment there was no difference between its selection of *Acartia* (*Acartiura*) sp. and the NIS copepod *Pseudodiaptomus forbesi* (15 vs. 21, $p > 0.05$, binomial test).

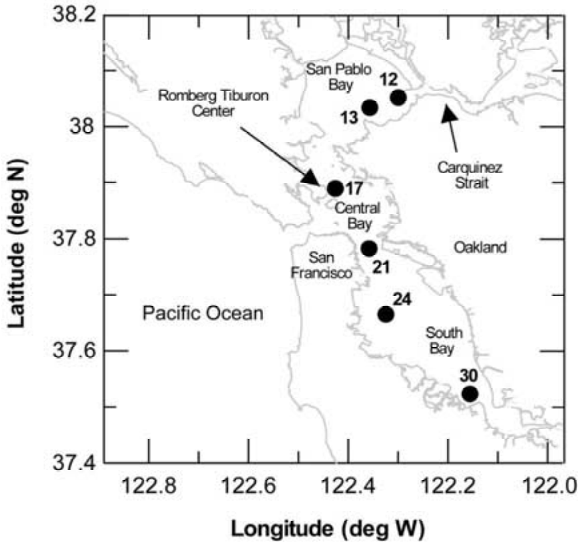

Figure 7. Map of San Francisco Bay, including South Bay, Central Bay, and San Pablo Bay. Numbers refer to the United States Geological Survey stations that were sampled for zooplankton abundance and composition.

Prey size seems to be a stronger discriminator, with the larger copepods being preferred.

In terms of community composition, *T. dextrilobatus* is now amongst the numerical dominants in the >500 μm size class of zooplankton in San Francisco Bay (Fig. 9). Given the relatively large size of this organism (ca. 3 mm for an adult female) compared to most other abundant zooplankters, this dominance is even greater if calculated in terms of biomass rather than numerical abundance (e.g. Purkerson et al., submitted). Thus the impacts of this copepod at the community level are likely to be great. This is hard to discern from the field data alone, however, because of the contemporaneous introduction of several other copepods (e.g. *Pseudodiaptomus marinus* and *Limnoithona tetraspina*) since the last comprehensive survey of zooplankton in San Francisco Bay was undertaken in 1980 (Ambler et al., 1985). Table 4 shows the dramatic change in the overall composition of the zooplankton community between 1980 and 1997, especially the prevalence of non-indigenous species in 1997. Evaluating community level impacts will require some combination of comparative field studies, manipulative experiments, and simulation modeling. Only in this way will we be able to unambiguously determine the degree to which changes such as those seen in San Francisco Bay are due to non-indigenous species *versus* other causes. Testing for possible community and ecosystem level impacts of NIS zooplankton would appear to be particularly pressing in the case of San Francisco Bay, where the rate of new introductions seems to be increasing (Cohen & Carlton, 1998), thus raising the specter that new invasions may be facilitated by earlier invaders (i.e. 'invasional meltdown', sensu Simberloff & Von Holle, 1999).

Table 4. Frequency of occurrence (% of samples) of various taxa of zooplankton, contrasting 1980 with 1997 (Jan.–May, and June–Dec.). Four copepods in bold are non-indigenous species. Note that three of these, *Tortanus dextrilobatus*, *Pseudodiaptomus marinus*, and *Limnoithona tetraspina*, have all been introduced since 1980, and are now extremely common. Correlation coefficients, τ, indicate no significant correlation between rank orders of occurrence, i.e. these communities are significantly different between 1980 and 1997

	Frequency of Occurrence (%)			
	Jan–May		June–Dec	
	1980	1997	1980	1997
Copepods				
Acartia (Acartiura) spp.	81	100	38	89
Acartia californiensis	1	11	51	44
Paracalanus sp.	12	78	17	67
Eurytemora affinis	26	44	23	0
Sinocalanus doerri	13	33	18	0
Oithona davisae	7	100	31	100
Oithona similis	3	22	6	56
Corycaeus sp.	7	22	7	44
Microsetella spp.	6	33	6	44
Tortanus dextrilobatus	0	67	0	78
Pseudodiaptomus marinus	0	33	0	89
Limnoithona tetraspina	0	100	0	67
Cladocerans	10	33	7	0
Meroplankton				
Cirripedia	43	0	55	33
Spionidae	52	33	66	22
	τ = 0.031, p <0.9		τ = −0.284, p <0.2	

Summary and conclusions

Our literature search on invasive or non-indigenous species (NIS) of zooplankton yielded a large body of work, measured as both numbers of papers published and number of taxa identified, which were concerned with zoogeographic distribution or range extensions. The basic biology and ecology of NIS zooplankton, on the other hand, have been less well studied: a modest number of papers have been published on dispersal, physiology, feeding or community interactions of freshwater zooplankton NIS, but vastly fewer on marine and estuarine forms, despite a larger number of taxa being identified from these latter habitats. For all

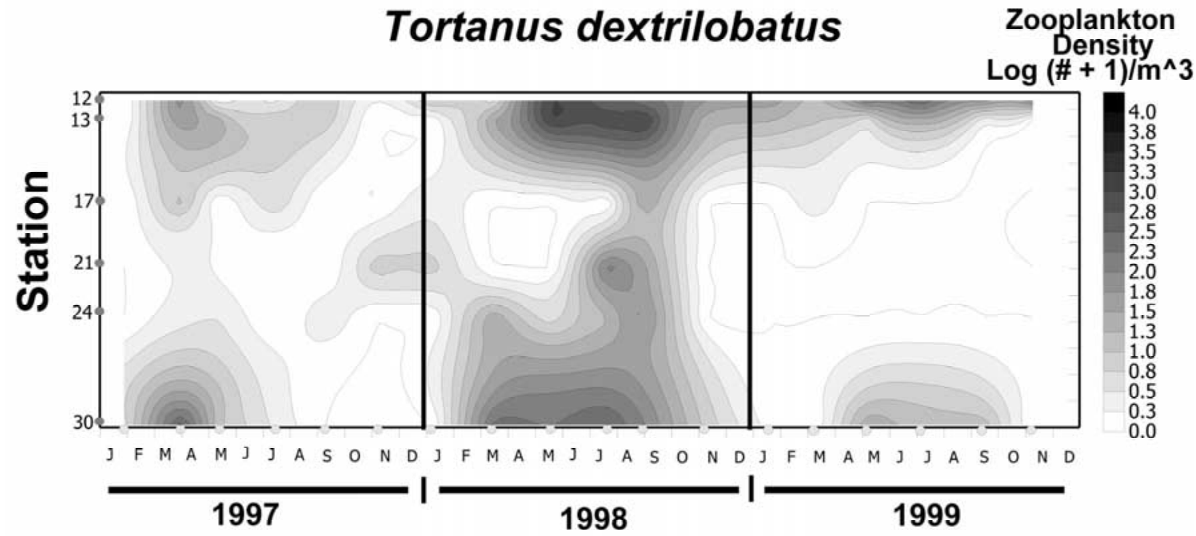

Figure 8. Abundance of *Tortanus dextrilobatus* (all copepodid stages combined) in San Francisco Bay, 1997–1999. Circles on x-axis are dates of sampling; circles on y-axis are locations of sampling.

habitat types, behavior and ecosystem dynamics have been particularly poorly studied, especially for meroplanktonic (*versus* holoplanktonic) organisms. The paucity of studies documenting community or ecosystem level impacts of NIS zooplankton may be due to the limited number of such impacts that actually occur in nature, or alternatively, to a lack of research on such possible impacts. We suspect the latter, and recommend that future work be directed at these questions (see recommendations for future research below).

By presenting our two case studies of invasive copepods in the Northeast Pacific Ocean, we have tried to go beyond the initial (but necessary) question of distribution and range extension, and to elucidate some of the basic biology and ecology of these invaders in their new habitats. The Asian copepod *Pseudodiaptomus inopinus*, first observed in the Northeast Pacific in 1990 (Cordell et al., 1992), is now broadly distributed throughout Washington and Oregon coastal river estuaries, and can at times and places (e.g. 2–6 psu) be very abundant (800 m^{-3}). Feeding experiments indicate that native vertebrate and invertebrate predators in the Chehalis River do not show striking preference for *P. inopinus versus* native copepods. Nevertheless, *P. inopinus* is an important, perhaps even dominant component of the diet of bentho-pelagic invertebrate predators (e.g. mysids and *Crangon* shrimp), and share a vertical distribution and migration pattern (on the bottom during the day, and up in the water column at night) with these predators. We hypothesize that this may have led to changes in the structure and function of the food webs in these estuarine ecosystems, with possible changes in the relative magnitudes of energy flow in benthic (i.e. bottom-feeding invertebrates and fishes) *versus* pelagic (i.e. truly planktonic copepods and zooplanktivorous fishes) food webs, although this remains to be tested.

The Asian copepod *T. dextrilobatus* was first observed in San Francisco Bay in 1992 (Orsi, 1995), and is now broadly distributed there, at times reaching extremely high abundances ($>10^3$ m^{-3}), which is especially noteworthy for a carnivore. This large, predatory copepod seems to select larger, native copepods (*Acartiura* sp.) over smaller, NIS copepods (*Oithona davisae). Tortanus dextrilobatus* is one of several NIS copepods that have resulted in a dramatic change in the composition of the zooplankton community in San Francisco Bay over the last 20 years, which raises the question of whether successfully established NIS may facilitate invasions by future NIS. The implications of this for planktonic food webs and ecosystem productivity are unknown.

We have several recommendations for future research. With regard to occurrences, certainly we need to keep looking for new NIS zooplankton introductions. Thus we are encouraged by the growing number of zooplankton monitoring programs that are being implemented by various state, federal and private institutions. However, greater attention needs to be paid to smaller forms (i.e. microzooplankton <200 μm),

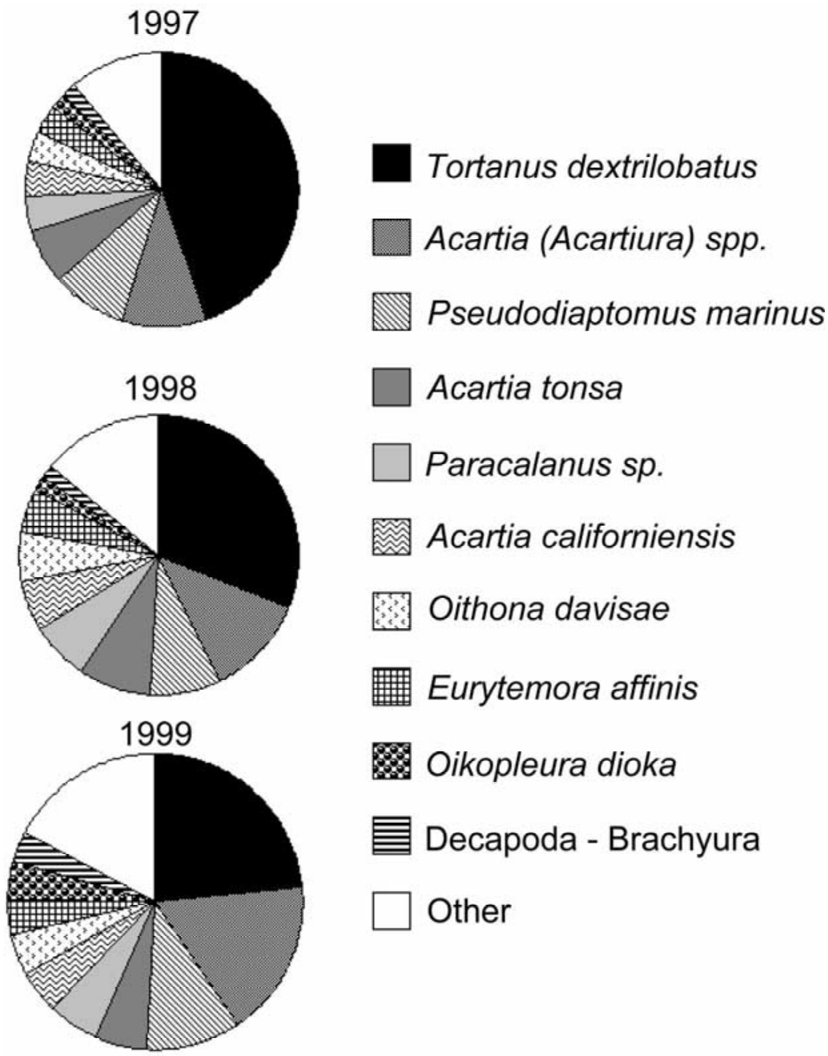

Figure 9. Numerical composition of the zooplankton community (> 500 μm) in San Francisco Bay, 1997–1999. Note the prevalence of *Tortanus dextrilobatus* in 1998 and 1999.

which have to date been largely ignored in studies of NIS. As for the causes of zooplankton invasions, a wide variety of vectors and mechanisms of dispersal are currently under study (e.g. ballast water transport, aquaculture, recreational boating, etc.), which needs to be continued and expanded. In particular we point to the need for population genetic studies. A related topic, namely, the ability of NIS zooplankton to persist in new habitats (e.g. their demographics and population dynamics, and the processes affecting these rates), also needs to be more extensively studied. Likewise for ecosystem resilience and resistance to invasions, e.g. why are some estuaries like Puget Sound apparently more resistant to invasion than some other estuaries such as San Francisco Bay?

With respect to consequences or ecological impacts of NIS zooplankton, the results of both our literature review and our two case studies suggest that more research on the community and ecosystem levels is needed. Specifically, we recommend that a combination of comparative field studies, simulation modeling, and manipulative field experiments (e.g. using well-controlled and replicated mesocosms or limnocorrals) be employed. Only in this way will we be able to discern whether NIS zooplankton are widespread but relatively harmless, or alternatively, that they are a serious and growing threat to the structure and function of native ecosystems.

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