Leonardo Kenji Miyashita

Biodiversity, distribution, feeding and trophic role of marine mysids (Crustacea, Peracarida, Mysida)

Thesis submitted to the Oceanographic Institute of the University of São Paulo, as part of the requirements to obtain the title of Doctor of Science, Oceanography Program, Biological Oceanography area.

Supervisor: Prof. Dr. Danilo L. Calliari

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Summary

Index of figures v

Index of tables vii

Abstract viii

Resumo x

Chapter 1. Introduction 1

- 1.1. References 4

Chapter 2. Revision of mysids (Crustacea: Peracarida: Mysida) zoogeographical distribution in the Southwest Atlantic (0° to 40°S) 11

- Abstract 11
- 2.1. Introduction 11
- 2.2. Material and methods 12
- 2.3. Results 13
- 2.4. Discussion 30
- 2.5. References 32

Chapter 3. Distribution, salinity tolerance and production of dominant mysids from the Cananeia-Iguape Coastal System, southeast Brazil 41

- Abstract 41
- 3.1. Introduction 41
- 3.2. Methods 43
  - 3.2.1. Study site 43
  - 3.2.2. Sample collection and analyses 43
  - 3.2.3. Salinity tolerance 46
- 3.3. Results 47
  - 3.3.1. Environmental variables 47
  - 3.3.2. Zooplankton 47
  - 3.3.3. Mysids 48
  - 3.3.4. Salinity tolerance 50

3.4. Discussion 50

3.5. Conclusions 57

3.6. References 57

Chapter 4. Species-specific and combined feeding rates and selectivity of dominant mysids from a subtropical estuary, Brazil 62

Abstract 62

4.1. Introduction 62

4.2. Materials and Methods 64

4.2.1. Study site 64

4.2.2. Mysid sampling 64

4.2.3. Feeding selectivity 64

4.2.4. Functional response 66

4.2.5. Intraguild predation 67

4.3. Results 67

4.3.1. Feeding rates and selectivity 67

4.3.2. Functional response 69

4.3.3. Intraguild predation 70

4.4. Discussion 70

4.4.1. Feeding rates and selectivity 70

4.4.2. Functional response 72

4.4.3. Mysid species interaction 73

4.5. Conclusions 75

4.6. References 76

Chapter 5. Effects of predator species number and spatial heterogeneity on prey suppression 79

5.1. Introduction 79

5.2. Methods 80

5.2.1. Experimental design 80

5.3. Results 82

5.3.1. First experiment.. 82

5.3.2. Second experiment 83

5.4. Discussion 84

5.5. References 87

Chapter 6. Concluding remarks 90

6.1. References 91

Index of figures

Fig. 2.1. Map of Southwest Atlantic. 13

Fig. 2.2. Cumulative number of currently valid species described (solid circle) and recorded (open circle) along the years in the Southwest Atlantic. 14

Fig. 3.1. Sampling stations in the Cananeia estuary, southeast Brazil. 44

Fig. 3.2. Rainfall data, and mean water temperature and salinity in the Cananeia estuary, between November 2011 and January 2013. Error bars represent the standard deviation. 48

Fig. 3.3. Abundance of the three main mysid species at five stations in the Cananeia estuary, from January 2012 through January 2013. 49

Fig. 3.4. Principal component analysis for abundance of the three main mysid species, and temperature, salinity, rainfall, and zooplankton abundance. 50

Fig. 3.5. Relative abundance and biomass temporal distribution of the different stages of *Metamysidopsis elongata atlantica*, from January 2012 through January 2013. 51

Fig. 3.6. Relationship between body length (BL) and brood size (BS) for *Metamysidopsis elongata atlantica* (solid line) and *Mysidopsis coelhoi* (dashed line). 51

Fig. 3.7. Relationship between body length (BL, mm) and dry weight (DW, mg) for *Metamysidopsis elongata atlantica*. 53

Fig. 3.8. Biomass and production of *Metamysidopsis elongata atlantica* and Copepoda in the Cananeia estuary, from January 2012 through January 2013. 54

Fig. 3.9. *Metamysidopsis elongata atlantica*, *Mysidopsis coelhoi* and *Chlamydopleon dissimile* surviving rate in the salinity tolerance experiment. 54

Fig. 4.1. Ingestion rate of each mysid species and combination of species, and biomass of the dominant zooplankton offered as food. Error bars represent the standard deviation. 68

Fig. 4.2. Clearance rate of each mysid species and combination of species, and abundance of the dominant zooplankton offered as food. Error bars represent the standard deviation. 69

Fig. 4.3. Zooplankton abundance, and clearance rate of each mysid species and combination of species separated by prey size class. Error bars represent the standard deviation. 72

Fig. 4.4. Zooplankton biomass, and ingestion rate of each mysid species and combination of species separated by prey size class. Error bars represent the standard deviation. 73

Fig. 4.5. Functional response of each mysid species and combination of species. Dotted (clearance rates) and continuous lines (ingestion rates) represent the model fitted to the respective data (see Table 4.4). 74

Fig. 5.1. Mysid final mean abundance in each predator treatment of the first mesocosm experiment. Error bars represent the standard deviation. 83

Fig. 5.2. Mean proportion of predator surviving at the end of the first experiment in each predator treatment. 83

Fig. 5.3. Mysid final mean abundance in each predator treatment of the second mesocosm experiment. Error bars represent the standard deviation. Ss: sand shrimp; Gs: grass shrimp; Bc: blue crab; St: structure (*Gracilaria* + oyster shells). 84

Fig. 5.4. Mean proportion of predator surviving at the end of the second experiment in each predator treatment. St: structure (*Gracilaria* + oyster shells). 85

Index of tables

Table 2.1. List of species recorded in the Southwest Atlantic with information on their body length, inshore/offshore and geographic distribution, and temperature (T) and salinity (S) range of occurrence. 15

Table 3.1. Reproductive parameters of *Metamysidopsis elongata atlantica* and *Mysidopsis coelhoi*: range and mean ± standard deviation of gravid female body length and brood size, and mean length of embryos separated by category. 52

Table 3.2. Annual production (mg C m^{-3} $year^{-1}$) of mysids from different marine environments. 52

Table 4.1. Design of the feeding selectivity experiments: species composition, number of organisms per bottle, mysid mean body length (± SD), salinity, and date of experiments. 66

Table 4.2. Electivity index (E*) of Vanderploeg & Scavia (1979) for the most abundant prey, and separated by prey size class for each mysid species and combination of species. 70

Table 4.3. Clearance (F) and ingestion (I) rates of the feeding selectivity experiments for each mysid species and combination of species. 70

Table 4.4. Maximum clearance (Fmax) and ingestion (Imax) rates for each mysid species and combination of species. Parameters were estimated by the exponential decay equation [$F = Fmax \times \exp(-bC)$] and the Ivlev model {$I = Imax \times [1 - \exp(-aC)]$}, where C is the food concentration. Parameter a of Ivlev's model is a measure of hunting efficiency. 71

Table 4.5. Number of juveniles predated when maintained with adults of the same or other mysid species. 75

Abstract

This thesis focuses on the role of mysids in coastal ecosystems. It considers aspects of their distribution, biology, and ecology, such as: zoogeographical distribution in the Southwest Atlantic; their population dynamics in the Cananeia estuary, exploring spatial and temporal distribution in relation to environmental variables and zooplankton abundance; reproductive traits, annual production and tolerance to salinity gradients; feeding rates, selectivity, and functional responses; inter- and intraspecific predation; and the suppression of mysid abundance by predators. Particular attention was put to the trophic role of mysids in the context of the Biodiversity and Ecosystem Functioning theory in ecology (BEF). Experimental approaches were employed to evaluate the effects of species richness of the mysid assemblage on their feeding selectivity and consumption fluxes. Also, the effect of species richness of the mysids predador assemblage was taken into account. Mysids are usually the dominant benthic epifauna in coastal waters, and thus they play a key role in marine coastal food webs. However, few studies focused on these organisms in the South American region: only 31 out of 1131 mysid species described worldwide have been registered in the Southwest Atlantic. In the Cananeia estuary, salinity and temperature were important factors influencing mysid spatio-temporal distribution. Higher abundance and production occurred in spring, when thermohaline conditions were more favorable and food availability was high. *Metamysidopsis elongata atlantica* was the numerically dominant species, probably because it is the single mysid species that effectively colonizes low salinity areas, where food is more abundant and other mysid species are absent, thus avoiding interspecific competition and intraguild predation. *Metamysidopsis e. atlantica* had high annual production values, confirming the importance of mysids in the carbon flux of tropical and subtropical coastal waters. *Chlamydopleon dissimile*, *M. e. atlantica*, and *Mysidopsis coelhoi* had opportunistic feeding behavior on the natural zooplankton assemblage, but there was evidence of avoidance of medium-size prey (300-400 µm), mostly comprised by *Oithona* spp. Ingestion rates showed a non-linear increase with increasing food concentrations, suggesting a type II functional response for the three mysid species. There were both positive (complementarity effect) and negative effects of species combinations on their feeding response. Negative interactions were probably linked to intraguild predation, resulting in a reduction of mysid predation over the zooplankton. An increase in the number of mysid predator species enhanced mysid suppression relative to the mean performance of predator monocultures, but not in comparison to the most effective predator. Positive effects of predator diversity increased with spatial heterogeneity, as it allowed interspecific complementarity effects between predators to be expressed. Moreover, mortality of predators was reduced in spatially heterogeneous treatments, most likely because it dampened intraguild predation and/or negative behavioral interactions between predators. Finally, trophic cascades were not observed, probably due to the omnivorous - generalist character of mysids.

Keywords: Mysida, biodiversity, ecosystem functioning, biogeography, distribution, feeding, predation, trophodynamics.

Resumo

Esta tese foca no papel dos misídeos em ecossistemas costeiros, considerando aspectos de sua distribuição, biologia e ecologia, tais como: distribuição zoogeográfica no Atlântico Sudoeste; dinâmica populacional dos misídeos no estuário de Cananéia, explorando sua distribuição espacial e temporal em relação às variáveis ambientais e abundância do zooplâncton; traços reprodutivos, produção anual e tolerância a gradientes de salinidade; taxas de alimentação, seletividade e respostas funcionais; predação inter- e intraespecífica; e predação sobre os misídeos. Atenção particular foi dada ao papel trófico dos misídeos no contexto da teoria da Biodiversidade e Funcionamento do Ecossistema em ecologia. Através de abordagens experimentais foram avaliados os efeitos da riqueza de espécies da comunidade de misídeos sobre sua seletividade alimentar e taxas de consumo. O efeito da riqueza de espécies da comunidade de predadores dos misídeos também foi considerado. Misídeos geralmente compõem a epifauna bêntica dominante em águas costeiras, tendo assim papel chave nas cadeias alimentares de regiões marinhas costeiras. No entanto, poucos estudos focaram esses organismos na América do Sul: apenas 31 de 1131 espécies de misídeos descritas no mundo foram registradas no Atlântico Sudoeste. No estuário de Cananéia, salinidade e temperatura foram parâmetros importantes na distribuição espacial e temporal dos misídeos. Maiores abundâncias e produção ocorreram na primavera, em decorrência de condições termohalinas mais favoráveis e a alta disponibilidade de alimento. *Metamysidopsis elongata atlantica* foi a espécie dominante numericamente, provavelmente por ser a única espécie de misídeo que consegue colonizar áreas de menor salinidade de forma efetiva, onde o alimento é mais abundante e as outras espécies de misídeos não ocorrem, evitando assim competição interespecífica e predação intraguilda. *Metamysidopsis e. atlantica* teve alta produção anual, fato que confirma a importância dos misídeos no fluxo de carbono em águas costeiras de regiões tropicas e subtropicais. *Chlamydopleon dissimile, M. e. atlantica* e *Mysidopsis coelhoi* tiveram comportamento alimentar oportunista sobre a comunidade de zooplâncton natural, mas houve evidência de que eles evitaram presas medindo entre 300 e 400 µm, compostas principalmente por *Oithona* spp. As taxas de ingestão tiveram um aumento não linear com o aumento da concentração de alimento, sugerindo resposta funcional do tipo II para as três espécies de misídeos. Houve tanto efeitos positivos (complementaridade) quanto negativos da combinação de espécies sobre a resposta alimentar das mesmas. Interações negativas estiveram provavelmente ligadas à predação intraguilda, resultando na redução da predação dos misídeos sobre o zooplâncton. Um aumento no número de espécies de predadores de misídeos resultou em um aumento na predação de misídeos em relação ao desempenho médio das monoculturas de predadores, mas não em comparação ao predador mais efetivo. Efeitos positivos da diversidade de predadores aumentaram com a heterogeneidade espacial, pois esta permitiu que efeitos de complementaridade interespecífica entre os predadores fossem melhor expressados. Além disso, a morte de predadores foi reduzida nos tratamentos com maior heterogeneidade espacial, provavelmente porque esta amenizou a ocorrência de predação intraguilda e/ou interações comportamentais negativas entre os predadores. E por último, efeitos de cascata trófica não foram observados, provavelmente em decorrência dos misídeos serem onívoros generalistas.

Palavras-chave: Mysida, biodiversidade, funcionamento do ecossistema, biogeografia, distribuição, alimentação, predação, trofodinâmica.

Chapter 1. Introduction

Organisms of the order Mysida (mysids or opossum-shrimps) have a ventral brood pouch, also known as marsupium, which differentiate members of the superorder Peracarida from other crustaceans (Murano 1999). Most of mysid species are marine (90%; Porter et al. 2008), occurring from subpolar to tropical estuarine, neritic and oceanic waters, at depths varying from few centimeters to >7 km (Mauchline 1980).

Mysids can be exclusively pelagic; however most species are hyperbenthic (>75%; Heard et al. 2006), i.e., they live on the sediment or in the water column adjacent to the sea bottom. Moreover, some species of the subfamily Gastrosaccinae have burrowing habits (Mauchline & Murano 1977). Because of their hyperbenthic habit, both classical plankton and benthos samplers are ineffective to collect these organisms (Jumars 2007). An epibenthic sledge is the most indicated sampling gear to collect hyperbenthic mysids, whereas pelagic species or vertical migrating individuals can be sampled with a plankton net, the latter usually only during night hours (Mauchline 1980).

Fecundation occurs externally in the marsupium, the structure where females carry their embryos during the entire larval development (Tattersall & Tattersall 1951; Mauchline 1980). The number of embryos in the marsupium varies inter- and intra-specifically according to female size (Baldó et al. 2001; Hanamura et al. 2009; Biju & Panampunnayil 2010; Feyrer 2010), embryo size (Saltzman 1996; Hanamura et al. 2008), and seasonally, with larger brood sizes usually occurring during warmer months (Mauchline 1980; Baldó et al. 2001). Embryos per female generally range from <5 to 245, this figure being usually higher for coastal and epipelagic species than for oceanic ones (Mauchline 1980). Larval development time is species-specific, varying from less than a week up to several months (Mauchline 1980; Wittmann 1981b; Astthorsson 1987; Johnston et al. 1997), and being influenced mainly by embryo size (Wittmann 1981a), temperature (Wittmann 1981a; Sudo 2003), and salinity (Fockedey et al. 2006).

Mysids usually are omnivorous and may feed on cyanobacteria (Gorokhova 2009), benthic algae (Webb et al. 1988; Kibirige et al. 2003; Carrasco & Perissinotto 2010), phytoplankton (Jerling & Wooldridge 1995; David et al. 2006a; Metillo et al. 2007; Lehtiniemi & Nordström 2008), detritus (Zagursky & Feller 1985; Fockedey & Mees 1999; David et al. 2006a; Carleton & McKinnon 2007; Lehtiniemi & Nordström 2008; Lesutienė et al. 2008), micro- and mesozooplankton, mainly copepods, but also cladocerans, rotifers and meroplankton (Aaser et al. 1995; Jerling & Wooldridge 1995; Fockedey & Mees 1999; David et al. 2006b; Gorokhova & Lehtiniemi 2007; Winkler et al. 2007; Barz & Hirche 2009; Carrasco & Perissinotto 2010, 2011), benthic invertebrates (harpacticoid copepods; Takahashi & Kawaguchi 1998; Lehtiniemi et al. 2009), zooplankton benthic eggs (Viitasalo & Viitasalo 2004; Viitasalo 2007; Karlson & Viitasalo-Frösen 2009; Lehtiniemi et al. 2009), and mysids from the same or different species (Wittmann 1978; Fenton 1992; Johnston & Ritz 2001).

Their wide diet varies seasonally (Viherluoto et al. 2000; Lehtiniemi & Nordström 2008; Lesutienė et al. 2008; Lehtiniemi et al. 2009) according to food availability (Viitasalo et al. 1998; Fockedey & Mees 1999; Winkler & Greve 2004; Kouassi et al. 2006; Carrasco & Perissinotto 2010), species (David et al. 2006a; Winkler et al. 2007; Lehtiniemi & Nordström 2008; Vilas et al. 2008), and ontogenetic stage (Froneman 2001; Gorokhova & Lehtiniemi 2007; Lesutienė et al. 2007), with herbivory and carnivory generally being predominant in juveniles and adults, respectively (Branstrator et al. 2000; Viherluoto et al. 2000). Mysids are suspension-feeders when feeding on detritus or algae (Webb et al. 1987), but may change to raptorial feeding when preying on other animals, depending on prey size and swimming behavior (Wooldridge & Webb 1988; Viitasalo & Rautio 1998).

Because of their high abundances and wide distribution, mysids represent a major trophic link between producers/primary consumers and upper level consumers (Jumars 2007; Latour et al. 2008; Rodríguez-Graña et al. 2008), such as large invertebrates (e.g., shrimp, lobster, and jellyfish; Chong & Sasekumar 1981; Cartes & Abelló 1992; Oh et al. 2001; Fanelli & Cartes 2004; Pitt et al. 2008), several fish species (Talbot & Baird 1985; Lasiak & McLachlan 1987; Bulman & Koslow 1992; Wakabara et al. 1993, 1996; Kock et al. 1994; Carrassón & Matallanas 2002; Teixeira et al. 2009), birds (Moran & Fishelson 1971; Schneider 1981; Sanger 1987; Hodum et al. 1998), and mammals (whales, seals; Darling et al. 1998; Dunham & Duffus 2002; Lake et al. 2003; Feyrer & Duffus 2011). Mysids can also alter their prey abundance and composition through predation pressure (Wooldridge & Webb 1988; Chigbu 2004; David et al. 2006b; Kouassi et al. 2006; Torniainen & Lehtiniemi 2008; Lasley-Rasher & Yen 2012), hence causing a trophic cascade (Aaser et al. 1995; Lindén & Kuosa 2004; Gal et al. 2006; Ellis et al. 2011). Moreover, because of their hyperbenthic habit they feed in the water column as well as on the sediment and have an important role in the benthic-pelagic coupling (Albertsson 2004; Jumars 2007; Lesutienė et al. 2008).

Currently, the influence of biodiversity on the functioning of ecosystems (Biodiversity and Ecosystem Functioning, BEF) is a major concern for ecologists (Loreau et al. 2001; Worm & Duffy 2003; Cardinale et al. 2012; Hooper et al. 2012; Naeem et al. 2012), mainly because the global biological diversity is decreasing drastically (Butchart et al. 2010; Barnosky et al. 2011). Such decline is already altering the fluxes of energy and matter that are essential for ecological processes, thus influencing the abundance, biomass and distribution of organisms, and the associated ecosystem services (Hooper et al. 2005, 2012). Empirical evidence showed that more diverse communities (in terms of genes, species or functional traits) are usually more effective in capturing resources and transforming them in new biomass (richness effects; Cardinale et al. 2006; Stachowicz et al. 2007). Moreover, these communities generally are more stable, i.e. biomass variability through time is lower than in less diverse systems (Griffin et al. 2009). Richness effects are consequence of two main mechanisms: complementarity and sampling effects. Complementarity results in better performance in more diverse communities because of resource partitioning and/or facilitation; whereas sampling effect results from the higher statistical probability of including species with a dominant effect when richness is higher.

Most studies regarding the BEF theme focused on producers (Cardinale et al. 2006, 2011). However, animals and plants respond differently to changes in diversity because of fundamental biological distinctions between these groups (Duffy 2002). In the marine environment the lack of studies focusing on animals is even more acute, especially for pelagic organisms (Duffy & Stachowicz 2006).

Thus, in this thesis I focused on the BEF theme using marine mysids as target organisms, addressing mainly their role in marine food webs, both as consumer and as prey. In addition, I studied relevant aspects concerning mysid biogeography, biology, distribution pattern, population structure, and feeding rates. This work is divided into five chapters, as follows:

In chapter 2 (published; Miyashita & Calliari 2014a), I revised mysids biogeographical distribution in the Southwest Atlantic, with the goal of complementing and updating previous records, and identifying venues for future research;

In chapter 3, I focused on mysid population dynamics in the Cananeia estuary (southeast Brazil), and provided estimates of their biomass and production to verify their importance to marine coastal food webs. I hypothesized that interspecific differences in physiological tolerance to salinity changes determines mysid spatial distribution, and consequently influences the life strategy of species present in the Cananeia estuary. To test this hypothesis, I evaluated the tolerance of the numerically dominant mysid species to salinity changes in the laboratory, and analyzed their *in situ* distribution in relation to environmental variables and food availability;

In chapter 4 (published; Miyashita & Calliari 2014b), I studied the influence of mysid species number on predation rates and prey selectivity to test how the structure of the mysid assemblage may affect carbon fluxes in the Cananeia environment. I hypothesized that species richness positively modulates feeding rates (resource use effectiveness), thus influencing carbon fluxes through that compartment;

In chapter 5, I investigated the role of predator diversity and spatial heterogeneity on mysid abundance, and evaluated its consequences, i.e. resource use effectiveness, competition among predators and trophic cascades. I hypothesized that predator species richness positively modulates resource use effectiveness (higher predation–complementarity), and consequently reduces mysid predation over their prey.

Finally, in chapter 6 I summarized the main results and conclusions related to the BEF theme.

1.1. References

Aaser HF, Jeppesen E, Søndergaard M. 1995. Seasonal dynamics of the mysid *Neomysis integer* and its predation on the copepod *Eurytemora affinis* in a shallow hypertrophic brackish lake. Mar Ecol Prog Ser 127:47–56.

Albertsson J. 2004. Trophic interactions involving mysid shrimps (Mysidacea) in the near-bottom habitat in the Baltic Sea. Aquat Ecol 38:457–469.

Astthorsson OS. 1987. Records and life history of *Praunus flexuosus* (Crustacea: Mysidacea) in Icelandic waters. J Plankton Res 9:955–964.

Baldó F, Taracido LJ, Arias AM, Drake P. 2001. Distribution and life history of the mysid *Rhopalophthalmus mediterraneus* in the Guadalquivir Estuary (SW Spain). J Crust Biol 21:961–972.

Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB, Marshall C, McGuire JL, Lindsey EL, Maguire KC, Mersey B, Ferrer EA. 2011. Has the Earth’s sixth mass extinction already arrived? Nature 471:51–57.

Barz K, Hirche HJ. 2009. Ecology of mysid shrimps in the Bornholm Basin (central Baltic Sea). Helgol Mar Res 63:317–326.

Biju A, Panampunnayil SU. 2010. Seasonality, reproductive biology and ecology of *Mesopodopsis zeylanica* (Crustacea: Mysida) from a tropical estuary (Cochin backwater) in India. Plankton Benthos Res 5:49–55.

Branstrator DK, Cabana G, Mazumder A, Rasmussen JB. 2000. Measuring life-history omnivory in the opossum shrimp, *Mysis relicta*, with stable nitrogen isotopes. Limnol Oceanogr 45:463–467.

Bulman CM, Koslow JA. 1992. Diet and food consumption of a deep-sea fish, orange roughy *Hoplostethus atlanticus* (Pisces: Trachichthyidae), off southeastern Australia. Mar Ecol Prog Ser 82:115–129.

Butchart SH, Walpole M, Collen B, Strien AV, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AN, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque JF, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Morcillo MH, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vié JC, Watson R. 2010. Global biodiversity: Indicators of recent declines. Science 328:1164–1168.

Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, Sankaran M, Jouseau C. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–992.

Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE, Duffy E, Gamfeldt L, Balvanera P, O’Connor MI, Gonzalez A. 2011. The functional role of producer diversity in ecosystems. Am J Bot 98:572–592.

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.

Carleton JH, McKinnon AD. 2007. Resident mysids: secondary production, consumption, and trophic role in a coral reef lagoon. Mar Ecol Prog Ser 336:89–98.

Carrasco NK, Perissinotto R. 2010. Spatial and temporal variations in the diet of the mysid *Mesopodopsis africana* in the St. Lucia Estuary (South Africa). Mar Ecol Prog Ser 417:127–138.

Carrasco NK, Perissinotto R. 2011. The comparative diet of the dominant zooplankton species in the St Lucia Estuary, South Africa. J Plankton Res 33:479–490.

Carrassón M, Matallanas J. 2002. Diets of deep-sea macrourid fishes in the western Mediterranean. Mar Ecol Prog Ser 234:215–228.

Cartes JE, Abelló P. 1992. Comparative feeding habits of polychelid lobsters in the Western Mediterranean deep-sea communities. Mar Ecol Prog Ser 84:139–150.

Chigbu P. 2004. Assessment of the potential impact of the mysid shrimp, *Neomysis mercedis*, on *Daphnia*. J Plankton Res 26:295–306.

Chong VC, Sasekumar A. 1981. Food and feeding habits of the white prawn *Penaeus merguiensis*. Mar Ecol Prog Ser 5:185–191.

Darling JD, Keogh KE, Steeves TE. 1998. Gray whale (*Eschrichtius robustus*) habitat utilization and prey species off Vancouver Island, B.C. Mar Mamm Sci 14:692–720.

David V, Chardy P, Sautour B. 2006b. Fitting a predator-prey model to zooplankton time-series data in the Gironde estuary (France): Ecological significance of the parameters. Estuar Coast Shelf Sci 67:605–617.

David V, Sautour B, Galois R, Chardy P. 2006a. The paradox high zooplankton biomass–low vegetal particulate organic matter in high turbidity zones: What way for energy transfer? J Exp Mar Biol Ecol 333:202–218.

Duffy JE. 2002. Biodiversity and ecosystem function: the consumer connection. Oikos 99:201–219.

Duffy JE, Stachowicz JJ. 2006. Why biodiversity is important to oceanography: potential roles of genetic, species, and trophic diversity in pelagic ecosystem processes. Mar Ecol Prog Ser 311:179–189.

Dunham JS, Duffus DA. 2002. Diet of gray whales (*Eschrichtius robustus*) in Clayoquot Sound, British Columbia, Canada. Mar Mamm Sci 18:419–437.

Ellis BK, Stanford JA, Goodman D, Stafford CP, Gustafson DL, Beauchamp DA, Chess DW, Craft JA, Deleray MA, Hansen BS. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. Proc Natl Acad Sci USA 108:1070–1075.

Fanelli E, Cartes JE. 2004. Feeding habits of pandalid shrimps in the Alboran Sea (SW Mediterranean): influence of biological and environmental factors. Mar Ecol Prog Ser 280:227–238.

Fenton GE. 1992. Population dynamics of *Tenagomysis tasmaniae* Fenton, *Anisomysis mixta australis* Zimmer and *Paramesopodopsis rufa* Fenton from south-eastern Tasmania (Crustacea: Mysidacea). Hydrobiologia 246:173–193.

Feyrer LJ. 2010. Differences in embryo production between sympatric species of mysids (family Mysidae) in the shallow coastal waters off Vancouver Island, BC. Mar Biol 157:2461–2465.

Feyrer LJ, Duffus DA. 2011. Predatory disturbance and prey species diversity: the case of gray whale (*Eschrichtius robustus*) foraging on a multi-species mysid (family Mysidae) community. Hydrobiologia 678:37–47.

Fockedey N, Mees J. 1999. Feeding of the hyperbenthic mysid *Neomysis integer* in the maximum turbidity zone of the Elbe, Westerschelde and Gironde estuaries. J Mar Syst 22:207–228.

Fockedey N, Ghekiere A, Bruwiere S, Janssen CR, Vincx M. 2006. Effect of salinity and temperature on the intra-marsupial development of the brackish water mysid *Neomysis integer* (Crustacea: Mysidacea). Mar Biol 148:1339–1356.

Froneman PW. 2001. Feeding ecology of the mysid, *Mesopodopsis wooldridgei*, in a temperate estuary along the eastern seaboard of South Africa. J Plankton Res 23:999–1008.

Gal G, Rudstam LG, Mills EL, Lantry JR, Johannsson OE, Greene CH. 2006. Mysid and fish zooplanktivory in Lake Ontario: quantification of direct and indirect effects. Can J Fish Aquat Sci 63:2734–2747.

Gorokhova E. 2009. Toxic cyanobacteria *Nodularia spumigena* in the diet of Baltic mysids: Evidence from molecular diet analysis. Harmful Algae 8:264–272.

Gorokhova E, Lehtiniemi M. 2007. A combined approach to understand trophic interactions between *Cercopagis pengoi* (Cladocera: Onychopoda) and mysids in the Gulf of Finland. Limnol Oceanogr 52:685–695.

Griffin JN, O’Gorman E, Emmerson MC, Jenkins SR, Klein A, Loreau M, Symstad A. 2009. Biodiversity and the stability of ecosystem functioning. In Naeem S, Bunker D, Loreau M, Hector A, Perring C. (eds), Biodiversity and human impacts. Oxford University Press, Oxford, pp.78–93.

Hanamura Y, Siow R, Chee PE. 2008. Reproductive biology and seasonality of the Indo-Australasian mysid *Mesopodopsis orientalis* (Crustacea: Mysida) in a tropical mangrove estuary, Malaysia. Estuar Coast Shelf Sci 77:467–474.

Hanamura Y, Siow R, Chee PE, Kassim FM. 2009. Seasonality and biological characteristics of the shallow-water mysid *Mesopodopsis orientalis* (Crustacea: Mysida) on a tropical sandy beach, Malaysia. Plankton Benthos Res 4:53–61.

Heard RW, Price WW, Knott DM, King RA, Allen DM. 2006. A taxonomic guide to the mysids of the South Atlantic Bight. NOAA Professional Paper NMFS 4:1–37.

Hodum PJ, Sydeman WJ, Visser GH, Weathers WW. 1998. Energy expenditure and food requirement of Cassin's Auklets provisioning nestlings. Condor 100:546–550.

Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, Matulich KL, Gonzalez A, Duffy JE, Gamfeldt L, O'Connor MI. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–108.

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol Monogr 75:3–35.

Jerling HL, Wooldridge TH. 1995. Feeding of two mysid species on plankton in a temperate South African estuary. J Exp Mar Biol Ecol 188:243–259.

Johnston NM, Ritz DA. 2001. Synchronous development and release of broods by the swarming mysids *Anisomysis mixta australis*, *Paramesopodopsis rufa* and *Tenagomysis tasmaniae* (Mysidacea: Crustacea). Mar Ecol Prog Ser 223:225–233.

Johnston NM, Ritz DA, Fenton GE. 1997. Larval development in the Tasmanian mysids *Anisomysis mixta australis*, *Tenagomysis tasmaniae* and *Paramesopodopsis rufa* (Crustacea: Mysidacea). Mar Biol 130:93–99.

Jumars PA. 2007. Habitat coupling by mid-latitude, subtidal, marine mysids: import-subsidised omnivores. Oceanogr Mar Biol Annu Rev 45:89–138.

Karlson AML, Viitasalo-Frösen S. 2009. Assimilation of ^{14}C-labelled zooplankton benthic eggs by macrobenthos. J Plankton Res 31:459–463.

Kibirige I, Perissinotto R, Nozais C. 2003. Grazing rates and feeding preferences of the mysid shrimp *Gastrosaccus brevifissura* in a temporarily open estuary in South Africa. Mar Ecol Prog Ser 251:201–210.

Kock KH, Wilhelms S, Everson I, Gröger J. 1994. Variations in the diet composition and feeding intensity of mackerel icefish *Champsocephalus gunnari* at South Georgia (Antarctic). Mar Ecol Prog Ser 108:43–57.

Kouassi E, Pagano M, Saint-Jean L, Sorbe JC. 2006. Diel vertical migrations and feeding behavior of the mysid *Rhopalophthalmus africana* (Crustacea: Mysidacea) in a tropical lagoon (Ebrié, Côte d'Ivoire). Estuar Coast Shelf Sci 67:355–368.

Lake S, Burton H, van den Hoff J. 2003. Regional, temporal and fine-scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica. Mar Ecol Prog Ser 254:293–305.

Lasiak T, McLachlan A. 1987. Opportunistic utilization of mysid shoals by surf-zone teleosts. Mar Ecol Prog Ser 37:1–7.

Lasley-Rasher RS, Yen J. 2012. Predation risk suppresses mating success and offspring production in the coastal marine copepod, *Eurytemora herdmani*. Limnol Oceanogr 57:433–440.

Latour RJ, Gartland J, Bonzek CF, Johnson RA. 2008. The trophic dynamics of summer flounder (*Paralichthys dentatus*) in Chesapeake Bay. Fish Bull 106:47–57.

Lehtiniemi M, Nordström H. 2008. Feeding differences among common littoral mysids, *Neomysis integer*, *Praunus flexuosus* and *P. inermis*. Hydrobiologia 614:309–320.

Lehtiniemi M, Kiljunen M, Jones RI. 2009. Winter food utilisation by sympatric mysids in the Baltic Sea, studied by combined gut content and stable isotope analyses. Mar Biol 156:619–628.

Lesutienė J, Gorokhova E, Gasiūnaitė ZR, Razinkovas A. 2007. Isotopic evidence for zooplankton as an important food source for the mysid *Paramysis lacustris* in the Curonian Lagoon, the South-Eastern Baltic Sea. Estuar Coast Shelf Sci 73:73–80.

Lesutienė J, Gorokhova E, Gasiūnaitė ZR, Razinkovas A. 2008. Role of mysid seasonal migrations in the organic matter transfer in the Curonian Lagoon, south-eastern Baltic Sea. Estuar Coast Shelf Sci 80:225–234.

Lindén E, Kuosa H. 2004. Effects of grazing and excretion by pelagic mysids (*Mysis* spp.) on the size structure and biomass of the phytoplankton community. Hydrobiologia 514:73–78.

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294:804–808.

Mauchline J. 1980. The biology of mysids and euphausiids. Adv Mar Biol 18:1–681.

Mauchline J, Murano M. 1977. World list of the Mysidacea, Crustacea. J Tokyo Univ Fish 64:39–88.

Metillo EB, Ritz DA, Swadling KM. 2007. In situ feeding rate and diet selectivity in Tasmanian mysid species (Crustacea, Mysidacea). Hydrobiologia 589: 207–218.

Miyashita LK, Calliari D. 2014a. Revision of mysids (Crustacea: Peracarida: Mysida) zoogeographical distribution in the south-west Atlantic (0° to 40°S). Mar Biodiv Rec 7:e5.

Miyashita LK, Calliari D. 2014b. Species-specific and combined feeding rates and selectivity of dominant mysids from a subtropical estuary, Brazil. J Exp Mar Biol Ecol 459:160–168.

Moran S, Fishelson L. 1971. Predation of sand-dwelling mysid crustacean *Gastrosaccus sanctus* by plover birds (Charadriidae). Mar Biol 9:63–64.

Murano M. 1999. Mysidacea. In Boltovskoy D. (ed.), South Atlantic zooplankton. Backhuys Publishers, Leiden, pp.1099–1140.

Naeem S, Duffy JE, Zavaleta E. 2012. The functions of biological diversity in an age of extinction. Science 336:1401–1406.

Oh CW, Hartnoll RG, Nash RDM. 2001. Feeding ecology of the common shrimp *Crangon crangon* in Port Erin Bay, Isle of Man, Irish Sea. Mar Ecol Prog Ser 214:211–223.

Pitt KA, Clement AL, Connolly RM, Thibault-Botha D. 2008. Predation by jellyfish on large and emergent zooplankton: Implications for benthic-pelagic coupling. Estuar Coast Shelf Sci 76:827–833.

Porter ML, Meland K, Pride W. 2008. Global diversity of mysids (Crustacea-Mysida) in freshwater. Hydrobiologia 595:213–218.

Rodríguez-Graña L, Calliari D, Conde D, Sellanes J, Urrutia R. 2008. Food web of a SW Atlantic shallow coastal lagoon: spatial environmental variability does not impose substantial changes in the trophic structure. Mar Ecol Prog Ser 362:69–83.

Saltzman J. 1996. Ecology and life history traits of the benthopelagic mysid *Boreomysis oparva* from the eastern tropical Pacific oxygen minimum zone. Mar Ecol Prog Ser 139:95–103.

Sanger GA. 1987. Winter diets of common murres and marbled murrelets in Kachemak Bay, Alaska. Condor 89:426–430.

Schneider D. 1981. Size-selective predation on mysids by birds (plovers). Mar Ecol Prog Ser 5:223–224.

Stachowicz J, Bruno JF, Duffy JE. 2007. Understanding the effects of marine biodiversity on communities and ecosystems. Annu Rev Ecol Evol Syst 38:739–766.

Sudo H. 2003. Effect of temperature on growth, sexual maturity and reproduction of *Acanthomysis robusta* (Crustacea: Mysidacea) reared in the laboratory. Mar Biol 143:1095–1107.

Takahashi K, Kawaguchi K. 1998. Diet and feeding rhythm of the sand-burrowing mysids, *Archaeomysis kokuboi* and *A. japonica* in Otsuchi Bay, northeastern Japan. Mar Ecol Prog Ser 162:191–199.

Talbot MMJF, Baird D. 1985. Feeding of the estuarine round herring *Gilchristella aestuarius* (G&T) (Stolephoridae). J Exp Mar Biol Ecol 87:199–214.

Tattersall WM, OS Tattersall. 1951. The British Mysidacea. The Ray Society, London, 460p.

Taylor MD. 2008. Spatial and temporal patterns of habitat use by three estuarine species of mysid shrimp. Mar Freshw Res 59:792–798.

Teixeira CM, Pinheiro A, Cabral HN. 2009. Feeding ecology, growth and sexual cycle of the sand sole, *Solea lascaris*, along the Portuguese coast. J Mar Biol Assoc UK 89:621–627.

Torniainen J, Lehtiniemi M. 2008. Potential predation pressure of littoral mysids on herring (*Clupea harengus membras* L.) eggs and yolk-sac larvae. J Exp Mar Biol Ecol 367:247–252.

Viherluoto M, Kuosa H, Flinkman J, Viitasalo M. 2000. Food utilisation of pelagic mysids, *Mysis mixta* and *M. relicta*, during their growing season in the northern Baltic Sea. Mar Biol 136:553–559.

Viitasalo M, Rautio M. 1998. Zooplanktivory by *Praunus flexuosus* (Crustacea: Mysidacea): functional responses and prey selection in relation to prey escape responses. Mar Ecol Prog Ser 174:77–87.

Viitasalo M, Kiørboe T, Flinkman J, Pedersen LW, Visser AW. 1998. Predation vulnerability of planktonic copepods: consequences of predator foraging strategies and prey sensory abilities. Mar Ecol Prog Ser 175:129–142.

Viitasalo S. 2007. Effects of bioturbation by three macrozoobenthic species and predation by necto-benthic mysids on cladoceran benthic eggs. Mar Ecol Prog Ser 336:131–140.

Viitasalo S, Viitasalo M. 2004. Predation by mysid shrimps (*Mysis mixta* and *M. relicta*) on benthic eggs of *Bosmina longispina maritima* (Cladocera) in the northern Baltic Sea. Mar Ecol Prog Ser 281:155–163.

Vilas C, Drake P, Fockedey N. 2008. Feeding preferences of estuarine mysids *Neomysis integer* and *Rhopalophthalmus tartessicus* in a temperate estuary (Guadalquivir Estuary, SW Spain). Estuar Coast Shelf Sci 77:345–356.

Wakabara Y, Tararam AS, Flynn MN. 1993. Importance of the macrofauna for the feeding of young fish species from infralittoral of Arrozal·Cananéia - lagoon estuarine region (25°02'S-47°56'W) Brazil. Bol Inst Oceanogr S Paulo 41: 39–52.

Wakabara Y, Flynn MN, Tararam AS. 1996. Ingestion and selection of suprabenthic crustaceans by small-sized fishes in a lower saltmarsh system. Rev Bras Oceanogr 44: 89–103.

Webb P, Perissinotto R, Wooldridge TH. 1987. Feeding of *Mesopodopsis slabberi* (Crustacea, Mysidacea) on naturally occurring phytoplankton. Mar Ecol Prog Ser 38:115–123.

Winkler G, Greve W. 2004. Trophodynamics of two interacting species of estuarine mysids, *Praunus flexuosus* and *Neomysis integer*, and their predation on the calanoid copepod *Eurytemora affinis*. J Exp Mar Biol Ecol 308:127–146.

Winkler G, Martineau C, Dodson JJ, Vincent WF, Johnson LE .2007. Trophic dynamics of two sympatric mysid species in an estuarine transition zone. Mar Ecol Prog Ser 332:171–187.

Wittmann KJ. 1978. Adoption, replacement, and identification of young in marine Mysidacea (Crustacea). J Exp Mar Biol Ecol 32:259–274.

Wittmann KJ. 1981a. On the breeding biology and physiology of marsupial development in Mediterranean *Leptomysis* (Mysidacea: Crustacea) with special reference to the effects of temperature and egg size. J Exp Mar Biol Ecol 53:261–279.

Wittmann KJ. 1981b. Comparative biology and morphology of marsupial development in *Leptomysis* and other Mediterranean Mysidacea (Crustacea). J Exp Mar Biol Ecol 52:243–270.

Wooldridge TH, Webb P. 1988. Predator–prey interactions between two species of estuarine mysid shrimps. Mar Ecol Prog Ser 50:21–28.

Worm B, Duffy JE. 2003. Biodiversity, productivity and stability in real food webs. Trends Ecol Evol 18:628–632.

Zagursky G, Feller RJ. 1985. Macrophyte detritus in the winter diet of the estuarine mysid, *Neomysis americana*. Estuaries 8:355–362.

Chapter 2. Revision of mysids (Crustacea: Peracarida: Mysida) zoogeographical distribution in the Southwest Atlantic (0° to 40°S)

Abstract

We revised the zoogeographical distribution of mysids in the Southwest Atlantic, from northern Brazil to Argentina (0° to 40°S), providing body length, and temperature and salinity range of occurrence for each species. All information concerning mysids from the Southwest Atlantic was obtained from published/unpublished studies. Of currently 1131 mysid species described worldwide, only 31 were recorded in the Southwest Atlantic which are distributed in 14 genera, 6 subfamilies and one family. This extremely low number of recorded species highlights the need for further studies focusing on mysids in the Southwest Atlantic.

Keywords: check list, biodiversity, Mysidacea, opossum shrimp, benthopelagic, hyperbenthic, Southwest Atlantic.

2.1. Introduction

The order Mysida contains 1131 species arranged in two families: Mysidae and Petalophthalmidae (cf. Mees & Meland 2014). Members of the order Mysida are known as mysids or opossum shrimps, the latter because mature females have a ventral brood pouch (marsupium). Most mysid species occur in the marine environment (>90%), from subpolar to tropical estuarine, neritic and oceanic waters (Mauchline 1980). They have a diverse diet, which may include algae, detritus, and small invertebrates (Zagursky & Feller 1985; Takahashi & Kawaguchi 1998; Lehtiniemi & Nordström 2008). Thus, mysids play an important link as intermediate consumers in marine food webs, serving as food for invertebrates, fish, birds, and mammals (Mauchline 1980). Mysids also have a major role in the benthic-pelagic coupling, a consequence of their hyperbenthic habit and strong vertical migratory behavior (Calliari et al. 2001; Taylor et al. 2005; Jumars 2007).

Most available knowledge about mysids is derived from studies carried out in temperate regions of the northern hemisphere. In the Southwest Atlantic, studies on mysids started with descriptions of new species collected sporadically in Brazilian coastal waters during international oceanographic expeditions (Dana 1852; Ortmann 1893; Tattersall 1923; Coifmann 1937). Later, studies by local and foreign scientists broadened the knowledge about regional mysid species richness with the description of new species from Brazilian (Băcescu 1968a, b, c, 1969, 1984, 1986; Silva 1970a, b, 1971a, b, 1972, 1974, 1979a; Reis & Silva 1987; Bond-Buckup & Tavares 1992) and Argentine waters (Hoffmeyer 1993; Carcedo et al. 2013). To date, a limited amount of investigations concerning their biology (Loureiro Fernandes & Gama 1996; Rörig et al. 1997; Gama & Zamboni 1999; Gama et al. 2002, 2006, 2011), distribution and/or population structure (Costa 1964; Almeida Prado 1973, 1974; González 1974; Silva 1979b; Hoffmeyer 1990; Tavares & Bond-Buckup 1990; Tararam et al. 1996; Bond-Buckup & Tavares 1998; Fries 1999; Calliari et al. 2001, 2007; Schiariti et al. 2004, 2006; Viñas et al. 2005; Cardelli et al. 2006; Borzone et al. 2007; Gama et al. 2007; Calil & Borzone 2008; Gama 2008) have been completed in the Southwest Atlantic. In the late nineties, Murano (1999) performed the most comprehensive review available to date of the mysidacean fauna (orders Mysida and Lophogastrida) of the South Atlantic Ocean, considering marine coastal and deep waters, including geographic and vertical distribution, detailed descriptions and illustrations of each species, and a taxonomic key for species identification. Since then, important results on regional mysids biodiversity have been gathered.

This work revisits the mysid biodiversity in the Southwest Atlantic with the goal of complementing and updating previous contributions, and identifying venues for future research. In particular, we add new species described or cited for the South Atlantic since Murano’s (1999) review and update known species distribution based on recent evidences. Synonymies, body length and temperature–salinity range of occurrence of each species are also provided.

2.2. Material and methods

Information was primarily obtained from published studies or reviews, and academic theses. Grey literature was also taken into consideration, because important information on regional biodiversity is often only present in journals of very restricted circulation. Search for information employed tools such as Google Scholar and Web of knowledge using terms [mysid*], [Brazil], [Uruguay], [Argentina], [Southwest Atlantic] as keywords. Search and identification of source information also relied on expert knowledge by authors. For the present study we considered species that occur in estuarine, coastal, and oceanic waters between 0° (northern Brazil) and 40°S (Argentina) off South America (Fig. 2.1). A list of all recorded species was compiled and is presented in Table 2.1 along with details of geographic distribution, body length, and temperature–salinity range of occurrence for each species. Species depth range of occurrence was not provided because this information was usually not available.

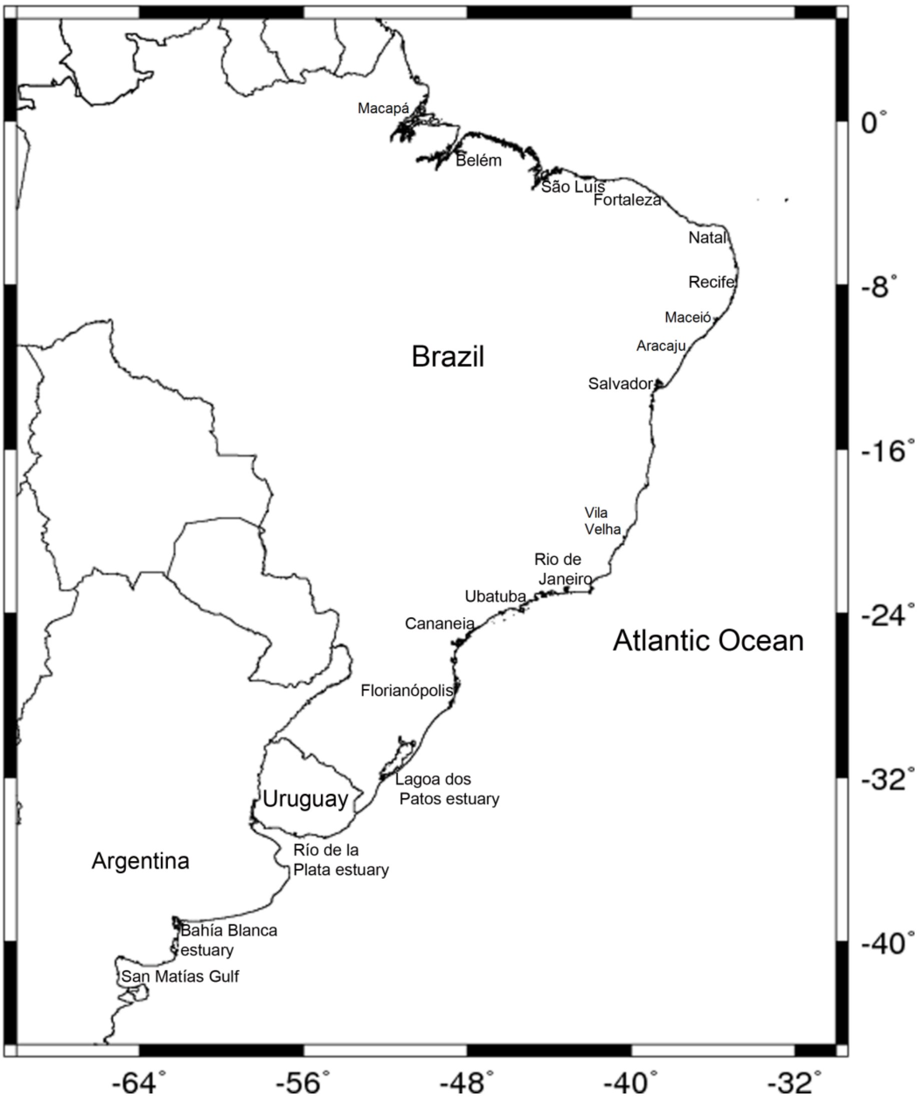


Fig. 2.1. Map of Southwest Atlantic.

2.3. Results

Available information indicated that in the Southwest Atlantic the order Mysida is represented by 31 species, distributed in 14 genera, 6 subfamilies, and one family

(Table 2.1). Species originally described from specimens collected in the Southwest Atlantic sum up to 20 (Fig. 2.2). Most of these species have been described between 1968 and 1993, mainly by Băcescu (1968a, b, c, 1969, 1984, 1986) and Silva (1970b, 1974, 1979a). After 1993, only one new mysid species (Carcedo et al. 2013) has been described in the Southwest Atlantic.

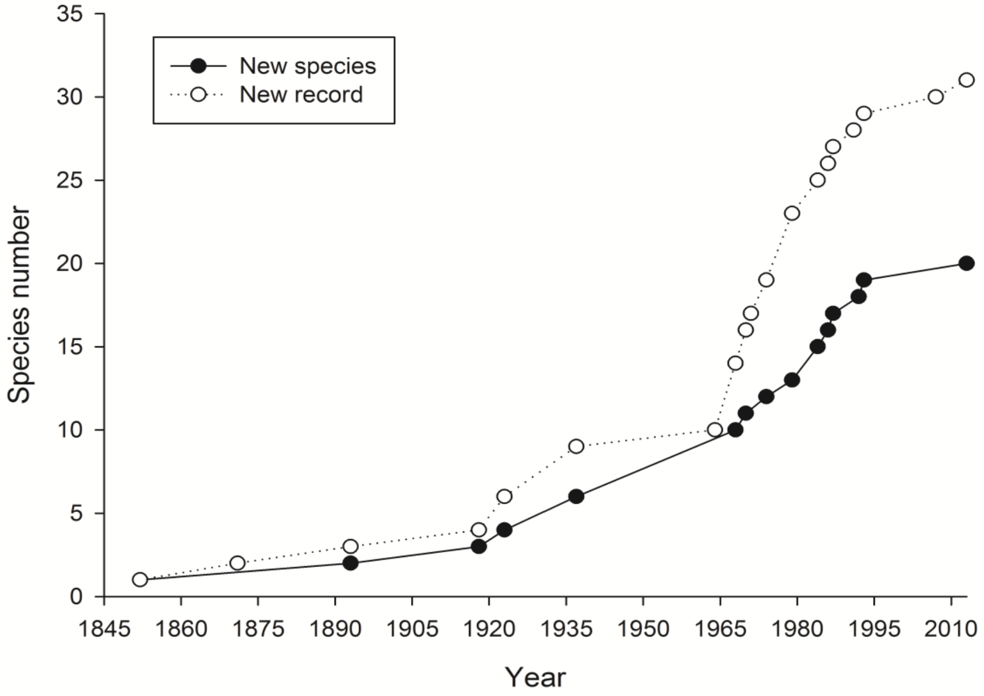


Fig. 2.2. Cumulative number of currently valid species described (solid circle) and recorded (open circle) along the years in the Southwest Atlantic.

SYSTEMATICS

Order MYSIDA Haworth, 1825

Family MYSIDAE Haworth, 1825

Subfamily SIRIELLINAE Norman, 1892

Genus *Siriella* Dana, 1850

Table 2.1. List of species recorded in the Southwest Atlantic with information on their body length, inshore/offshore and geographic distribution, and temperature (T) and salinity (S) range of occurrence.

Species	**Length (mm)**		**In/offshore distribution**	**Geographic distribution**	**T (°C)**	**S (psu)**
	Female	**Male**				
Subfamily Siriellinae Norman, 1892						
Siriella chierchiae Coifmann, 1937	5.0-10.2	8.6-10.2	Coastal	Off Brazil north of 23°S	-	-
Siriella melloi Silva, 1974	-	9	Coastal	Off NE Brazil, 5°S	26.1	36.1
Siriella thompsonii (Milne Edwards, 1837)	4.5-10.2	5.5-11.5	Oceanic	North of 40°S	-	-
Subfamily Gastrosaccinae Norman, 1892						
Anchialina typica typica (Krøyer, 1861)	4.5-5.7	4.6-7.2	Oceanic	Off N/NE Brazil, 1°N-8°S	25.6-27.8	35.4-36.5
Chlamydopleon aculeatum Ortmann, 1893	6.2	6.4	Coastal/Estuarine	Off N Brazil, 0.7°S	28.0	11.4
Chlamydopleon dissimile (Coifmann, 1937)	7.5-13	7.5-10	Coastal/Estuarine	Off Brazil north of 23°S	17.7-31.9	4.25-37
Coifmanniella johnsoni (Tattersall, 1937)	8.8-10.4	8.4-10	Coastal	Off N Brazil, 0°	27.4	36.4
Coifmanniella merjonesi (Băcescu, 1968)	9-11	9-11	Coastal	Off N/NE Brazil, 3°S-8°S	25.7-26.5	36.0-36.5
Coifmanniella mexicana (Tattersall, 1951)	9-11	8-9	Coastal	Off Brazil north of 23°S	-	-
Subfamily Erythropinae Hansen, 1910						
Amathimysis brasiliana (Băcescu, 1984)	2.8-3.0	2.8	Coastal	Off NE Brazil, 5°S	-	-
Subfamily Leptomysinae Hansen, 1910						
Brasilomysis castroi Băcescu, 1968	5.6-9.1	8.0-9.0	Coastal/Estuarine	Off Brazil north of 25°S	18.9-27.7	17.4-32.5
Promysis atlantica Tattersall, 1923	3.6-5.5	4.0-5.5	Coastal	North of 35°S	11.8-27.7	0-36.4
Promysis orientalis Dana, 1852*	7	7	Coastal	Lagoa dos Patos, 32°S	24.2-24.9	33.8-34.1
Mysidopsis coelhoi Băcescu, 1968	5.0-6.1	5.5-6.0	Coastal/Estuarine	Off Brazil north of 32°S	12-31.9	4-36.4
Mysidopsis juniae Silva, 1979	4.0-4.1	4.2-4.8	Coastal	Off SE Brazil, 23°S	-	-
Mysidopsis rionegrensis Hoffmeyer, 1993	5.6-7.2	5-5.6	Coastal	Between 36°S-42°S	13-18	33.7-33.9

Continued

Table 2.1. Continued

Mysidopsis robustispina Brattegard, 1969	>3.1	>2.0	Coastal	Off N/NE Brazil, 2°S	26.3	36.3
Mysidopsis sankarankuttyi Băcescu, 1984	2.6	-	Coastal	Off NE Brazil, 5°S	-	-
Mysidopsis scintilae Reis & Silva, 1987	-	5.2	Coastal	Off SE Brazil, 23°S	-	-
Mysidopsis tortonesei Băcescu, 1968	4.6-7.5	5.0-7.5	Coastal/Estuarine	North of 36°S	10.8-32	0-36.6
Metamysidopsis elongata atlantica Băcescu, 1968	5.0-8.0	4.5-7.0	Coastal/Estuarine	Between 23°S-32°S	10.8-32	0-35
Metamysidopsis macaensis Silva, 1970	-	-	Coastal	Off SE Brazil, 23°S	-	-
Metamysidopsis munda (Zimmer, 1918)	6-10.1	6-9.2	Coastal	Between 23°S-30°S	11.3-24.1	6.1-31.5
Metamysidopsis neritica Bond-Buckup & Tavares, 1992	3.1-6.5	2.8-6.1	Coastal	Between 25°S-30°S	17.3-28.0	31.8-37.1
Metamysidopsis swifti Băcescu, 1969	3.6-7.0	4.5-6.5	Coastal	Off SE Brazil, 23°S	-	-
Pseudobranchiomysis arenae Carcedo, Fiori & Hoffmeyer, 2013	22.4-29.0	14.6-19.5	Coastal	Off Argentina, 38°59´S	11.5-23.3	25.3-36.6
Subfamily Mysinae Haworth, 1825						
Arthromysis magellanica (Cunningham, 1871)	22-31	22-30	Coastal/Estuarine	Between 38°S-53°S	8.8-23.3	17.2-34.0
Neomysis americana (Smith, 1873)**	6.7-8.7	6.5-9.0	Coastal/Estuarine	Between 30°S-40°S	10.0-27.8	0-34.5
Mysidium columbiae (Zimmer, 1915)	5.7-7.3	4.7	Coastal	Off Brazil north of 8°S	25.6-26.5	36.1-36.5
Mysidium gracile (Dana, 1852)	5.6-6	5-7	Coastal	Off Brazil north of 23°S	26.5	36.5
Subfamily Heteromysinae Norman, 1892						
Heteromysis mureseanui Băcescu, 1986.	4	3.5	Coastal	Off SE Brazil, 20°S	-	-

*Alien species; **Cryptogenic species (potentially alien, not confirmed)

GENERAL REMARKS

Of 80 *Siriella* species currently described (Mees & Meland 2013) only three were recorded in the Southwest Atlantic, with *S. melloi* Silva, 1974 being exclusive to Brazilian waters. Identification uncertainties of *Siriella* species may arise as a result of the fact that organisms belonging to this genus usually continue growing after sexual maturity, thus showing some morphological variation compared with available descriptions (Tattersall 1955). Species identification depends on the analysis of the male, as females of congeneric species are very similar and may not be distinguished from one another (Ii 1964). The three *Siriella* species that were recorded in the Southwest Atlantic can be distinguished from each other by the analysis of the male third and fourth pleopods.

Siriella species usually perform diel vertical migration, staying at deeper waters during daytime and closer to the surface at night (Tattersall 1955).

Siriella chierchiae Coifmann, 1937

Siriella occidentalis Tattersall, 1937: 6, figures 3, 4.

Siriella chierchiae Coifmann, 1937: 3, figure 1; Tattersall, 1951: 66, figures 15, 16; Costa, 1964: 3, figure 57; Brattegard, 1970a: 2, figure 1; Brattegard, 1970b: 116, figure 2; Escobar-Briones & Soto, 1989: 33, figure 3; Price et al., 2002: 40, figures 3B, 4C; Price & Heard, 2004: 149, figure 3A.

GENERAL REMARKS

Siriella chierchiae is abundant in the western tropical Atlantic, mainly in coastal waters (Tattersall 1951).

DISTRIBUTION

Southwest Atlantic

Brazil: Rio Grande do Norte, mouth of Potengy River (Băcescu 1984); Bahia (Coifmann 1937); and Rio de Janeiro, Urca (Costa 1964).

Others

Caribbean Sea (Tattersall 1951; Brattegard 1970a, b, 1973, 1974a, b, 1975; Băcescu & Ortiz 1984; Modlin 1987); Gulf of Mexico (Modlin 1984; Escobar-Briones & Soto 1988, 1989, 1991); and Key West, Florida (Tattersall 1951).

Siriella melloi Silva, 1974

Siriella melloi Silva, 1974: 1, figures 1–7.

DISTRIBUTION

Northeast Brazil (Silva 1974, 1979b).

Siriella thompsonii (Milne Edwards, 1837)

Cynthia thompsoni Milne Edwards, 1837: 462.

Siriella thompsonii: Sars, 1885: 205, plate 36, figures 1–24; Ii, 1964: 62, figures 14–15; Pillai, 1965: 1693, figure 19; Stuck et al., 1979a: 234, figures 2F–5F; Heard et al., 2006: 25, figure 22.

DISTRIBUTION

Southwest Atlantic

Off Brazil (Coifmann 1937; W.M. Tattersall 1951; O.S. Tattersall 1955; own unpublished data).

Others

Worldwide between 40°N and 40°S (W.M. Tattersall, 1923, 1951; O.S. Tattersall, 1955, 1962; Ii, 1964; Stuck et al., 1979b; Price et al., 1986).

Subfamily GASTROSACCINAE Norman, 1892

Genus *Anchialina* Norman & Scott, 1906

GENERAL REMARKS

There are 17 described species of *Anchialina* (cf. Mees & Meland 2013), but only one has been registered in the southwestern Atlantic.

Anchialina typica typica (Krøyer, 1861)

Anchialus typicus Krøyer, 1861: 53, plate 2, figures 7A–L.

Anchialina typica: Brattegard, 1970a: 24, figure 6; Nouvel, 1943: 70, plate 4, figures 109–110; Stuck et al., 1979a: 227, figures 2a–5a; Băcescu & Ortiz, 1984: 16, figure 1B; Price et al., 2002: 41, figure 4E; Price & Heard, 2004: 149, figure 3D; Heard et al., 2006: 25, figure 6.

Anchialina typica typica: Nouvel, 1971: 327, figure 1.

GENERAL REMARKS

Nouvel (1971) separated *Anchialina typica* (Krøyer, 1861) in two subspecies: *Anchialina typica typica* from Atlantic waters and *Anchialina typica orientalis* Nouvel, 1971 from the Indo-Pacific.

DISTRIBUTION

Southwest Atlantic

Brazil: off north and northeast coasts (Silva 1979b); and Rio de Janeiro (Tattersall 1923).

Others

Caribbean Sea (Brattegard 1973, 1974a, 1975; Băcescu & Ortiz 1984; Price et al. 2002; Price & Heard 2004); Gulf of Mexico (Stuck et al. 1979b; Price et al. 1986; Escobar-Briones & Soto 1991); Bahamas and Florida (Brattegard 1970a); and USA Atlantic coast (Wigley & Burns 1971).

Genus *Chlamydopleon* Ortmann, 1893

GENERAL REMARKS

Wittmann (2009) re-described the type material of *Chlamydopleon aculeatum* Ortmann, 1893, as the original description made by Ortmann (1893) was considered inadequate (Tattersall 1951). Thus, Wittmann (2009) revalidated the genus *Chlamydopleon*, and consequently invalidated the junior synonym *Bowmaniella* Heard & Price, 2006. He also provided a taxonomic key to identify the three species of *Chlamydopleon* (cf. Wittmann 2009). This genus can be easily distinguished from other Gastrosaccinae genera by the presence of the articulated dorsal process on the fifth abdominal segment (Heard & Price 2006).

Chlamydopleon aculeatum Ortmann, 1893

Chlamydopleon aculeatum Ortmann, 1893: 25, plate 2, figure 1; Wittmann, 2009: 23, figure 1A–H.

DISTRIBUTION

Brazil: Pará, Tocantis River mouth (Ortmann 1893).

Chlamydopleon dissimile (Coifmann, 1937)

Gastrosaccus dissimilis Coifmann, 1937: 5, figures 2–3; Tattersall, 1951: 97, figure 29; Costa, 1964: 4, plate 1, figures 1–4.

Bowmaniella (*Coifmanniella*) *dissimilis*: Băcescu, 1968a: 363, figure 4.

Bowmaniella dissimilis: Brattegard, 1970a: 11, figure 2; Heard & Price, 2006: 7, figures 1, 2C–D, 4A, 5A, 6A–B, 8F; Heard et al., 2006: 26, figure 8.

Bowmaniella (*Coifmanniella*) *brasiliensis* Băcescu, 1968a: 363, figures 5–6; Almeida Prado, 1974: 49, figures 2–4.

Bowmaniella brasiliensis: Stuck et al., 1979a: 233, figures 2D, 3D, 4C, 5D, 7; Price, 1982: 13, figure 4.

Bowmaniella floridana Holmquist, 1975: 68; Stuck et al., 1979a: 227, figures 2C, 3C, 4D, 5C, 6; Price, 1982: 14, figures 2–3. Escobar-Briones & Soto, 1989: 34, figure 4.

Chlamydopleon dissimile: Wittmann, 2009: 24, figure 1J–L.

GENERAL REMARKS

This burrowing species is one of the most common and abundant Gastrosaccinae in the Southwest Atlantic.

DISTRIBUTION

Southwest Atlantic

Brazil: Rio Grande do Norte, mouth of Potengy River (Băcescu 1984); Bahia (Coifmann 1937); Rio de Janeiro, Mangaratiba Bay (Costa 1964; Băcescu 1968a), and Sepetiba Bay (Băcescu 1968a); São Paulo, Cananeia estuary (Almeida Prado 1973, 1974; Tararam et al. 1996; Chapter 3); Paraná, Atami and Mansa beaches (Borzone et al. 2007); and Rio Grande do Sul, Lagoa dos Patos estuary (Gama 2008).

Others

Caribbean Sea (Brattegard 1973, 1974a, b); Gulf of Mexico (Băcescu 1968a; Stuck et al. 1979b; Escobar-Briones & Soto 1988, 1989, 1991); Florida (Brattegard 1970a); and USA Atlantic coast (Hopkins 1965; Heard et al. 2006 and references therein).

Genus *Coifmanniella* Heard & Price, 2006

GENERAL REMARKS

This genus differs from *Chlamydopleon* by the absence of the articulated process in the posterodorsal margin of the abdominal segment 5 (Heard & Price 2006).

Coifmanniella johnsoni (Tattersall, 1937)

Gastrosaccus johnsoni Tattersall, 1937: 9, figures 5–7; Tattersall, 1951: 93, figures 26–28.

Bowmaniella (*Bowmaniella*) *johnsoni*: Băcescu, 1968a: 356, figures 2F, 3C; Price et al., 2002: 41, figure 4F; Price & Heard, 2004: 150, figure 3E.

Bowmaniella bacescui Brattegard, 1970a: 20, figure 5; Silva, 1979b: 4, figure 3.

Coifmanniella johnsoni: Heard & Price, 2006: 15, figures 2A, B, 3A–D, 4C, 5C.

DISTRIBUTION

Southwest Atlantic

North Brazil (Silva 1979b).

Others

Caribbean Sea (Tattersall 1937; Brattegard 1974b, 1975; Price et al. 2002; Price & Heard 2004); Gulf of Mexico (Modlin 1984; Escobar-Briones & Soto 1991); and Bahamas (Brattegard 1970a).

Coifmanniella merjonesi (Băcescu, 1968)

Bowmaniella (*Coifmanniella*) *merjonesi* Băcescu, 1968a: 356, figures 7–9.

Bowmaniella recifensis Silva, 1971b: 185, figures 1–2.

Bowmaniella inarticulata Silva, 1972: 161, figure 1.

Coifmanniella merjonesi: Heard & Price, 2006: 21, figures 3 G, H, 4E, 5E.

DISTRIBUTION

Southwest Atlantic

Northeast Brazil (Silva 1971b, 1972, 1979b).

Others

Caribbean Sea (Băcescu 1968a; Heard & Price, 2006).

Coifmanniella mexicana (Tattersall, 1951)

Gastrosaccus mexicanus Tattersall, 1951: 98, figure 30.

Bowmaniella (*Coifmanniella*) *mexicana*: Băcescu, 1968a: 356.

Bowmaniella mexicana: Brattegard, 1970a: 9, tables 7–8; Heard et al., 2006: 27, figure 9.

Bowmaniella (*Bowmaniella*) *atlantica* Silva, 1971a: 159 (=*Gastrosaccus brasiliensis* sensu Silva, 1970a: 35, figure 1).

Bowmaniella portoricensis Băcescu, 1968a: 357, figures 1, 2A–E, 3A–B; Brattegard, 1970a: 9, tables 7–8; Stuck et al., 1979a: 227, figures 2B–5B.

Bowmaniella gutzui Ortiz, 1988: 4, figure 1.

Coifmanniella mexicana: Heard & Price, 2006: 18, figures 3E, F, 4D, 5D.

DISTRIBUTION

Southwest Atlantic

Brazil: Rio de Janeiro, Sepetiba Bay (Silva 1970a, 1971a).

Others

Gulf of Mexico (Tattersall 1951; Stuck et al. 1979b); Cuba (Ortiz 1988); USA Atlantic coast (Băcescu 1968a; Wigley & Burns 1971; Heard et al. 2006); and Pacific coast of Panama (Tattersall 1951).

Subfamily ERYTHROPINAE Hansen, 1910

Genus *Amathimysis* Brattegard, 1969

GENERAL REMARKS

Amathimysis was considered a subgenus of *Katerythops* Holt & Tattersall, 1905, but was elevated to a valid genus (Murano & Chess 1987).

Amathimysis brasiliana (Băcescu, 1984)

Katerythops (*Amathimysis*) *brasiliana* Băcescu, 1984: 3, figure 1.

DISTRIBUTION

Brazil: Rio Grande do Norte, mouth of Potengy River (Băcescu 1984).

Subfamily LEPTOMYSINAE Hansen, 1910

Genus *Brasilomysis* Băcescu, 1968

GENERAL REMARKS

There are two species of *Brasilomysis*: *B. castroi* Băcescu, 1968 and *B. inermis* (Coifmann, 1937). The latter occurs in the Pacific coast of South America (Coifmann 1937), whereas *B. castroi* is limited to Atlantic waters (Murano 1999).

Brasilomysis castroi Băcescu, 1968

Brasilomysis castroi Băcescu, 1968b: 81, figures 3–4; Brattegard, 1969: 61, figure 18; Almeida Prado, 1974: 50, figures 5–7; Stuck et al., 1979a: 236, figures 2N, 3N, 4N, 5O; Price, 1982: 16, figures 13–14; Escobar-Briones & Soto, 1989: 34, figure 5; Heard et al., 2006: 30, figure 24.

DISTRIBUTION

Southwest Atlantic

Brazil: Rio de Janeiro, Sepetiba Bay (Băcescu 1968b); São Paulo, Ubatuba (Băcescu 1968b), and Cananeia estuary (Almeida Prado 1973, 1974; Tararam et al. 1996; Chapter 3); Paraná, Atami and Mansa beaches (Borzone et al. 2007).

Others

Caribbean Sea (Brattegard 1973, 1974a, b); Gulf of Mexico (Stuck et al. 1979b; Price et al. 1986); Florida (Brattegard 1969); and USA Atlantic coast (Heard et al. 2006).

Genus *Promysis* Dana, 1850

GENERAL REMARKS

The two valid *Promysis* species, *P. atlantica* Tattersall, 1923 and *P. orientalis* Dana, 1852, were recorded in the Southwest Atlantic. However, *P. orientalis* is an alien species (see “Discussion”).

Promysis atlantica Tattersall, 1923

Promysis atlantica Tattersall, 1923: 286, plate 1, figures 5–6; Tattersall, 1951: 245, figure 56; Clarke, 1956: 1, figures 1–6; Costa, 1964: 8, plate 2, figures 1–2; Brattegard, 1973: 44, figure 18; Almeida Prado, 1974: 52, figures 15–17; Silva, 1979b: 8, figure 4; Stuck et al., 1979a: 234, figures 2G–5G; Price, 1982: 15, figures 5–6; Tavares & Bond-Buckup, 1990: 55, figures 24–28; Heard et al., 2006: 31, figure 12.

DISTRIBUTION

Southwest Atlantic

Brazil: Ceará (Silva 1979b); Espírito Santo, Vitória Bay (Sterza & Loureiro Fernandes 2006); Rio de Janeiro, six miles off Rio de Janeiro Harbour (Tattersall 1923), and Guanabara Bay (Costa 1964); São Paulo, Ubatuba (Băcescu 1968c), Santos (own unpublished data), and Cananeia estuary (Almeida Prado 1973, 1974); Paraná, Atami Beach (Borzone et al. 2007); Santa Catarina (Resgalla 2011); and Rio Grande do Sul, Tramandaí (Tavares & Bond-Buckup 1990), and Lagoa dos Patos estuary (Gama 2008); Uruguay: Río de la Plata estuary (Calliari et al. 2007).

Others

Caribbean Sea (Brattegard, 1973, 1974a); Gulf of Mexico (Stuck et al., 1979b; Price et al., 1986); and USA Atlantic coast (Clarke, 1956; Williams, 1972; Heard et al., 2006).

Promysis orientalis Dana, 1852

Promysis orientalis Dana, 1852: 651; Dana, 1855: plate 43, figure 4A–C; Ii, 1964: 392, figure 99; Pillai, 1965: 1713, figure 71; Pillai, 1973: 98, figure 53.

Uromysis armata Hansen, 1910: 72, plate 11, figure 2A–N.

DISTRIBUTION

Southwest Atlantic

Brazil: Rio Grande do Sul, Lagoa dos Patos estuary (Gama et al. 2007; Gama 2008).

Others

Indo-Pacific (Hansen 1910; Tattersall 1951; Ii 1964; Pillai 1965, 1973).

Genus *Mysidopsis* Sars, 1864

GENERAL REMARKS

Mysidopsis is the most speciose genus in the Southwest Atlantic, with 7 registered species. However, most of these species were recorded only once. A taxonomic key to identify *Mysidopsis* species from warm waters of the western Atlantic was provided by Brattegard (1969).

Mysidopsis coelhoi Băcescu, 1968

Mysidopsis coelhoi Băcescu, 1968c: 245, figure 5; Almeida Prado, 1974: 51, figures 10–12.

DISTRIBUTION

Brazil: northeast Brazil (Silva 1979b); São Paulo, Ubatuba (Băcescu 1968c), and Cananeia estuary (Almeida Prado 1973, 1974; Tararam et al. 1996; Chapter 3); Paraná, Atami and Mansa beaches (Borzone et al. 2007); Rio Grande do Sul, Lagoa dos Patos estuary (Gama 2008).

Mysidopsis juniae Silva, 1979

Mysidopsis juniae Silva, 1979a: 1, figure 1.

GENERAL REMARKS

In Brazil, this species is frequently used in toxicity tests (e.g., Nipper et al. 1993; Lopes et al. 1997).

DISTRIBUTION

Brazil: São Paulo, São Sebastião (Silva 1979a; Fries 1999), and Cananeia estuary (Chapter 3).

Mysidopsis rionegrensis Hoffmeyer, 1993

Mysidopsis rionegrensis Hoffmeyer, 1993: 15, figures1–2; Schiariti et al., 2004: 890, figure 2B.

DISTRIBUTION

Uruguay: Río de la Plata estuary (own unpublished data); Argentina: Buenos Aires coastal waters (Schiariti et al. 2004), San Matías Gulf (Hoffmeyer 1993), and Nuevo Gulf (Menéndez et al. 2011).

Mysidopsis robustispina Brattegard, 1969

Mysidopsis robustispina Brattegard, 1969: 56, figures 16–17; Brattegard, 1973: 26, figure 9.

DISTRIBUTION

Southwest Atlantic

Northeast Brazil (Silva 1979b).

Others

Bahamas (Brattegard 1969).

Mysidopsis sankarankuttyi Băcescu, 1984

Mysidopsis sankarankuttyi Băcescu, 1984: 6, figure 2.

DISTRIBUTION

Brazil: Rio Grande do Norte, mouth of Potengi River (Băcescu 1984).

Mysidopsis scintilae Reis & Silva, 1987

Mysidopsis scintilae Reis & Silva, 1987: 5, plates 1, 5.

DISTRIBUTION

Brazil: Rio de Janeiro (Reis & Silva 1987).

Mysidopsis tortonesei Băcescu, 1968

Mysidopsis tortonesei Băcescu, 1968c: 242, figure 4; Tavares & Bond-Buckup, 1990: 55, figures 10–23; Schiariti et al., 2004: 888, figure 2A.

Mysidopsis tortonesi: Brattegard, 1973: 27, figure 10; Almeida Prado, 1974: 52, figures 13–14.

DISTRIBUTION

Southwest Atlantic

Brazil: Paraíba (Silva 1979b); São Paulo, Ubatuba (Băcescu 1968c), and Cananeia estuary (Almeida Prado 1973, 1974; Tararam et al. 1996); Paraná, Atami Beach (Borzone et al. 2007); Rio Grande do Sul, Tramandaí (Tavares & Bond-Buckup 1990), and Lagoa dos Patos estuary (Gama 2008); Uruguay: Río de la Plata estuary (Calliari et al. 2007); Argentina: Río de la Plata estuary (Schiariti et al. 2004).

Others

Caribbean coast of Colombia (Brattegard 1973, 1974a).

Genus *Metamysidopsis* Tattersall, 1951

GENERAL REMARKS

Four species and one subspecies of *Metamysidopsis* were recorded in the Southwest Atlantic. A taxonomic key to identify the *Metamysidopsis* species can be found in Băcescu (1969) and Brattegard (1970b).

Metamysidopsis elongata atlantica Băcescu, 1968

Metamysidopsis elongata atlantica Băcescu, 1968c: 237, figure 2; Almeida Prado 1974: 51, figures 8–9.

GENERAL REMARKS

Băcescu (1968c) described *M. e. atlantica* to separate from the Pacific subspecies *M. e. elongata* (Holmes, 1900). *Metamysidopsis e. atlantica* usually is the most abundant and common species in coastal and estuarine waters of the south/southeast Brazilian coast (Bersano 1994; Tararam et al. 1996; Chapter 3), consequently it is the most studied species in this region. Studies relating to rearing techniques, feeding rates, molting cycle, growth and response to gradients of temperature and salinity were carried out under laboratory conditions (Rörig et al. 1997; Gama & Zamboni 1999; Gama et al. 2002, 2006, 2011).

DISTRIBUTION

Brazil: São Paulo, Ubatuba (Băcescu 1968c), São Sebastião (Fries 1999), Una do Prelado River (Lansac Tôha & Lima 1993), and Cananeia estuary (Almeida Prado 1973, 1974; Tararam et al. 1996; Chapter 3); Santa Catarina (Rörig et al. 1997; Resgalla 2011); Rio Grande do Sul, Tramandaí Beach (Avila et al. 2009), Lagoa dos Patos estuary (Gama 2008; Avila et al. 2011), and Cassino Beach (Bersano 1994; Avila et al. 2011).

Metamysidopsis macaensis Silva, 1970

Metamysidopsis macaensis Silva, 1970b: 199, figures 1–4.

DISTRIBUTION

Brazil: Rio de Janeiro and São Paulo (Silva 1970b).

Metamysidopsis munda (Zimmer, 1918)

Mysidopsis munda Zimmer, 1918: 17, figures 8–15.

Metamysidopsis munda: Băcescu, 1969: 352, figures 2A–J; Tavares & Bond-Buckup, 1990: 49, 1–7.

GENERAL REMARKS

Loureiro Fernandes & Gama (1996) studied the molting cycle of *M. munda* under laboratory conditions.

DISTRIBUTION

Brazil: Rio de Janeiro, Armação dos Búzios (Zimmer 1918); Rio Grande do Sul, Tramandaí (Tavares & Bond-Buckup 1990), and Lagoa dos Patos estuary (Gama 2008).

Metamysidopsis neritica Bond-Buckup & Tavares, 1992

Metamysidopsis neritica Tavares & Bond-Buckup, 1990: 49, 8–15; Bond-Buckup & Tavares, 1992: 66, figures 1–2.

GENERAL REMARKS

This species usually is the dominant mysid in littoral waters of the state of Paraná, south Brazil (Borzone et al. 2007).

DISTRIBUTION

Brazil: Paraná, Atami and Mansa beaches (Borzone et al. 2007; Calil & Borzone 2008); and Rio Grande do Sul, Tramandaí (Tavares & Bond-Buckup 1990; Bond-Buckup & Tavares 1992).

Metamysidopsis swifti Băcescu, 1969

Metamysidopsis munda: Costa, 1964: 8, plate 2, figures 3–4.

Metamysidopsis swifti Băcescu, 1969: 350, figure 1; Brattegard, 1970: 30, figure 8; Brattegard, 1973: 21, figure 7; Stuck et al., 1979a: 234, figures 2h–5h; Price, 1982: 16, figures 15–16; Heard et al., 2006: 30, figure 28.

DISTRIBUTION

Southwest Atlantic

Brazil: Rio de Janeiro, Sepetiba Bay (Costa 1964).

Others

Caribbean Sea (Brattegard 1974a, b); Gulf of Mexico (Băcescu 1969; Stuck et al. 1979b); Florida, Cape Haze (Brattegard 1970a); and USA Atlantic coast (Heard et al. 2006).

Genus *Pseudobranchiomysis* Carcedo, Fiori & Hoffmeyer, 2013

Pseudobranchiomysis arenae Carcedo et al., 2013: 480, figures 1–6.

GENERAL REMARKS

This gregarious species is the only member of the genus *Pseudobranchiomysis*.

DISTRIBUTION

Argentina: surf zone (0-1 m) of Monte Hermoso and Pehuen Có sandy beaches (Carcedo et al. 2013).

Subfamily MYSINAE Haworth, 1825

Genus *Arthromysis* Colosi, 1924

GENERAL REMARKS

This genus is monospecific, containing only *Arthromysis magellanica* (Cunningham, 1871). Details regarding taxonomic classification can be found elsewhere (W.M. Tattersall 1951; O.S. Tattersall 1955).

Arthromysis magellanica (Cunningham, 1871)

Macromysis magellanica Cunningham, 1871: 497.

Arthromysis chierchiae Colosi, 1924: 4, figures 1–3.

Arthromysis magellanica: Tattersall, 1955: figures 45A–O; 46A–P.

DISTRIBUTION

Argentina: Bahía Blanca estuary (Hoffmeyer 2004; Cardelli et al. 2006; Fernández Severini et al. 2011); Strait of Magellan (Cunningham 1871; Colosi 1924; Tattersall 1955); and Patagonian shelf (Tattersall 1955).

Genus *Neomysis* Czerniavsky, 1882

GENERAL REMARKS

This genus comprises 17 valid species (Mees & Meland 2013).

Neomysis americana (Smith, 1873)

Mysis americana Smith, 1873: 552.

Neomysis americana: Williams et al., 1974: 838, figures 4–5; Hoffmeyer, 1990: 186, figures 2–3; Tavares & Bond-Buckup, 1990: 55, figures 29–33; Heard et al., 2006: 32, figure 26; Wittmann et al., 2012: 62, figures 1B, 1E, 1H.

DISTRIBUTION

Southwest Atlantic

Brazil: Rio Grande do Sul, Tramandaí (Tavares & Bond-Buckup 1990), and Lagoa dos Patos estuary (Gama 2008). Uruguay: Laguna de Rocha estuary (Rodriguez-Graña et al. 2008), Solis Grande estuary (Calliari et al. 2001), and Río de la Plata estuary (González 1974; Calliari et al. 2007). Argentina: Río de la Plata estuary (Schiariti et al. 2004, 2006; Viñas et al. 2005); and Bahía Blanca estuary (Hoffmeyer 1990, 2004; Cardelli et al. 2006; Fernández Severini et al. 2011; Menéndez et al. 2012).

Others

North American Atlantic coast (Hulburt 1957; Herman 1963; Wigley & Burns 1971; Williams 1972; Williams et al. 1974; Zagursky & Feller 1985; Prouse 1986; Brown et al. 2005; Taylor et al. 2005; Heard et al. 2006 and references therein); and Holland (Wittmann et al. 2012).

Genus *Mysidium* Dana, 1852

GENERAL REMARKS

Two of the six valid species of *Mysidium* were recorded in the Southwest Atlantic.

Mysidium columbiae (Zimmer, 1915)

Diamysis columbiae Zimmer, 1915: 172, figures 23–29.

Mysidium columbiae: Brattegard, 1969: 86, figure 27; Silva, 1979b: 11, figure 6; Băcescu & Ortiz, 1984: 22, figure 2L; Price et al., 2002: 44, figure 4G; Price & Heard, 2004: 154, figure 3I.

DISTRIBUTION

Southwest Atlantic

Brazil: Paraíba and Pernambuco (Silva 1979b).

Others

Caribbean Sea (Zimmer 1915; Tattersall 1951; Steven 1961; Goodbody 1965; Brattegard 1970b, 1973, 1974a, b, 1975; Băcescu & Ortiz 1984; Modlin 1987); Bahamas and Florida (Brattegard 1969, 1970b).

Mysidium gracile (Dana, 1852)

Macromysis gracilis Dana, 1852: 653; Dana, 1855: plate 43, figure 5A–M.

Mysidia gracilis: Zimmer, 1918: 24, figures 33–44.

Mysidium gracile: Costa, 1964: 8, plate 2, figures 5–6; Brattegard, 1969: 80, figure 25; Silva, 1979b: 10, figure 5; Price et al., 2002: 45, figure 4I; Price & Heard, 2004: 155, figure 3K.

DISTRIBUTION

Southwest Atlantic

Brazil: Paraíba and Pernambuco (Silva 1979b); Espírito Santo (Cividanes da Hora & Joyeux 2009); Rio de Janeiro (Dana 1852, Zimmer 1918, Costa 1964); and São Paulo, São Sebastião (Fries 1999).

Others

Caribbean Sea (Tattersall 1951; Brattegard 1970b, 1974a, b); and Florida (Brattegard 1969).

Subfamily HETEROMYSINAE Norman, 1892

Genus *Heteromysis* Smith, 1873

GENERAL REMARKS

Despite the high number of *Heteromysis* species described (82, Mees & Meland 2013), only *Heteromysis mureseanui* Băcescu, 1986 was recorded in the Southwest Atlantic.

Heteromysis mureseanui Băcescu, 1986

Heteromysis mureseanui Băcescu, 1986: 93, figure 1.

DISTRIBUTION

Brazil: at 29 m depth, 12 km off the coast of the state of Espírito Santo (Băcescu 1986).

2.4. Discussion

In relation to the previous review (Murano 1999), this contribution adds 8 species to the mysid species list in the South Atlantic, and updates the geographic distribution range or the temperature and salinity ranges of occurrence of 13 species.

Out of 1131 currently known mysid species worldwide (Mees & Meland 2014), only 31 have been recorded in this region, i.e., ca. 2.7%. These figures are extremely low considering the extension of the geographic area covered. This situation contrasts to that of other marine taxa, e.g., planktonic copepods, for which the same area hosts 15% of the world's marine planktonic copepod species (Razouls et al. 2012). It is likely that the low mysid species richness in the Southwestern Atlantic is an artefact resulting from limited research effort and knowledge, rather than a real pattern. Despite their ecological importance, few works focused on these organisms in the Southwest Atlantic (Murano 1999).

One major problem limiting research on mysids is related to sampling difficulties, as either classical plankton or benthos samplers are ineffective to collect these evasive organisms (Jumars 2007). Moreover, their strong migratory (vertical and horizontal) and schooling behavior (patchy distribution) make them difficult to locate and quantify. The most indicated sampling gear to collect hyperbenthic mysids is an epibenthic sledge, whereas pelagic species or vertical migrating individuals can be sampled with large plankton nets, but usually only during night hours (Mauchline 1980).

Current results strongly suggest that several further mysid species should be found in the Southwest Atlantic if a stronger research effort and specific sampling designs and methods were applied to target that group. Likewise, under that scenario new mysid species would be expected to be described in this region. Two subfamilies are acutely underrepresented in this region: the Erythropinae and Heteromysinae. There are currently 243 and 123 species described worldwide in each subfamily (Mees & Meland 2013), respectively, but only one species of each has been recorded in the Southwest Atlantic (Băcescu 1984, 1986). The former is represented mainly by deep-sea species, where studies are rare, whereas species of Heteromysinae are usually symbionts of benthic invertebrates (e.g., Wittmann 2008), which makes this taxon even more complicated to sample.

Because of mysids’ omnivorous diet and voracious predatory behavior, the introduction of an alien mysid species may result in deleterious ecological consequences (e.g., Ketelaars et al. 1999; Ellis et al. 2011). The species list here presented (Table 2.1) includes two cases of potentially alien and invasive mysids: *P. orientalis* and *N. americana*. *Promysis orientalis* is endemic from the Indo-Pacific (Hansen 1910; Tattersall 1951; Ii 1964; Pillai 1973), but was found in the South Atlantic, in the Lagoa dos Patos estuary (~32°S), south Brazil, probably transported by ballast water (Gama et al. 2007; Gama 2008). However, there are no data regarding if this alien species is already established in Brazilian waters, i.e. if there is a self-sustaining, reproducing population. *Neomysis americana* occurs in the North Atlantic from ca. 46°N along Canadian and USA coastal waters (Hulburt 1957; Herman 1963; Williams 1972; Williams et al. 1974; Prouse 1986; Brown et al. 2005), but it is not reported for Central America or northern South American waters. It was first cited for South America in Montevideo Harbour, Uruguay (35°S, González 1974), and since then it has been found in other Uruguayan sites (Calliari et al. 2001, 2007; Rodriguez-Graña et al. 2008), in southern Brazil (Tramandaí and Lagoa dos Patos, ca. 30°–32°S, Tavares & Bond-Buckup 1990; Gama 2008) and Argentina (36°–40°S, Hoffmeyer 1990; Viñas et al. 2005). In these localities, *N. americana* is usually the dominant or single mysid species present. *Neomysis americana* is probably an invasive species in South America, but its alien character has not been clarified yet; it is thus considered cryptogenic (Orensanz et al. 2002) and further research is needed to fill that gap in knowledge. Interestingly, *N. americana* has been recently found in the eastern North Atlantic (Holland, Wittmann et al. 2012).

In summary, few works concerning mysids have been carried out in the Southwest Atlantic. Taxonomically, more effort should be made to sample symbiotic and deep-sea species. In addition, for a better understanding of mysids’ role in the marine food webs, experimental works should be conducted to complement studies of composition and spatial distribution.

2.5. References

Almeida Prado M.S. (1973) Distribution of Mysidacea (Crustacea) in the Cananeia region. *Boletim de Zoologia e Biologia Marinha, Nova Série* 30, 395–417.

Almeida Prado M.S. (1974) Sistemática dos Mysidacea (Crustacea) na região de Cananéia. *Boletim do Instituto Oceanográfico, São Paulo* 23, 47–87.

Avila T.R., Machado A.A.S. and Bianchini A. (2011) Chitobiase of planktonic crustaceans from South Atlantic coast (Southern Brazil): Characterization and influence of abiotic parameters on enzyme activity. *Journal of Experimental Marine Biology and Ecology* 407, 323–329.

Avila T.R., Pedrozo C.S. and Bersano J.G.F. (2009) Variação temporal do zooplâncton da Praia de Tramandaí, Rio Grande do Sul, com ênfase em Copepoda. *Iheringia Série Zoologia* 99, 18–26.

Băcescu M. (1968a) Contributions to the knowledge of the Gastrosaccinae Psammobionte of the tropical America, with the description of a new genus (*Bowmaniella*, n.g.) and three new species of its frame. *Travaux du Muséum d´Histoire Naturelle «Grigore Antipa»* 8, 355–373.

Băcescu M. (1968b) *Afromysis guinensis* n. sp. and *Brasilomysis castroi* n. g. n. sp., from the waters of tropical Atlantic. *Revue Roumaine de Biologie, Zoologie* 13, 75–86.

Băcescu M. (1968c) Étude des quelques Leptomysini (Crustacea Mysidacea) des eaux du Brésil et de Cuba: description d'un genre et de cinq autres taxons nouveaux. *Annali Museo Civico di Storia Naturale Genova* 77, 232–249.

Băcescu M. (1969) Contribution à la connaissance du genre *Metamysidopsis* W. Tattersall 1951, *M. swifti* n. sp., *M. mexicana* n. n, confondues avec *M. munda* Zimmer. *Revue Roumaine de Biologie, Zoologie* 14, 349–357.

Băcescu M. (1984) *Katerythrops* s.gen. *Amathimsysis brasiliana* n.sp. and *Mysidopsis sankarankuttyi* n.sp. of the NE Brazilian littoral waters. *Revue Roumaine de Biologie, Biologie Animale* 29, 3–7.

Băcescu M. (1986) *Heteromysis mureseanui* n.sp. and *Kalliapseudes viridis,* ssp. *brasiliensis* n.ssp., from the Brazilian littoral waters. *Revue Roumaine de Biologie, Biologie Animale* 31, 93–97.

Băcescu M. and Ortiz M. (1984) Contribution to the knowledge of the Mysidacea (Crustacea) of the Cuban insular shelf waters. *Travaux du Muséum d´Histoire Naturelle «Grigore Antipa»* 26, 15–23.

Bersano J.G. (1994) *Zooplâncton da zona de arrebentação de praias arenosas, situadas ao sul de Rio Grande R.S.. Primavera de 1990, verão de 1991*. Master thesis. Fundação Universidade Federal do Rio Grande, Rio Grande, Brasil.

Bond-Buckup G. and Tavares L.M.G. (1992) *Metamysidopsis neritica* a new peracarid from the coastal waters of south Brazil (Crustacea, Mysidacea). *Atlântica* 14, 65–71.

Bond-Buckup G. and Tavares L.M.G. (1998) Malacostraca - Peracarida. Mysidacea. In Young P.S. (ed) *Catalogue of Crustacea of Brazil*. Rio de Janeiro: Museu Nacional, pp. 525–531.

Borzone C.A., Lorenzi L. and Calil P. (2007) Cross-shore Mysidacea (Crustacea) distribution in two sandy beaches with contrasting morphodynamics. *Revista Brasileira de Zoologia* 24, 943–949.

Brattegard T. (1969) Marine biological investigations in the Bahamas. 10. Mysidacea from shallow water in the Bahamas and Southern Florida. Part I. *Sarsia* 39, 17–106.

Brattegard T. (1970a) Marine biological investigations in the Bahamas 11. Mysidacea from shallow water in the Bahamas and southern Florida. Part 2. *Sarsia* 41, 1–35.

Brattegard T. (1970b) Mysidacea from shallow water in the Caribbean Sea. *Sarsia* 43, 111–154.

Brattegard T. (1973) Mysidacea from shallow water on the Caribbean coast of Colombia. *Sarsia* 54, 1–65.

Brattegard T. (1974a) Additional Mysidacea from shallow water on the Caribbean coast of Colombia. *Sarsia* 57, 47–86.

Brattegard T. (1974b) Mysidacea from shallow water on the Caribbean coast of Panama. *Sarsia* 57, 87–108.

Brattegard T. (1975) Shallow-water Mysidacea from the Lesser Antilles and other Caribbean regions. *Studies on the Fauna of Curaçao and Other Caribbean Islands* 157, 102–115.

Brown H., Bollens S.M., Madin L.P. and Horgan E.F. (2005) Effects of warm water intrusions on populations of macrozooplankton on Georges Bank, Northwest Atlantic. *Continental Shelf Research* 25, 143–156.

Calil P. and Borzone C.A. (2008) Population structure and reproductive biology of *Metamysidopsis neritica* (Crustacea: Mysidacea) in a sand beach in south Brazil. *Revista Brasileira de Zoologia* 25, 403–412.

Calliari D., Cervetto G., Bastreri D. and Gómez M. (2001) Short-term variability in abundance and vertical distribution of the opossum-shrimp *Neomysis americana* in the Solís Grande river estuary, Uruguay. *Atlântica* 23, 117–125.

Calliari D., Cervetto G., Castiglioni R. and Rodríguez L. (2007) Salinity preferences and habitat partitioning between dominant mysids at the Río de la Plata estuary (Uruguay). *Journal of the Marine Biological Association of the United Kingdom* 87, 501–506.

Carcedo C., Fiori S. and Hoffmeyer M. (2013) *Pseudobranchiomysis arenae*, a new genus and species of Leptomysinae (Crustacea: Mysida) in Argentinian sandy beaches. *Zootaxa* 3647, 479–487.

Cardelli N.V., Cervellini P.M. and Piccolo M.C. (2006) Abundancia estacional y distribución espacial de Mysidacea en el Atlántico sudoccidental, estuario de Bahía Blanca (38°42'- 39°26'S y 62°28'- 61°40'W). *Revista de Biología Marina y Oceanografía* 41, 177–185.

Cividanes da Hora M.D.S. and Joyeux J.C. (2009) Closing the reproductive cycle: Growth of the seahorse *Hippocampus reidi* (Teleostei, Syngnathidae) from birth to adulthood under experimental conditions. *Aquaculture* 292, 37–41.

Clarke W.D. (1956) A further description of *Promysis atlantica* Tattersall (Crustacea, Mysidacea). *American Museum Novitates* 1755, 1–5.

Coifmann I. (1937) Misidacei raccolti dalla R. Corvetta « Vettor Pisani » negli anni 1882–85. *Annuario del Museo Zoologico della Reale Università di Napoli, Nuova Serie* 7, 1–14.

Colosi G. (1924) Euphausiacea e Mysidacea raccolti dalla R. Nave « Vettor Pisani » nel 1882–1885. *Annuario del Museo Zoologico della Reale Università di Napoli, Nuova Serie* 5, 1–7.

Costa H.R. (1964) Notas sôbre os Mysidacea da costa brasileira. *Boletim do Museu Nacional, Rio de Janeiro, Nova Série* 247, 1–9.

Cunningham R.O. (1871) Notes on the Reptiles, Amphibia, Fishes, Mollusca, and Crustacea obtained during the voyage of H.M.S. 'Nassau' in the years 1866-69. *Transactions of the Linnean Society of London* 27, 465–502.

Czerniavsky V. (1882) Monographia Mysidarum inprimis Imperii Rossici. Fasc. 1, 2. *Trudy Sankt-Peterburgskago Obschestva Estestvoispytatelei* 12, 1–170; 13, 1–85.

Dana J.D. (1850) Synopsis generum crustaceorum ordinis "Schizopoda". *The American Journal of Science and Arts, Series 2* 9, 129–133.

Dana J.D. (1852) Crustacea, part I. *United States Exploring Expedition, during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes* 13, 1–685.

Dana J.D. (1855) Crustacea, part I. *United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes* 13, Folio atlas, 96 pls.

Ellis B.K., Stanford J.A., Goodman D., Stafford C.P., Gustafson D.L., Beauchamp D.A., Chess D.W., Craft J.A., Deleray M.A. and Hansen B.S. (2011) Long-term effects of a trophic cascade in a large lake ecosystem. *Proceedings of the National Academy of Sciences of the United States of America* 108, 1070–1075.

Escobar-Briones E. and Soto L.A. (1988) Mysidacea from Términos Lagoon, southern Gulf of Mexico, and description of a new species of *Taphromysis*. *Journal of Crustacean Biology* 8, 639–655.

Escobar-Briones E. and Soto L.A. (1989) Los misidáceos (Crustacea: Peracarida) epibenticos de Laguna de Términos, Campeche: distribución, notas ecológicas y clave taxonómica ilustrada para su identificación. *Anales Instituto de Biologia, Universidade Nacional Autonoma de Mexico, Serie Zoologia* 59, 29–44.

Escobar-Briones E. and Soto L.A. (1991) Biogeografía de los misidáceos (Crustacea: Peracarida) del Golfo de México. *Caribbean Journal of Science* 27, 80–89.

Fernández Severini M.D., Botté S.E., Hoffmeyer M.S. and Marcovecchio J.E. (2011) Lead concentrations in zooplankton, water, and particulate matter of a southwestern Atlantic temperate estuary (Argentina). *Archives of Environmental Contamination and Toxicology* 61, 243–260.

Fries B.G. (1999) *Composição, frequência e abundância dos Mysidacea (Crustacea, Peracarida) do Saco do Segredo, São Sebastião, SP*. Master thesis. Universidade de São Paulo, São Paulo, Brasil.

Gama A.M.S. (2008) *Fatores ambientais e mecanismos comportamentais determinantes da ocorrência de Mysida (Crustacea) no estuário da Laguna dos Patos e região costeira adjacente*. PhD thesis. Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brasil.

Gama A.M.S. and Zamboni A.J. (1999) Aspectos da biologia e do cultivo de *Metamysidopsis elongata atlantica* para uso em testes de toxicidade. *Nauplius* 7, 127–139.

Gama A.M.S., Calazans D. and Fontoura N.F. (2011) Dial behavioral responses of *Metamysidopsis elongata atlantica* (Crustacea, Mysida) to gradients of salinity and temperature. *Iheringia Série Zoologia* 101, 103–108.

Gama A.M.S., Cardozo A.P. and Fontoura N.F. (2007) Occurrence of *Promysis orientalis* Dana, 1852 (Crustacea: Mysidacea) in Patos Lagoon estuary, RS, Brazil. *Atlântica* 29, 127–128.

Gama A.M.S., Montú M.A. and D'Incao F. (2006) Ciclo de mudas e taxas de crescimento de *Metamysidopsis elongata atlantica* (Crustacea, Mysidacea) cultivado em diferentes temperaturas e salinidades. *Iheringia Série Zoologia* 96, 67–70.

Gama A.M.S., Montú M.A. and Gusmão L.F.M. (2002) Ciclo de vida pós-marsupial e crescimento de *Metamysidopsis elongata atlantica* (Crustacea, Mysidacea, Mysidae) em cultivo de laboratório. *Iheringia Série Zoologia* 92, 77–83.

González L.A. (1974) Hallazgo de *Neomysis americana* Smith (1873) (Crustacea: Mysidacea) en el Río de la Plata. *Revista de Biología del Uruguay* 2, 119–130.

Goodbody I. (1965) Continuous breeding in populations of two tropical crustaceans, *Mysidium columbiae* (Zimmer) and *Emerita portoricensis* Schmidt. *Ecology* 46, 195–197.

Hansen H.J. (1910) The Schizopoda of the Siboga Expedition. *Siboga Expeditie* 37, 1–123.

Haworth A.H. (1825) A new binary arrangement of the macrurous Crustacea. *The Philosophical Magazine and Journal* 65, 183–184.

Heard R.W. and Price W.W. (2006) Revision of *Bowmaniella* sensu Băcescu, 1968 (Crustacea: Mysida: Mysidae: Gastrosaccinae): a taxonomic conundrum. *Zootaxa* 1269, 1–29.

Heard R.W., Price W.W., Knott D.M., King R.A. and Allen D.M. (2006) A taxonomic guide to the mysids of the South Atlantic Bight. *NOAA Professional Paper NMFS* 4, 1–37.

Herman S.S. (1963) Vertical migration of the opossum shrimp, *Neomysis americana* Smith. *Limnology and Oceanography* 8, 228–238.

Hoffmeyer, M. (1990) The occurrence of *Neomysis americana* in two new localities of the South American coast (Mysidacea). *Crustaceana* 58, 186–192.

Hoffmeyer M.S. (1993) *Mysidopsis rionegrensis*, a new species of Mysidacea from San Matias Gulf, Argentina. *Physis, Sección A* 48, 15–19.

Hoffmeyer M.S. (2004) Decadal change in zooplankton seasonal succession in the Bahía Blanca estuary, Argentina, following introduction of two zooplankton species. *Journal of Plankton Research* 26, 181–189.

Holmes S.J. (1900) Synopsis of California stalk-eyed Crustacea. *Occasional papers of the California Academy of Sciences* 7, 1–262.

Holmquist C. (1975) A revision of the species *Archaeomysis grebnitzkii* Czerniavsky and *A. maculata* (Holmes) (Crustacea, Mysidacea*). Zoologische Jahrbuecher. Abteilung fuer Systematik, Oekologie und Geographie der Tiere* 102, 51-71.

Holt E.W.L. and Tattersall W.M. (1905) Schizopodous Crustacea from the north-east Atlantic slope. *Appendix to the Report on the Sea and Inland Fisheries of Ireland for 1903-1903. Part II. Scientific Investigations* 4, 99–152.

Hopkins T.L. (1965) Mysid shrimp abundance in surface waters of Indian River Inlet, Delaware. *Chesapeake Science* 6, 86–91.

Hulburt E.M. (1957) The distribution of *Neomysis americana* in the estuary of the Delaware River. *Limnology and Oceanography* 2, 1–11.

Ii N. (1964) *Mysidae (Crustacea) Fauna Japonica*. Tokyo: Biogeographical Society of Japan.

Jumars P.A. (2007) Habitat coupling by mid-latitude, subtidal, marine mysids: import-subsidised omnivores. *Oceanography and Marine Biology: An Annual Review* 45, 89–138.

Ketelaars H.A.M., Lambregts-van de Clundert F.E., Carpentier C.J., Wagenvoort A.J. and Hoogenboezem W. (1999) Ecological effects of the mass occurrence of the Ponto-Caspian invader, *Hemimysis anomala* G.O. Sars, 1907 (Crustacea: Mysidacea), in a freshwater storage reservoir in the Netherlands, with notes on its autecology and new records. *Hydrobiologia* 394, 233–248.

Krøyer H. (1861) Et bidrag til kundskab om Krebsdyrfamilien Mysidæ. *Naturhistorisk Tidsskrift 3* 1, 1–75.

Lansac Tôha F.A. and Lima A.F. (1993) Ecologia do zooplâncton do estuário do Rio Una do Prelado (São Paulo, Brasil). *Acta Limnologica Brasiliensia* 6, 82–96.

Lehtiniemi M. and Nordström H. (2008) Feeding differences among common littoral mysids, *Neomysis integer*, *Praunus flexuosus* and *P. inermis*. *Hydrobiologia* 614, 309–320.

Lopes C.F., Milanelli J.C.C., Prosperi V.A., Zanardi E. and Truzzi A.C. (1997) Coastal monitoring program of São Sebastião channel: Assessing the effects of 'Tebar V' oil spill on rocky shore populations. *Marine Pollution Bulletin* 34, 923–927.

Loureiro Fernandes L. and Gama A.M.S. (1996) Molting cycle in *Metamysidopsis munda* (Crustacea: Mysidacea). *Nauplius* 4, 171–172.

Mauchline J. (1980) The biology of mysids and euphausiids. *Advances in Marine Biology* 18, 1–681.

Mees J. and Meland K. (2013) *World List of Lophogastrida, Stygiomysida and Mysida*. Available from: http://www.marinespecies.org/mysidacea (accessed 10 October 2013).

Mees J. and Meland K. (2014) *World List of Lophogastrida, Stygiomysida and Mysida*. Available from: http://www.marinespecies.org/mysidacea (accessed 11 June 2014).

Menéndez M.C., Biancalana F., Berasategui A.A., Fernández Severini M.D., Hoffmeyer M. and Esteves J.L. (2011) Mesozooplankton composition and spatial distribution, Nuevo Gulf, Patagonia, Argentina. *Check List* 7, 101–107.

Menéndez M.C., Dutto M.S., Piccolo M.C. and Hoffmeyer M. (2012) The role of the seasonal and semi-diurnal tidal cycle on mesozooplankton variability in a shallow mixed estuary (Bahía Blanca, Argentina). *ICES Journal of Marine Science* 69, 389–398.

Milne Edwards H. (1837) *Histoire naturelle des crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux*. Volume 2. Paris: Librairie encyclopédique de Roret.

Modlin R.F. (1984) Mysidacea from the Florida Middle Ground, northeast Gulf of Mexico with descriptions of three new species of *Heteromysis* and a key to the Heteromysini of the western Atlantic. *Journal of Crustacean Biology* 4, 278–297.

Modlin R.F. (1987) Mysidacea from shallow waters in the vicinity of Carrie Bow Cay, Belize, Central America, with descriptions of two new species. *Journal of Crustacean Biology* 7, 106–121.

Murano M. (1999) Mysidacea. In Boltovskoy D. (ed) *South Atlantic Zooplankton*. Leiden: Backhuys Publishers, pp. 1099–1140.

Murano M. and Chess J.R. (1987) Four new mysids from Californian coastal waters. *Journal of Crustacean Biology* 7, 182–197.

Nipper M.G., Badaró-Pedroso C., José V.F. and Melo S.L.R. (1993) Toxicity testing with coastal species of Southeastern Brazil. Mysids and copepods. *Bulletin of Environmental Contamination and Toxicology* 51, 99–106.

Norman A.M. (1892) On British Mysidae, a family of Crustacea Schizopoda. *Annals and Magazine of Natural History, Series 6* 10, 143–166.

Norman A.M. and Scott T. (1906) *The Crustacea of Devon and Cornwall*. London: William Wesley and Son.

Nouvel, H. (1943) Mysidacés provenant des campagnes du Prince Albert Ier de Monaco. *Résultats des campagnes scientifiques accomplies sur son yacht par Albert Ier de Monaco* 105, 1–128.

Nouvel H. (1971) Mysidacés récoltés par S. Frontier à Nosy-Bé. VI. *Anchialina typica* (Kroyer) avec distinction de deux sous-espèces, et *Anchialina latifrons* n. sp. *Bulletin de la Société d'Histoire Naturelle de Toulouse* 107, 325–338.

Orensanz J.M., Schwindt E., Pastorino G., Bortolus A., Casas G., Darrigran G., Elías R., López Gappa J.J., Obenat S., Pascual M., Penchaszadeh P., Piriz M.L., Scarabino F., Spivak E.D. and Vallarino E.A. (2002) No longer the pristine confines of the world ocean: a survey of exotic marine species in the southwestern Atlantic. *Biological Invasions* 4, 115–143.

Ortiz M. (1988) Una nueva especie de misidáceo del género *Bowmaniella* (Crustacea: Mysidacea), de aguas cubanas. *Revista de Investigaciones Marinas* 9, 3–7.

Ortmann A.E. (1893) Decapoden und Schizopoden. In Hensen V. (ed) *Ergebnisse der Plankton–Expedition der Humboldt-Stiftung.* Kiel und Leipzig: Lipsius und Tischer, pp. 1–120.

Pillai N.K. (1965) A review of the work on the shallow water Mysidacea of the Indian waters. *Proceedings of the Symposium on Crustacea, Mandapam Camp, 12–15 January 1965*. Ernakulam: Marine Biological Association of India, pp. 1681–1728.

Pillai N.K. (1973) Mysidacea of the Indian Ocean. *Handbook to the International Zooplankton Collections* 4, 1–125.

Price W.W. (1982) Key to the shallow water Mysidacea of the Texas coast with notes on their ecology. *Hydrobiologia* 93, 9–21.

Price W.W. and Heard R.W. (2004) Studies on the Crustacea of the Turks and Caicos Islands, British West Indies. V. Records of mysids from Pine Cay, Fort George Cay, Water Cay, and adjacent waters. *Gulf and Caribbean Research* 16, 147–159.

Price W.W., Heard R.W., Harris J.T., and McCoy C.M.R. (2002) Crustacea of the Cayman Islands, British West Indies. I. Records of mysids from shallow water non-reef habitats. *Gulf and Caribbean Research* 14, 35–52.

Price W.W., McAllister A.P., Towsley R.M. and DelRe, M. (1986) Mysidacea from continental shelf waters of the northwestern Gulf of Mexico. *Contributions in Marine Science* 29, 45–58.

Prouse N.J. (1986) Distribution and abundance of mysids in the Cumberland basin, upper Bay of Fundy. *Proceedings of the Nova Scotian Institute of Science* 36, 1–11.

Razouls C., de Bovée F., Kouwenberg J. and Desreumaux N. (2005-2012) *Diversity and geographic distribution of marine planktonic copepods*. Available from: http://copepodes.obs-banyuls.fr/en (accessed March 06 2013).

Reis J.M.L. and Silva V.M.P. (1987) *Mysidopsis scintilae* espécie nova de Crustacea-Mysidacea. *Avulso, Departamento de Zoologia, Instituto de Biologia, UFRJ*, 33, 1–14.

Resgalla Jr C. (2011) The holoplankton of the Santa Catarina coast, southern Brazil. *Annals of the Brazilian Academy of Sciences* 83, 575–588.

Rodríguez-Graña L., Calliari D., Conde D., Sellanes J. and Urrutia R. (2008) Food web of a SW Atlantic shallow coastal lagoon: spatial environmental variability does not impose substantial changes in the trophic structure. *Marine Ecology Progress Series* 362, 69–83.

Rörig L.R., Resgalla Jr C., Pezzuto P.R., Alves E.S. and Morelli F. (1997) Análise ecológica de um processo de acumulação da diatomácea *Anaulus* sp. na zona de arrebentação da praia de Navegantes (Santa Catarina, Brasil). *Oecologia Brasiliensis* 3, 29–43.

Sars G.O. (1864) Beretning om en i Sommeren 1863, foretagen Zoologisk Reise i Christiania Stift. *Nyt Magazin for Naturvidensskaberne* 13, 225–260.

Sars G.O. (1885) Report on the Schizopoda collected by H.M.S. Challenger during the years 1873-76. *Report on the scientific results of the voyage of H.M.S. Challenger, Zoology* 13, 1–228.

Schiariti A., Mianzan H.W. and Ramírez F.C. (2004) New records of *Mysidopsis tortonesei* Băcescu, 1968 and *M. rionegrensis* Hoffmeyer, 1993 (Mysidacea) from the Río de la Plata estuary and Buenos Aires coastal waters. *Crustaceana* 77, 887–893.

Schiariti A., Berasategui A.D., Giberto D.A., Guerrero R.A., Acha E.M. and Mianzan H.W. (2006) Living in the front: *Neomysis americana* (Mysidacea) in the Río de la Plata estuary, Argentina-Uruguay. *Marine Biology* 149, 483–489.

Silva V.M.A.P. (1970a) *Gastrosaccus brasilensis* nova espécie de Crustacea Mysidacea. *Atas da Sociedade de Biologia do Rio de Janeiro* 13, 35–36.

Silva V.M.A.P. (1970b) *Metamysidopsis macaensis*, nova espécie de Crustacea Mysidacea. *Atas da Sociedade de Biologia do Rio de Janeiro* 13: 199–201.

Silva V.M.A.P. (1971a) *Bowmaniella (Bowmaniella) atlantica*, nôvo nome para *Gastrosaccus brasilensis* (da Silva, 1970) (Crustacea, Mysidacea). *Atas da Sociedade de Biologia do Rio de Janeiro* 14, 159.

Silva V.M.A.P. (1971b) *Bowmaniella (Bowmaniella) recifensis* n. sp. de Crustacea Mysidacea. *Atas da Sociedade de Biologia do Rio de Janeiro* 14, 185–187.

Silva V.M.A.P. (1972) *Bowmaniella (Coifmanniella) inarticulata* sp. n. de Crustacea Mysidacea. *Atas da Sociedade de Biologia do Rio de Janeiro* 15, 161–163.

Silva V.M.A.P.. (1974) *Siriella melloi*, nova espécie de Crustacea Mysidacea. *Avulso, Departamento de Zoologia, Instituto de Biologia, UFRJ* 22, 1–4.

Silva V.M.A.P. (1979a) *Mysidopsis juniae*, nova espécie de Crustacea-Mysidacea. *Avulso, Departamento de Zoologia, Instituto de Biologia, UFRJ* 30, 1–4.

Silva V.M.A.P. (1979b) Mysidacea (Crustacea) da costa brasileira 1 “Operação Norte/Nordeste I”. *Avulsos, Departamento de Zoologia, Instituto de Biologia, UFRJ* 32, 1–18.

Smith S.I. (1873) Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. *Report of the Commissioner, US Commission of Fish and Fisheries, Part 1, 1871-72 (1873)* 18, 295–747.

Sterza J.M. and Loureiro Fernandes L. (2006) Zooplankton community of the Vitória Bay estuarine system (southeastern Brazil). Characterization during a three-year study. *Brazilian Journal of Oceanography* 54, 95–105.

Steven D.M. (1961) Shoaling behaviour in a mysid. *Nature* 192, 280–281.

Stuck K., Perry H.M. and Heard R.W. (1979a) An annotated key to the Mysidacea of the North central Gulf of Mexico. *Gulf Research Reports* 6, 225–238.

Stuck K., Perry H.M. and Heard R.W. (1979b) Records and range extensions of Mysidacea from coastal and shelf waters of the eastern Gulf of Mexico. *Gulf Research Reports* 6, 239–248.

Takahashi K. and Kawaguchi K. (1998) Diet and feeding rhythm of the sand-burrowing mysids, *Archaeomysis kokuboi* and *A. japonica* in Otsuchi Bay, northeastern Japan. *Marine Ecology Progress Series* 162, 191–199.

Tararam A.S., Wakabara Y. and Flynn M.N. (1996) Suprabenthic community of the Cananeia lagoon estuarine region, Southeastern Brazil. *Cahiers de Biologie Marine* 37, 295–308.

Tavares L.M.G. and Bond-Buckup G. (1990) Os Mysidacea da região litorânea e estuarina de Tramandaí, RS, Brasil (Crustacea, Peracarida, Mysidacea). *Revista Brasileira de Zoologia* 7, 47–57.

Tattersall O.S. (1955) Mysidacea. *Discovery Reports* 28, 1–190.

Tattersall O.S. (1962) Report on a collection of Mysidacea from South African coastal and off-shore waters (1957-59) and from Zanzibar (1961). *Proceedings of the Zoological Society of London* 139, 221–247.

Tattersall W.M. (1923) Crustacea. Part VII.–Mysidacea. *British Antarctic ("Terra Nova" Expedition, 1910, Natural History Reports, Zoology* 3, 273–304.

Tattersall W.M. (1937) New species of mysidacid crustaceans. *Smithsonian Miscellaneous Collections* 91, 1–18.

Tattersall W.M. (1951) A review of the Mysidacea of the United States National Museum. *Bulletin of the United States National Museum* 201, 1–292.

Taylor L.H., Shellito S.M., Abello H.U. and Jumars P.A. (2005) Tidally phased emergence events in a strongly tidal estuary. *Estuaries* 28, 500–509.

Viñas M.D., Ramírez F.C. and Mianzan H.W. (2005) Annual population dynamics of the opossum shrimp *Neomysis americana* Smith, 1873 (Crustacea: Mysidacea) from an estuarine sector of the Argentine Sea. *Scientia Marina* 69, 493–502.

Wigley R.L. and Burns C.R. (1971) Distribution and biology of mysids (Crustacea, Mysidacea) from the Atlantic coast of the United States in the NMFS Woods Hole collection. *Fishery Bulletin* 69, 717–746.

Williams A.B. (1972) A ten-years study of meroplankton in North Carolina estuaries: Mysid shrimps. *Chesapeake Science* 13, 254–262.

Williams A.B., Bowman T.E. and Damkaer D.M. (1974) Distribution, variation, and supplemental description of the opossum shrimp, *Neomysis americana* (Crustacea, Mysidacea). *Fishery Bulletin* 72, 835–842.

Wittmann K.J. (2008) Two new species of Heteromysini (Mysida, Mysidae) from the island of Madeira (N.E. Atlantic), with notes on sea anemone and hermit crab commensalisms in the genus *Heteromysis* S. I. Smith, 1873. *Crustaceana* 81, 351–374.

Wittmann K.J. (2009) Revalidation of *Chlamydopleon aculeatum* Ortmann, 1893, and its consequences for the taxonomy of Gastrosaccinae (Crustacea: Mysida: Mysidae) endemic to coastal waters of America. *Zootaxa* 2115, 21–33.

Wittmann K.J., Vanagt T.J., Faasse M.A. and Mees J. (2012) A new transoceanic invasion? First records of *Neomysis americana* (Crustacea: Mysidae) in the East Atlantic. *The Open Marine Biology Journal* 6, 62–66.

Zagursky G. and Feller R.J. (1985) Macrophyte detritus in the winter diet of the estuarine mysid, *Neomysis americana*. *Estuaries* 8, 355–362.
Zimmer C. (1915) Schizopoden des Hamburger Naturhistorischen (Zoologischen) Museums. *Mitteilungen aus dem Naturhistorischen Museum in Hamburg* 32, 159–182.
Zimmer C. (1918) Neue und wenig bekannte Mysidaceen des Berliner Zoologischen Museums. *Mitteilungen aus dem Zoologischen Museum in Berlin* 9, 15–26.

Chapter 3. Distribution, salinity tolerance and production of dominant mysids from the Cananeia-Iguape Coastal System, southeast Brazil

Abstract

We studied the population dynamics of marine mysids from the Cananeia-Iguape Coastal System, southeast Brazil, exploring their spatial and temporal distribution pattern in relation to environmental variables and zooplankton abundance. We also analyzed mysid reproductive traits, estimated their annual production, and tested their tolerance to salinity gradients in laboratory experiments. Salinity and temperature were important factors influencing mysid spatio-temporal distribution in the studied region. Mysids were more abundant in spring, when thermohaline conditions were more favorable and food availability was high. The minimum salinity tolerated by *Metamysidopsis elongata atlantica* and *Mysidopsis coelhoi* in the salinity gradient experiment was similar to the minimum salinity of their respective *in situ* occurrence. The former was the numerically dominant species, probably because it is the single mysid species that may occur in lower salinity areas, where food is more abundant and other mysid species are absent, thus avoiding interspecific competition and intraguild predation. *Metamysidopsis e. atlantica* had high annual production values, probably consequence of the warm water (>19°C) and high food availability that predominates throughout the year in the Cananeia-Iguape Coastal System, which favors continuous breeding and high growth rates. These results confirm the importance of mysids in the carbon flux of tropical and subtropical coastal waters.

Keywords: Mysidacea, benthopelagic, subtropical estuary, salinity gradient, production, biomass.

3.1. Introduction

Mysids distinguish from other crustaceans by the presence of a ventral brood pouch (only adult females) and a statocyst in the uropods. These peracaridan crustaceans have a wide distribution in the marine environment, occurring from subpolar to tropical estuarine, neritic and oceanic waters, at depths varying from few centimeters to >7 km (Murano 1999). However, they are particularly abundant and have an important trophic role in marine coastal ecosystems. Mysids total length varies according to species, with coastal and neritic species measuring between 5-25 mm, whereas oceanic species are usually larger (25-80 mm; Mauchline 1980).

Most mysid species are hyperbenthic, i.e. they live on the sediment or in the water column adjacent to the sea bottom. Interestingly, some species of the subfamily Gastrosaccinae are even capable of burrowing. Furthermore, several mysids species perform vertical migration, i.e. they stay close to the bottom during the day and migrate to the water column at nighttime (Almeida Prado 1973; Rudstam et al. 1989; Kouassi et al. 2006). Coastal species also perform horizontal migrations, with such behavior varying in relation to ontogenetic stage and sex (Webb & Wooldridge 1990; Takahashi & Kawaguchi 1997; Suzuki et al. 2009). Besides migration, most mysid species have gregarious habits (Mauchline 1980). Both migration and schooling are performed to reduce predation pressure, and/or to enhance feeding and reproduction success (Webb & Wooldridge 1990; Takahashi & Kawaguchi 1997; Lesutienė et al. 2008).

Mysids are omnivorous and may feed on cyanobacteria, algae, detritus and small invertebrates (Rudstam et al. 1989; Kouassi et al. 2006; Gorokhova 2009; Carrasco & Perissinotto 2011). They are frequently the dominant benthic epifauna in coastal waters (Tararam et al. 1996; Rappé et al. 2011), thus representing a key trophic link between producers/primary consumers and upper level consumers, such as large invertebrates, fish, birds and mammals (Sanger 1987; Wakabara et al. 1996; Lake et al. 2003; Rodríguez-Graña et al. 2008; Feyrer & Duffus 2011). Moreover, because of their hyperbenthic and diel migratory behavior, mysids have a major role in the benthic-pelagic coupling (Jumars 2007).

Despite the ecological importance of mysids, few studies focused on this group, especially in the Southwest Atlantic (Miyashita & Calliari 2014). In this region, the few existing investigations have emphasized the taxonomy and distribution of mysids (e.g., Almeida Prado 1973; Murano 1999; Borzone et al. 2007; Calliari et al. 2007), and no data on biomass and production is available (but see Viñas et al. 2005 for the Rio de la Plata). During an extensive study in the early '70s of the 20th century (over 40 years back), Almeida Prado (1973) found six mysid species within the Cananeia-Iguape Coastal System (CICS; southeast Brazil). Her results also suggested that salinity was a key variable influencing the spatial distribution of different species. Since then no further investigation focused on mysids from the CICS, which has been subject to increasing anthropogenic influence, for instance coastal land use, boat activities, and pollution. Also, despite generally assumed to play an important trophic role, the production of mysids in the CICS has not been so far assessed.

The present investigation was intended to update existing knowledge on the mysid fauna of the CICS, to evaluate the role of salinity as determinant of species distribution, and to provide an estimate of mysid secondary production. We hypothesized that species-specific salinity tolerances determines the spatial distribution of individual species, and thus the spatial pattern in the structure of the mysid assemblage. To test this hypothesis, we evaluated the tolerance of dominant species to salinity in the laboratory; and analyzed mysid *in situ* distribution in relation to environmental variables and food availability. We also quantified biomass and production of dominant mysid species to verify their importance to marine coastal food webs.

3.2. Methods

3.2.1. Study site

The CICS (24°35’- 25°10’S, 47°30’ - 48°05’W) is located in the south coast of the state of São Paulo, southeast Brazil. Annual mean precipitation and air temperature are 2269 mm and 23.8°C, respectively (Miyao et al. 1986; Silva 1989). This estuarine system is surrounded by a coastal plain area, salt marshes, mangroves and the Atlantic rainforest. It is composed by a complex system of meandering channels delimited by four main islands (Cardoso, Cananeia, Comprida and Iguape), with two main connections to the Atlantic Ocean. Circulation along the estuary is driven by semidiurnal tidal currents, with amplitudes of 0.83 m and 0.13 m during spring and neap tides, respectively. The estuary is classified as partially mixed and weakly stratified (Type 2a; Miranda et al. 1995), with several small rivers being responsible for the freshwater discharge (Miyao & Harari 1989).

3.2.2. Sample collection and analyses

Sampling was carried out every second month during daytime, at five sites in the southern part of the CICS (Cananeia estuary; Fig. 3.1), from January 2012 through January 2013, and usually over flood tides. Stations were chosen according to a salinity gradient, with stations 1 to 4 located within the estuary, and station 5 on the outside. On some occasions, some stations could not be sampled because of technical problems or severe weather conditions. Three hyperbenthic samples and one zooplankton sample were collected per site, with an epibenthic sledge (500 µm) and a conic plankton net (90 µm), respectively. For both, the filtered volume was calculated with a Hydro-Bios flow meter. All samples were preserved in 4% formaldehyde–seawater buffered solution. Water temperature and salinity were measured with a multiparameter meter (Oakton, 600 series). Rainfall data were obtained from a permanent meteorological station located near station 3.

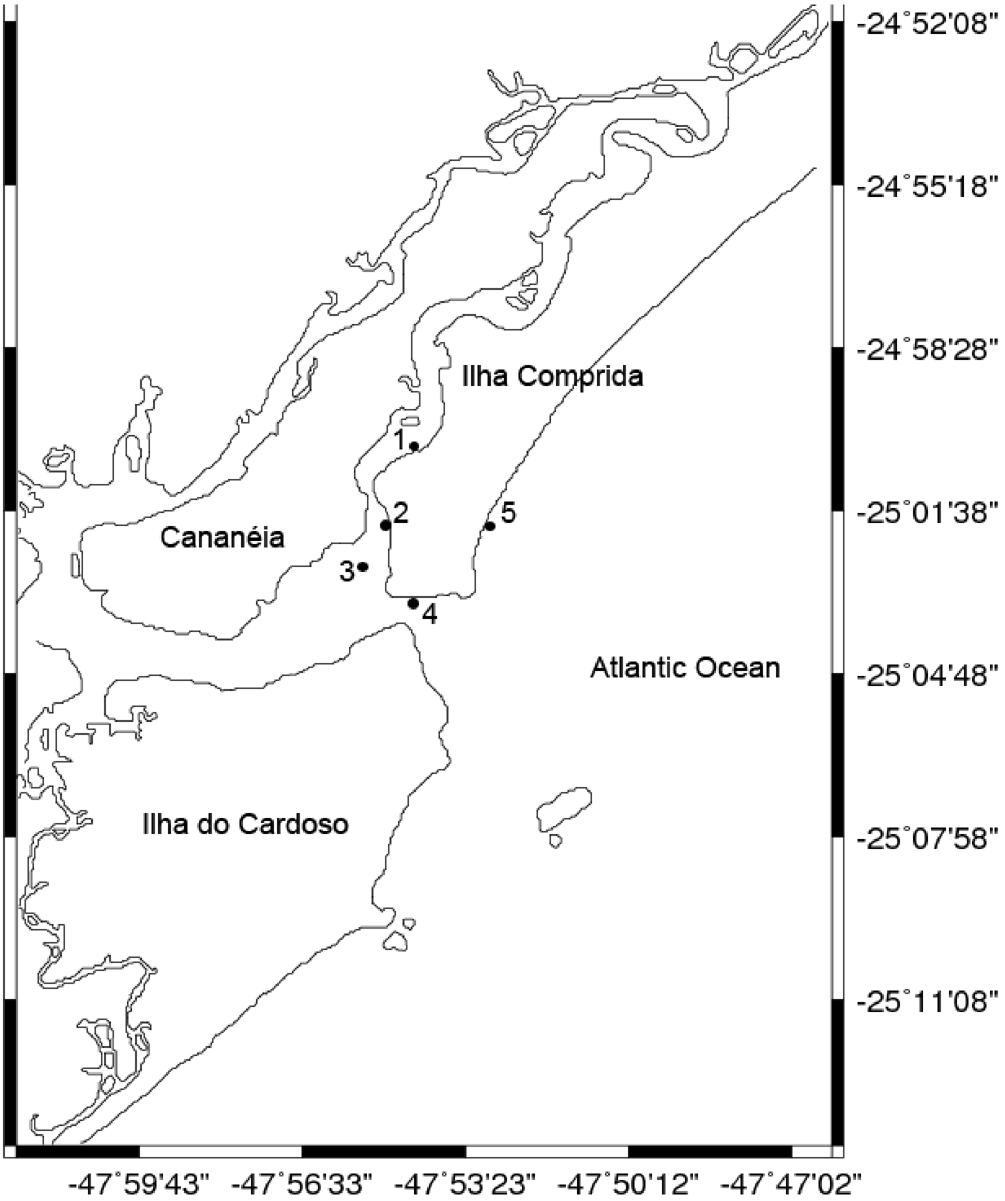


Fig. 3.1. Sampling stations in the Cananeia estuary, southeast Brazil.

Whenever mysids were available, aliquots from the epibenthic sledge samples containing at least 140 individuals of each species per sample were inspected for species identification (Almeida Prado 1974; Murano 1999), enumeration, and measurement. Individuals were categorized as follows (Mauchline 1980):

Juvenile: secondary sexual characteristics absent;

Immature male: secondary sexual characteristics in development process;

Mature male: secondary sexual characteristics totally developed;

Immature female: marsupium without embryos, under developed and smaller compared to a mature female marsupium;

Mature female: marsupium completely developed, but with no embryos.

Gravid female: mature female with embryos. Embryonic development was further categorized into three stages: “egg”, embryo without eye, and eyed embryo (Mauchline 1980).

For each sample, up to 20 individuals per category were measured (body length, BL; from the tip of the rostrum to the end of the telson) by digital image analysis using public domain Image-J software (Schneider et al. 2012). Embryos from up to 20 randomly sorted gravid females per sample were carefully dissected and counted, and the total length of five embryos per female was measured (Image-J software).

For zooplankton, at least 300 individuals per sample were randomly sorted (Motoda splitter; Omori & Ikeda 1984), counted, identified under a stereomicroscope to species level whenever possible (Björnberg 1972, 1981; Bradford-Grieve et al. 1999), and measured (20 individuals per taxon or stage; Image-J software). For less abundant species, larger aliquots were inspected (Frontier 1981). Mysid and zooplankton abundance were expressed as number of individuals per m^3.

Length-weight regression was derived only for the dominant mysid *M. e. atlantica*. Mysids used to obtain the length-weight relationship were collected employing the same sampling design described above. Mysids were diluted in 12–18 L buckets and brought to the laboratory. In the laboratory, live mysids were sorted, identified, and photographed. Body length was measured by digital image analysis using the Image-J software. Each individual was rinsed with distilled water, separated by size-class (1–8 individuals per size class), and placed in pre-weighed aluminum capsules. These capsules were dried at 55°C for 30 hours, cooled in a desiccator, and weighed to ± 0.05 mg. The dry weight (DW, mg) for each size-class was obtained as the difference between the final (aluminum capsule + mysids) and initial (aluminum capsule) weight, divided by the number of organisms present in the capsule. The relationship between BL and DW was described using the following equation:

$\log DW = \log a + b \log BL$.

For each sample DW, ash-free dry weight (AFDW) or carbon weight (CW) of copepods and mysids were estimated based on body length and allometric equations (Uye 1982; Berggreen et al. 1988; Hansen & Ockelmann 1991; Webber & Roff 1995; Fotel et al. 1999; Hansen 1999; Ara 2001; Turner et al. 2001; Uye et al. 2002; Almeda et al. 2010). For copepods, AFDW was converted to DW assuming AFDW = 0.89 DW (Båmstedt 1986). DW was converted to CW using a conversion factor of 0.40 and 0.46 for mysids (Uye 1982) and copepods (Ara 2001), respectively. Biomass (B; mg C m^{-3}) of each taxon was estimated by multiplying its mean CW by its *in situ* density.

Metamysidopsis elongata atlantica daily growth rates (g; d^{-1}) were estimated using the following equation:

$g = -0.0097 + 1.98\ T \times 10^{-3}$ ($r^2 = 0.41$),

where T is water temperature (°C). We obtained this equation from growth rates measured by Gama et al. (2006) during experiments conducted in the laboratory at different combinations of temperature and salinity. These authors observed that *M. e. atlantica* growth rates were not affected by salinity, only by temperature (Gama et al. 2006).

Copepods daily growth rates were estimated through the Hirst & Lampitt (1998) empirical model, which considers water temperature and body weight to its calculation. Mysid and copepod production (mg C m^{-3} d^{-1}) were calculated from the product of g and B.

Spatial differences were analyzed with one-way ANOVA ($\alpha = 0.05$). Principal component analysis was used to explore the influence of abiotic variables (temperature, salinity, and rainfall) and zooplankton density on mysid abundance. All data from each month and station were considered.

3.2.3. Salinity tolerance

Mysids were collected through the same sampling design described above, in January and May 2012, in the Cananeia estuary. Water temperature and salinity were measured with a multiparameter sensor (Oakton, 600 series). In the laboratory, live mysids were sorted, identified, categorized (female, male, or juvenile), and incubated individually in plastic cups (300 mL) with filtered seawater (10 µm). Cups were maintained in darkness and at constant temperature (mean of 25.7 ± 0.3ºC), similar to that of the sampling site at the time of mysid collection. The three dominant mysid species were used in the experiments: *Chlamydopleon dissimile*, *M. e. atlantica* and *Mysidopsis coelhoi*. For each species, 10 control and 10 experimental cups were established to test their tolerance to salinity gradients. Control replicates consisted of mysids incubated in seawater from the site where they had been collected (salinity of 27.4 for *C. dissimile*, and 30.0 for *M. e. atlantica* and *M. coelhoi*). Water of different salinities was prepared by seawater dilution with distilled water. To test tolerance to salinity changes, organisms were subjected to successive changes in salinity at steps of 5 (except for salinity below 5: 30, 25, 20, 15, 10, 5 and 3), and allowing for a 3 h acclimatization period between changes. Before each salinity reduction, the condition of each individual was checked (live or dead). The experiment ended when at least 50% of the organisms were found dead.

3.3. Results

3.3.1. Environmental variables

There were no significant differences in temperature between sampling sites (ANOVA, $p > 0.05$), but there was a clear seasonality, temperatures were higher from late spring to summer (ranged from 25.4 to 32.6°C), and lower during autumn/winter (ranged from 20.0 to 23.3°C). Salinity increased seaward (from stations 1 to 5); lower salinity values were associated with rainfall during sampling day, which occurred in July 2012 and January 2013. Rainfall was more intense in summer (rainy season) and lower in winter and early spring (dry season; Fig. 3.2).

3.3.2. Zooplankton

Zooplankton community was dominated by copepod nauplii and copepodites, mainly *Oithona* spp. (*Oithona hebes* and *Oithona oswaldocruzi*), followed by *Pseudodiaptomus acutus*, *Acartia lilljeborgii*, and *Temora turbinata*. Other taxa that were numerically important at certain periods were *Oikopleura dioica*, cladocerans, and larvae of Bivalvia, Cirripedia, Gastropoda, and Polychaeta. Zooplankton was abundant during the entire study period, but highly variable (ranged from 5,539 to 202,666 ind. m^{-3}), peaking in November 2012 and January 2013 (Fig. 3.3). Zooplankton biomass and production (only copepods) mirrored the abundance pattern.

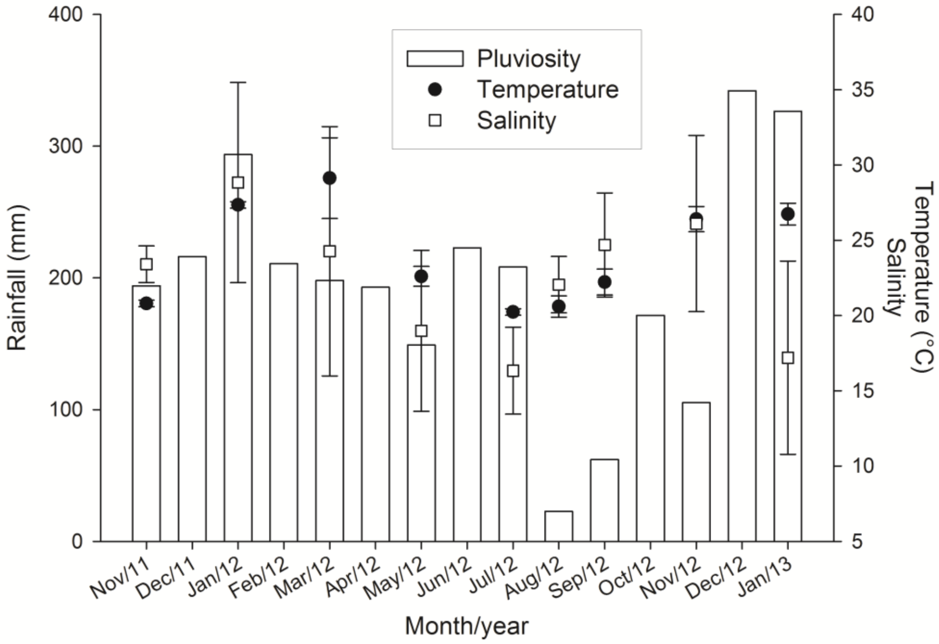


Fig. 3.2. Rainfall data, and mean water temperature and salinity in the Cananeia estuary, between November 2011 and January 2013. Error bars represent the standard deviation.

3.3.3. Mysids

We found 5 mysids species: *Brasilomysis castroi*, *Chlamydopleon dissimile*, *Metamysidopsis elongata atlantica*, *Mysidopsis coelhoi*, and *Mysidopsis juniae*. *B.castroi* and *M. juniae* were rare, the former occurred only at the outermost station (station 5) in January and November 2012, whereas *M. juniae* was found once at station 4 in March 2012. The other three species were frequently found along the study period (Fig. 3.3), but with different distributional patterns.

Chlamydopleon dissimile and *M. coelhoi* did not show a clear seasonal pattern, both species occurred at low abundances along the year and were limited to salinity values higher than 18 (stations 2 through 5; Fig. 3.3). *Metamysidopsis e. atlantica* had the widest spatial distribution, occurring at all sampling stations. It was also the dominant species (Fig. 3.3), attaining higher abundances in spring (September and November 2012; up to 35,964 ind. m^{-3}) at station 3. Principal component analysis showed that mysid lower abundances were related to lower salinities and increasing rainfall (Fig. 3.4).

Juveniles were the dominant stage for the three main species: *C. dissimile, M. coelhoi*, and *M. e. atlantica*. However, for *M. e. atlantica* the other stages were also observed all year long, except in May 2012 (Fig. 3.5). Males and females of *M. e.*

atlantica were more abundant in September and November 2012, when population abundance peaked. During these months sex ratio was close to 1.

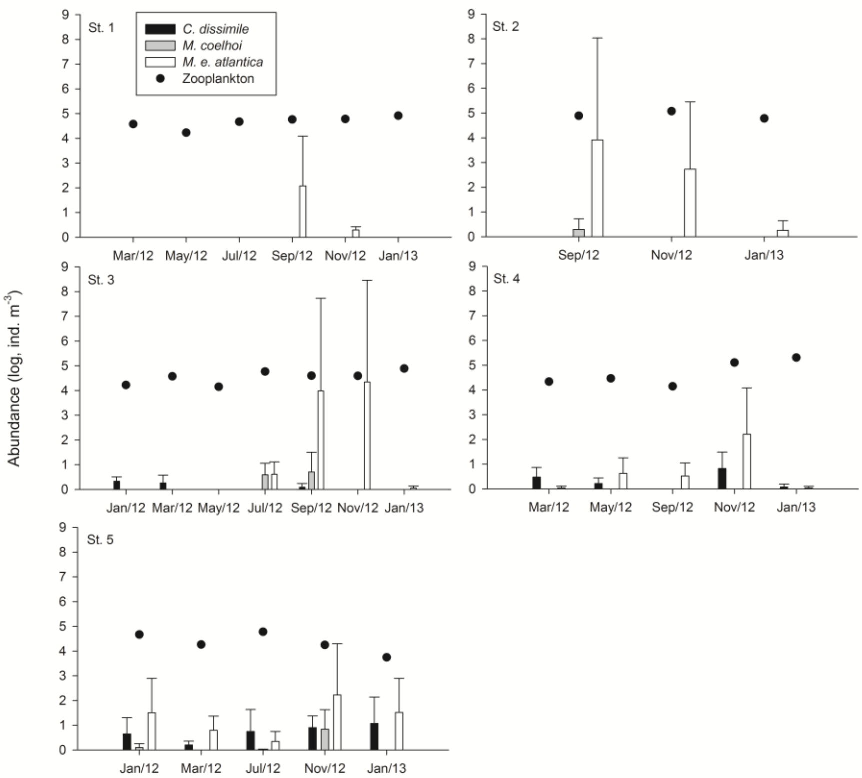
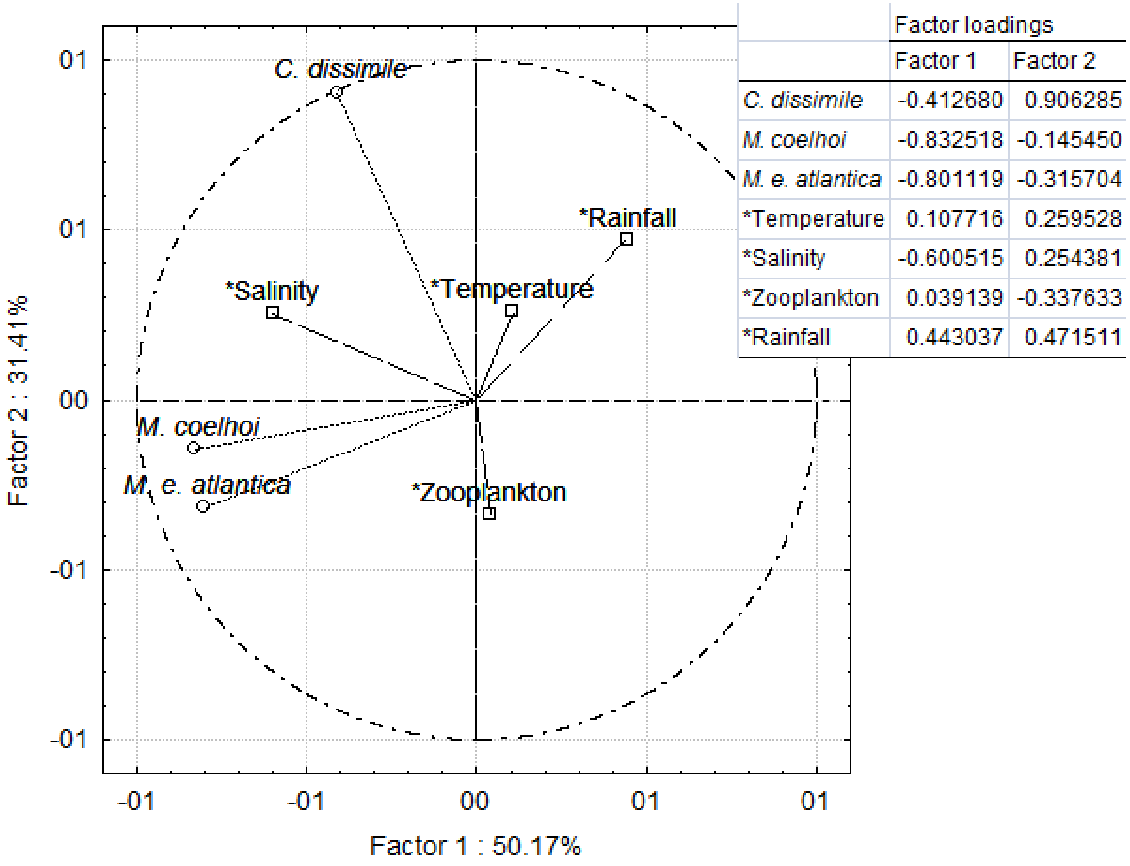


Fig. 3.3. Abundance of the three main mysid species at five stations in the Cananeia estuary, from January 2012 through January 2013.

The brood size of *M. e. atlantica* and *M. coelhoi* increased with body length (Fig. 3.6). Gravid females of both species had similar mean body length, but *M. coelhoi* had larger brood sizes (Table 3.1). The brood size of *C. dissimile* ranged from 29 to 50 (mean ± SD = 40 ± 11), but only three gravid females were found and analyzed. No gravid *B. castroi* and *M. juniae* females were found.

The relationship between BL and DW was obtained only for the numerically dominant species *M. e. atlantica*: log DW = 2.30 log BL – 2.38 (r^2 = 0.99; Fig. 3.7). Growth rate, biomass and production were also only calculated for *M. e. atlantica* (Table 3.2). Growth rates were higher during warmer months. Biomass and production followed the abundance distribution pattern, with low values during most of the year (Fig. 3.8), except in spring (September and November 2012) when high biomass and production values were observed.



	Factor loadings	
	Factor 1	Factor 2
C. dissimile	-0.412680	0.906285
M. coelhoi	-0.832518	-0.145450
M. e. atlantica	-0.801119	-0.315704
*Temperature	0.107716	0.259528
*Salinity	-0.600515	0.254381
*Zooplankton	0.039139	-0.337633
*Rainfall	0.443037	0.471511

Fig. 3.4. Principal component analysis for abundance of the three main mysid species, and temperature, salinity, rainfall, and zooplankton abundance.

3.3.4. Salinity tolerance

No mortality was observed in any of the control cups. *Chlamydopleon dissimile* was the most tolerant species to low-salinity, surviving well down to 5. At salinity 3, 50% of the individuals died (Fig. 3.9). *Metamysidopsis e. atlantica* tolerated a minimum salinity of 15 with 70% survival rate. At salinity 10, 100% of the specimens deceased. *Mysidopsis coelhoi* survived down to a salinity of 20; mortality was 80% at salinity 15 (Fig. 3.9). Low abundance of *B. castroi* and *M. juniae* prevented evaluation of their salinity tolerance.

3.4. Discussion

We observed a similar number of mysid species compared to that previously

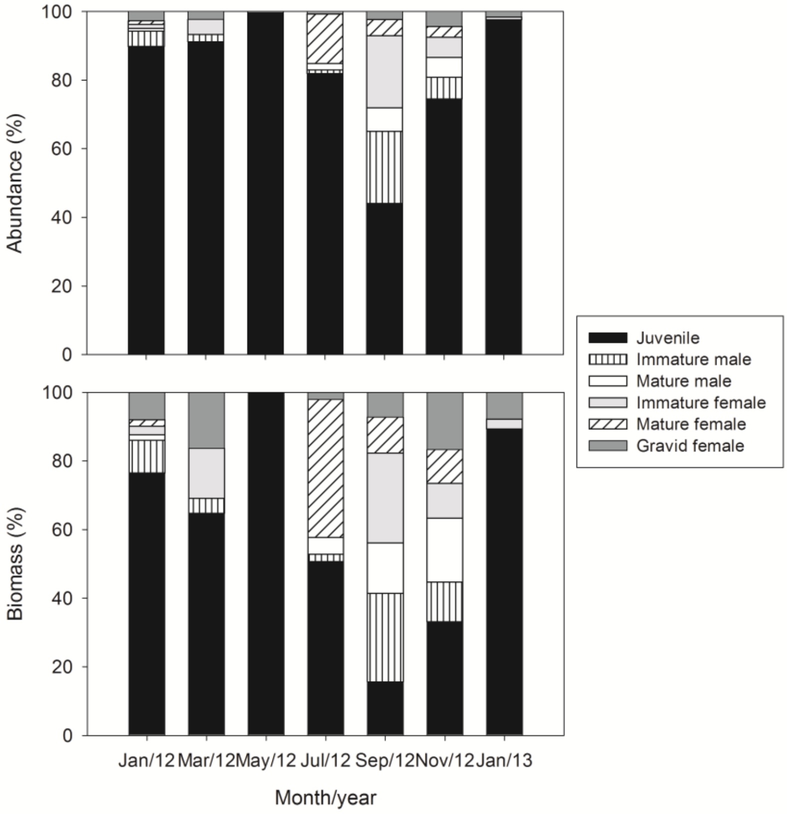


Fig. 3.5. Relative abundance and biomass temporal distribution of the different stages of *Metamysidopsis elongata atlantica*, from January 2012 through January 2013.

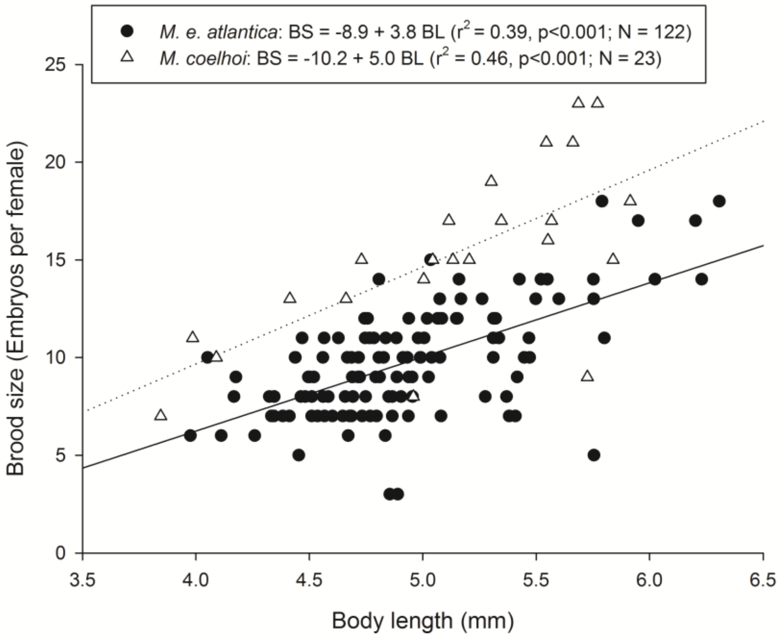


Fig. 3.6. Relationship between body length (BL) and brood size (BS) for *Metamysidopsis elongata atlantica* (solid line) and *Mysidopsis coelhoi* (dashed line).

Table 3.1. Reproductive parameters of *Metamysidopsis elongata atlantica* and *Mysidopsis coelhoi*: range and mean ± standard deviation of gravid female body length and brood size, and mean length of embryos separated by category.

Species	Body length (mm)			Brood size (N)			Embryos length (mean ± SD; mm)		
	Range	Mean ± SD	N	Range	Mean ± SD	N	Stage 1	Stage 2	Stage 3
M. e. atlantica	3.9-6.3	4.9 ± 0.5	123	3-18	9.7 ± 2.9	122	0.35 ± 0.03 (N=294)	0.68 ± 0.10 (N=262)	0.94 ± 0.11 (N=48)
M. coelhoi	3.8-5.9	5.1 ± 0.6	25	7-23	15.3 ± 4.4	23	0.37 ± 0.03 (N=44)	0.81 ± 0.16 (N=38)	0.95 ± 0.14 (N=35)

Table 3.2. Annual production (mg C m^{-3} $year^{-1}$) of mysids from different marine environments.

Species	T (°C)	Depth (m)	Production	Location	Source
Metamysidopsis elongata atlantica	20.0 - 32.6	0.3 - 1.5	425.0	Cananeia estuary, Brazil	This study
Anisomysis mixta australis	10.4 - 17.8	2 - 4	9.2	One Three Point, Tasmania	Fenton (1996)
Paramesopodopsis rufa	10.4 - 17.8	2 - 4	12.1	One Three Point, Tasmania	Fenton (1996)
Tenagomysis tasmaniae	10.4 - 17.8	2 - 4	31.84	One Three Point, Tasmania	Fenton (1996)
Mesopodopsis slabberi	11 - 26	<4	6.4	Mondego estuary, Portugal	Azeiteiro et al. (1999)
Rhopalophthalmus terranatalis	14 - 26	<2 - 6	1150.0	Sundays estuary, South Africa	Wooldridge (1986)
Schistomysis spiritus	10.1 - 18.9	31	12.3	Bay of Biscay, Spain	Vicente and Sorbe (1995)

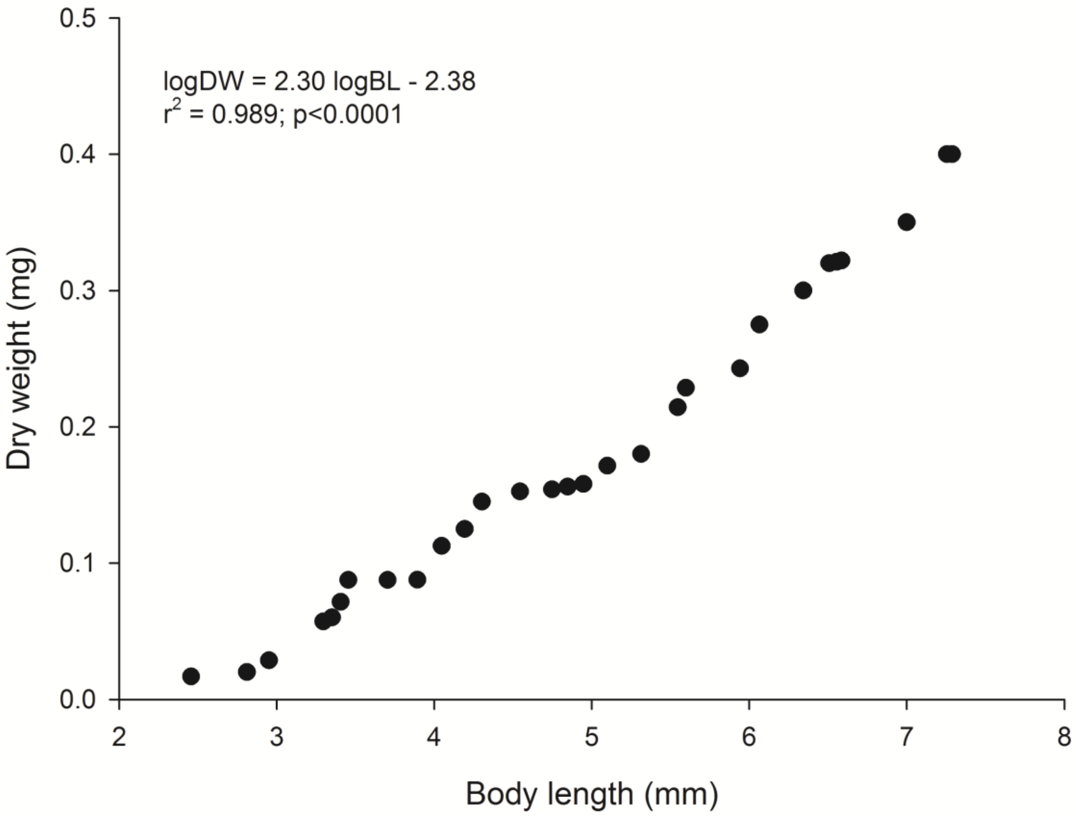


Fig. 3.7. Relationship between body length (BL, mm) and dry weight (DW, mg) for *Metamysidopsis elongata atlantica*.

recorded in the same region (Almeida Prado 1973; Tararam et al. 1996), but with some important differences in the assemblage composition. The main difference was that on the one hand we registered *M. juniae* for the first time in the Cananeia estuary, but on the other hand, we did not find two species that were previously recorded: *Mysidopsis tortonesei* (Almeida Prado 1973; Tararam et al. 1996; Wakabara et al. 1996) and *Promysis atlantica* (Almeida Prado 1973). Interestingly, *M. tortonesei* was the dominant species in the Cananeia region in the early 1970's, followed by *B. castroi* (Almeida Prado 1973). However, in the next decade, *M. tortonesei* was found at low abundances, being replaced by *M. e. atlantica* as the dominant species (Tararam et al. 1996; Wakabara et al. 1996), as observed here. This shift in species composition in the Cananeia estuary might be related to anthropogenic impacts, such as eutrophication, and the ongoing alteration in freshwater discharge and sediment transport caused by the construction of an artificial channel in the 19th century (Barrera-Alba et al. 2007).

All mysid species observed here are coastal water species that may migrate into the estuary (Almeida Prado 1973). Therefore, salinity can be thought of as the main

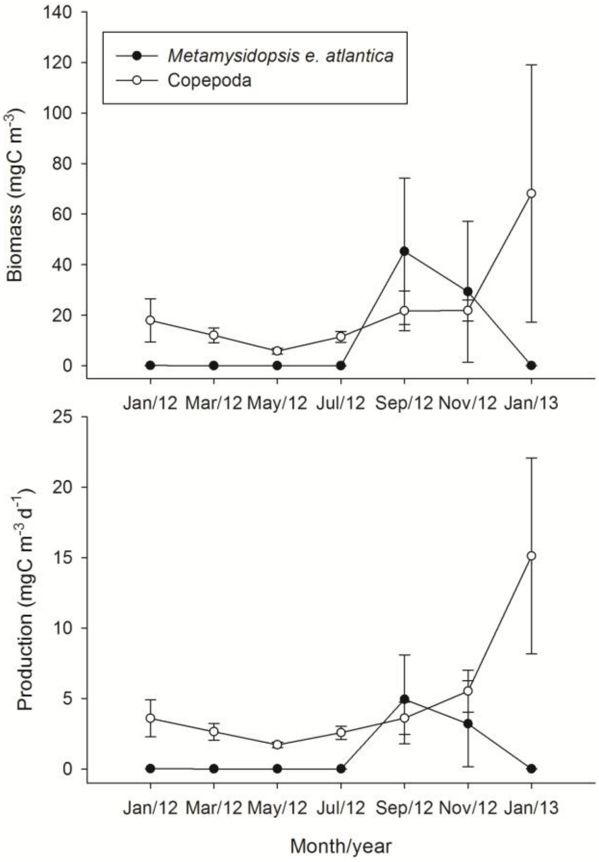


Fig. 3.8. Biomass and production of *Metamysidopsis elongata atlantica* and Copepoda in the Cananeia estuary, from January 2012 through January 2013.

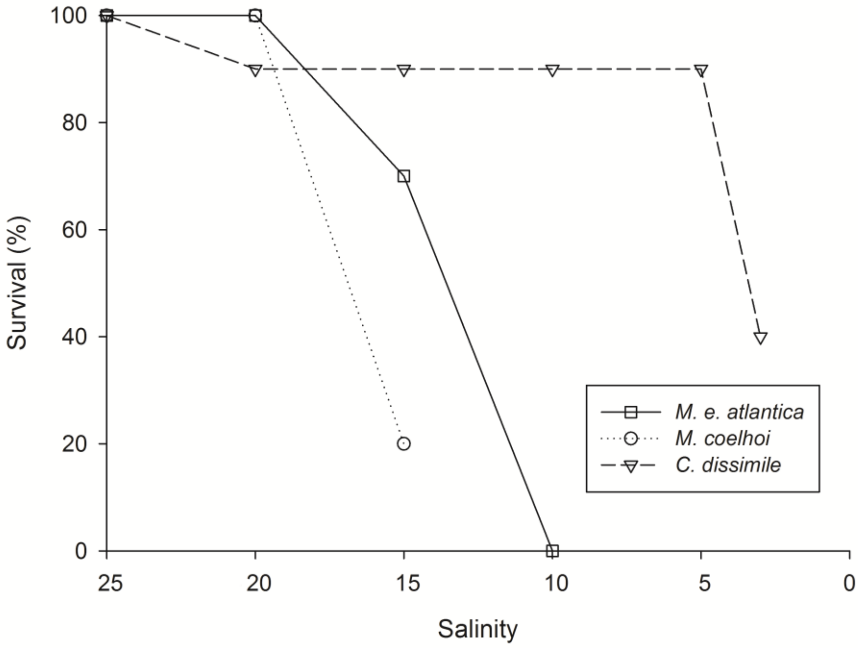


Fig. 3.9. *Metamysidopsis elongata atlantica*, *Mysidopsis coelhoi* and *Chlamydopleon dissimile* surviving rate in the salinity tolerance experiment.

factor influencing mysid spatio-temporal distribution in the Cananeia estuary, as commonly observed in estuaries worldwide (Rio de la Plata, Calliari et al. 2007; Guadalquivir, Vilas et al. 2009; Westerschelde, Rappé et al. 2011). In our study, *M. e. atlantica* had the widest spatial distribution along the estuary, whereas *M. coelhoi* and *C. dissimile* were limited to higher salinities regions. The minimum salinity tolerated by *M. e. atlantica* (15) and *M. coelhoi* (20) in the laboratory experiments was similar to the minimum salinity where they occurred *in situ*, i.e. 13 and 18, respectively. The wider distribution of *M. e. atlantica* along the estuary is probably associated to its numerical dominance in relation to other mysid species. That occurs because the lower salinity areas are usually richer in food concentration due to the influence of rivers discharge and the mangrove forest (Jorcin 2000; Barrera-Alba et al. 2008). Moreover, *M. e. atlantica* is highly benefited by the absence of other mysid species in these regions, as it avoids interspecific competition and intraguild predation (Chapter 4).

Conversely, *C. dissimile* was the most tolerant species to low salinities (5) according to experimental results, but its distribution in the natural environment did not match such capability, as it was restricted to the upper salinity range (18-36). Higher tolerance of *C. dissimile* to low salinities may be an evolutionary adaptation related to limited mobility linked to burrowing behavior to avoid unfavorable haline conditions (e.g., during tidal cycles), especially at daytime when this species tends to stay within the sediments (personal observation). Occurrence of *C. dissimile* over a narrow salinity range points to factors other than salinity as determinant of its distribution in the Cananeia estuary. For example, sediment characteristics in low salinity sites of this estuary is composed mostly by a fine muddy sand (Jorcin 2000), which seems inappropriate for burrowing (e.g., Nel et al. 1999).

Besides salinity, temperature was also important in structuring mysid seasonal distribution, although temperature was not detected as a first-order variable for explaining mysid abundance. Mysids attained higher biomass and production during warmer months because of higher metabolic rates (Ikeda 2013) and individual growth rates with increased temperature (Gama et al. 2006), thus favoring a faster population growth. Abundance peaks in spring are usually observed in the Cananeia region (Almeida Prado 1973; Tararam et al. 1996), when most favorable thermohaline conditions for mysids to thrive occur, i.e. temperature starts to increase and salinity is not as low as in summer (rainy season). Furthermore, mysid production peaks are coupled to the higher zooplankton production observed during warmer months, seeing that zooplankton comprises an important food item for mysids (Rudstam et al. 1989; Kouassi et al. 2006; Carrasco & Perissinotto 2011). Moreover, other likely food sources such as phytoplankton (Barrera-Alba et al. 2008) and detritus (Jorcin 2000) are also more abundant during the warmer season.

Conversely, predation pressure is likely to represent a major limiting factor for mysid populations in the Cananeia estuary, as parasites or diseases were not observed (e.g., Ohtsuka et al. 2011). Wakabara et al. (1993) analyzed the diet of 30 fish species from the Cananeia region, and observed that mysids were preyed by 18 of them, mainly by juveniles of the whitemouth croaker (*Micropogonias furnieri*), the leatherjacket (*Oligoplites* sp.), the tonguefish (*Symphurus jenynsii*), and the little croaker (*Stellifer stellifer*). The importance of mysids as the main prey for upper level consumers (e.g., fish, birds, seals, whales) has already been described for other coastal systems (Sanger 1987; Lake et al. 2003; Rodríguez-Graña et al. 2008; Feyrer & Duffus 2011).

Mysids seem to breed continuously in the Cananeia estuary (Almeida Prado 1973), as indicated by the presence of juveniles and gravid females throughout the year. Even in May 2012, when we found only juveniles in our samples, we did observe high abundances of all mysid stages when collecting mysids for another experiment (Chapter 4). This inconsistency occurred because mysids have a strong migratory behavior, which makes them complicated to locate and quantify (Miyashita & Calliari 2014).

Mysids brood size varied inter- and intraspecifically, being positively correlated to female body size, as usually observed (Baldó et al. 2001; Hanamura et al. 2009; Feyrer 2010). The differences in brood size between the three main mysid species suggest that they have distinct reproductive strategies (Feyrer 2010), although based on current results it is not clear how brood size relates to *in situ* abundance. The dominant species *M. e. atlantica* had the smallest brood size. To outnumber the other mysid species and maintain high abundances, *M. e. atlantica* probably (i) compensates the smaller brood sizes with faster embryonic development and/or faster sexual maturation, to attain a fecundity similar to that of other mysid species; (ii) exploits a different suite of resources (e.g., food types); or (iii) is more efficient in the use of common resources. In contrast, *C. dissimile* and *M. coelhoi* have low abundances, but are able to sustain their population producing larger brood sizes. These are issues that deserve further attention in future studies in order to gain a better understanding of community dynamics of the mysid assemblage of the Cananeia estuary.

Metamysidopsis e. atlantica had high annual production value compared with mysid production from other coastal systems (Table 3.2). In spring, its production was even comparable to copepod production. This high production value is probably consequence of the combination of warm water (>19°C) and high food availability that predominates throughout the year in the Cananeia estuary, but mainly in spring, which favors continuous breeding and high growth rates. This suggests that mysids play a key role in the Cananeia estuary linking producers/primary consumers and upper trophic levels (Wakabara et al. 1993, 1996), thus being essential for the sustenance of both commercial and subsistence fisheries in the region.

3.5. Conclusions

Salinity, followed by temperature, were the main factors influencing mysid spatio-temporal distribution in the Cananeia estuary. Mysids showed higher abundance and production in spring, when more favorable thermohaline conditions coupled with higher food availability were observed.

Metamysidopsis e. atlantica was the most abundant species. Its numerical dominance in relation to other mysid species was a result of a combination of factors: (i) *M. e. atlantica* had wider spatial distribution, occurring in lower-salinity areas than the other mysid species, thus avoiding interspecific competition and intraguild predation (Chapter 4). Moreover, these estuarine inner areas usually provide higher food concentration (Jorcin 2000; Barrera-Alba et al. 2008); and (ii) *M. e. atlantica* probably compensates the smaller brood sizes with a faster life cycle, i.e. earlier sexual maturation and shorter embryonic development.

Mysid high annual production confirms their importance in the carbon flux of marine coastal waters. Therefore, despite all the difficulties related to mysid sampling (Miyashita & Calliari 2014), mysids should be considered in future trophodynamics studies and models.

3.6. References

Almeda R., C.B. Augustin, M. Alcaraz, A. Calbet, and E. Saiz. 2010. Feeding rates and gross growth efficiencies of larval developmental stages of *Oithona davisae* (Copepoda, Cyclopoida). *Journal of Experimental Marine Biology and Ecology* 387: 24–35.

Almeida Prado, M.S. 1973. Distribution of Mysidacea (Crustacea) in the Cananéia region. *Boletim de Zoologia e Biologia Marinha, Nova Série* 30: 395–417.

Almeida Prado, M.S. 1974. Sistemática dos Mysidacea (Crustacea) na região de Cananéia. *Boletim do Instituto Oceanográfico São Paulo* 23: 47–87.

Ara, K. 2001. Length-weight relationships and chemical content of the planktonic copepods in the Cananéia Lagoon estuarine system, São Paulo, Brazil. *Plankton Biology and Ecology* 48: 121–127.

Azeiteiro, U.M.M., L. Jesus, and J.C. Marques. 1999. Distribution, population dynamics, and production of the suprabenthic mysid *Mesopodopsis slabberi* in the Mondego Estuary, Portugal. *Journal of Crustacean Biology* 19: 498–509.

Baldó, F., L.J. Taracido, A.M. Arias, and P. Drake. 2001. Distribution and life history of the mysid *Rhopalophthalmus mediterraneus* in the Guadalquivir Estuary (SW Spain). *Journal of Crustacean Biology* 21: 961–972.

Båmstedt, U. 1986. Chemical composition and energy content. In The biological chemistry of marine copepods, eds. E.D.S. Corner, and S.C.M. O´Hara, 1–58. New York: Oxford University Press.

Barrera-Alba, J.J., S.M.F. Gianesella, F.M.P. Saldanha-Corrêa, and G.A.O Moser. 2007. Influence of an artificial channel in a well-preserved sub-tropical estuary. *Journal of Coastal Research SI* 50: 1137–1141.

Barrera-Alba, J.J., S.M.F. Gianesella, G.A.O. Moser, and F.M.P. Saldanha-Corrêa. 2008. Bacterial and phytoplankton dynamics in a sub-tropical estuary. *Hydrobiologia* 598: 229–246.

Berggreen, U., B. Hansen, and T. Kiørboe. 1988. Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. *Marine Biology* 99: 341–352.

Björnberg, T.K.S. 1972. Developmental stages of some tropical and subtropical planktonic marine copepods. *Studies on the Fauna of Curaçao and Other Caribbean Islands* 40: 1–185.

Björnberg, T.K.S. 1981. Copepoda. In Atlas del Zooplancton del Atlántico Sudoccidental y Métodos de Trabajo con el Zooplancton Marino, ed. D. Boltovskoy, 587–679. Mar del Plata: INIDEP.

Bradford-Grieve, J.M., E.L. Markhaseva, C.E.F. Rocha, and B. Abiahy. 1999. Copepoda. In South Atlantic Zooplankton, ed. D. Boltovskoy, 869–1098. Leiden: Backhuys Publishers.

Calliari, D., G. Cervetto, R. Castiglioni, and L. Rodríguez. 2007. Salinity preferences and habitat partitioning between dominant mysids at the Río de la Plata estuary (Uruguay). *Journal of the Marine Biological Association of the United Kingdom* 87: 501–506.

Carrasco, N.K., and R. Perissinotto. 2011. The comparative diet of the dominant zooplankton species in the St Lucia Estuary, South Africa. *Journal of Plankton Research* 33:479–490.

Fenton, G.E. 1996. Production and biomass of *Tenagomysis tasmaniae* Fenton, *Anisomysis mixta australis* (Zimmer) and *Paramesopodopsis rufa* Fenton from south-eastern Tasmania (Crustacea: Mysidacea). *Hydrobiologia* 323: 23–30.

Feyrer, L.J. 2010. Differences in embryo production between sympatric species of mysids (family Mysidae) in the shallow coastal waters off Vancouver Island, BC. *Marine Biology* 157: 2461–2465.

Feyrer, L.J., and D.A. Duffus. 2011. Predatory disturbance and prey species diversity: the case of gray whale (*Eschrichtius robustus*) foraging on a multi-species mysid (family Mysidae) community. *Hydrobiologia* 678: 37–47.

Fotel, F.L., N.J. Jensen, L. Wittrup, and B.W. Hansen. 1999. *In situ* and laboratory growth by a population of blue mussel larvae (*Mytilus edulis* L.) from a Danish embayment, Knebel Vig. *Journal of Experimental Marine Biology and Ecology* 233: 213–230.

Frontier, S. 1981. Diseño de muestros. In Atlas del Zooplancton del Atlántico Sudoccidental y Métodos de Trabajo con el Zooplancton Marino, ed. D. Boltovskoy, 103–108. Mar del Plata: INIDEP.

Gama, A.M.S., M.A. Montú, and F. D'Incao. 2006. Ciclo de mudas e taxas de crescimento de *Metamysidopsis elongata atlantica* (Crustacea, Mysidacea) cultivado em diferentes temperaturas e salinidades. *Iheringia Série Zoologia* 96: 67–70.

Gorokhova, E. 2009. Toxic cyanobacteria *Nodularia spumigena* in the diet of Baltic mysids: Evidence from molecular diet analysis. *Harmful Algae* 8: 264–272.

Hanamura, Y., R. Siow, P.E. Chee, and F.M. Kassim. 2009. Seasonality and biological characteristics of the shallow-water mysid *Mesopodopsis orientalis* (Crustacea: Mysida) on a tropical sandy beach, Malaysia. *Plankton Benthos Research* 4: 53–61.

Hansen, B., and K.W. Ockelmann. 1991. Feeding behaviour in larvae of the opistobranch *Philine aperta* I. Growth and functional response at different developmental stages. *Marine Biology* 111: 255–261.

Hansen, B.W. 1999. Cohort growth of planktotrophic polychaete larvae–are they food limited? *Marine Ecology Progress Series* 178: 109–119.

Hirst, A.G., and R. S. Lampitt. 1998. Towards a global model of in situ weight-specific growth in marine planktonic copepods. *Marine Biology* 132: 247–257.

Ikeda, T. 2013. Synthesis towards a global-bathymetric model of metabolism and chemical composition of mysid crustaceans. *Journal of Experimental Marine Biology and Ecology* 445: 79–87.

Jorcin, A. 2000. Physical and chemical characteristics of the sediment in the estuarine region of Cananéia (SP), Brazil. *Hydrobiologia* 431: 59–67.

Jumars, P.A. 2007. Habitat coupling by mid-latitude, subtidal, marine mysids: import-subsidised omnivores. *Oceanography and Marine Biology: An Annual Review* 45: 89–138.

Kouassi, E., M. Pagano, L. Saint-Jean, and J.C. Sorbe. 2006. Diel vertical migrations and feeding behavior of the mysid *Rhopalophthalmus africana* (Crustacea: Mysidacea) in a tropical lagoon (Ebrié, Côte d'Ivoire). *Estuarine, Coastal and Shelf Science* 67: 355–368.

Lake, S., H. Burton, and J. van den Hoff. 2003. Regional, temporal and fine-scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica. *Marine Ecology Progress Series* 254: 293–305.

Lesutienė, J., E. Gorokhova, Z.R. Gasiūnaitė, and A. Razinkovas. 2008. Role of mysid seasonal migrations in the organic matter transfer in the Curonian Lagoon, south-eastern Baltic Sea. *Estuarine, Coastal and Shelf Science* 80: 225–234.

Mauchline, J. 1980. The biology of mysids and euphausiids. *Advances in Marine Biology* 18: 1–681.

Miranda, L.B., A.R. Mesquita, and C.A.S. França. 1995. Estudo da circulação e dos processos de mistura no extremo sul do mar de Cananéia: condições de dezembro de 1991. *Boletim do Instituto Oceanográfico São Paulo* 43: 153–164.

Miyao, S.Y., and J. Harari. 1989. Estudo preliminar da maré e das correntes de maré da região estuarina de Cananéia (25°S-48°W). *Boletim do Instituto Oceanográfico São Paulo* 37: 107–123.

Miyao, S.Y., L. Nishihara, and C.C. Sarti. 1986. Características físicas e químicas do sistema estuarino-lagunar de Cananéia-Iguape. *Boletim do Instituto Oceanográfico São Paulo* 34: 23–36.

Miyashita, L.K., and D. Calliari. 2014. Revision of mysids (Crustacea: Peracarida: Mysida) zoogeographical distribution in the south-west Atlantic (0° to 40°S). *Marine Biodiversity Records* 7: e5.

Murano, M. 1999. Mysidacea. In South Atlantic Zooplankton, ed. D. Boltovskoy, 1099–1140. Leiden: Backhuys Publishers.

Nel, R., A. McLachlan, and D. Winter. 1999. The effect of sand particle size on the burrowing ability of the beach mysid *Gastrosaccus psammodytes* Tattersall. *Estuarine, Coastal and Shelf Science* 48: 599–604.

Ohtsuka, S., T. Horiguchi, Y. Hanamura, A. Yamaguchi, M. Shimomura, T. Suzaki, K. Ishiguro, H. Hanaoka, K. Yamada, and S. Ohtani. 2011. Symbiosis of planktonic copepods and mysids with epibionts and parasites in the north pacific: diversity and interactions. In *New Frontiers in Crustacean Biology,* eds. A. Asakura et al., 1–14. Leiden: Brill.

Omori, M., and T. Ikeda. 1984. Methods in Marine Zooplankton Ecology. New York: John Wiley & Sons.

Rappé, K., N. Fockedey, C.V. Colen, A. Cattrijsse, J. Mees, and M. Vincx. 2011. Spatial distribution and general population characteristics of mysid shrimps in the Westerschelde estuary (SW Netherlands). *Estuarine, Coastal and Shelf Science* 91: 187–197.

Rodríguez-Graña, L., D. Calliari, D. Conde, J. Sellanes, and R. Urrutia. 2008. Food web of a SW Atlantic shallow coastal lagoon: spatial environmental variability does not impose substantial changes in the trophic structure. *Marine Ecology Progress Series* 362: 69–83.

Rudstam, L.G., K. Danielsson, S. Hansson, and S. Johansson. 1989. Diel vertical migration and feeding patterns of *Mysis mixta* (Crustacea, Mysidacea) in the Baltic Sea. *Marine Biology* 101: 43–52.

Sanger, G.A. 1987. Winter diets of common murres and marbled murrelets in Kachemak Bay, Alaska. *Condor* 89: 426–430.

Schneider, C.A., W.S. Rasband, and K.W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671–675.

Silva, J.F. 1989. Dados climatológicos de Cananéia e Ubatuba (Estado de São Paulo). *Boletim Climatológico do Instituto Oceanográfico* 6: 1–21.

Takahashi, K, and K. Kawaguchi. 1997. Diel and tidal migrations of the sand-burrowing mysids, *Archaeomysis kokuboi*, *A. japonica* and *Iiella ohshimai,* in Otsuchi Bay, northeastern Japan. *Marine Ecology Progress Series* 148: 95–107.

Tararam, A.S., Y. Wakabara, and M.N. Flynn. 1996. Suprabenthic community of the Cananeia lagoon estuarine region, Southeastern Brazil. *Cahiers de Biologie Marine* 37: 295–308.

Turner, J.T., H. Levinsen, T.G. Nielsen, and B.W. Hansen. 2001. Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay, West Greenland. *Marine Ecology Progress Series* 221: 209–219.

Uye, S. 1982. Length-weight relationships of important zooplankton from the Inland Sea of Japan. *Journal of the Oceanographical Society of Japan* 38: 149–158.

Uye, S., I. Aoto, and T. Onbé. 2002. Seasonal population dynamics and production of *Microsetella norvegica*, a widely distributed but little-studied marine planktonic harpacticoid copepod. *Journal of Plankton Research* 24: 143–153.

Vicente, C.S., and J.C. Sorbe. 1995. Biology of the suprabenthic mysid *Schistomysis spiritus* (Norman, 1860) in the southeastern part of the Bay of Biscay. *Scientia Marina* 59: 71–86.

Vilas, C., P. Drake, and E. Pascual. 2009. Inter- and intra-specific differences in euryhalinity determine the spatial distribution of mysids in a temperate European estuary. *Journal of Experimental Marine Biology and Ecology* 369: 165–176.

Viñas, M.D., F.C. Ramírez, and H.W. Mianzan. 2005. Annual population dynamics of the opossum shrimp *Neomysis americana* Smith, 1873 (Crustacea: Mysidacea) from an estuarine sector of the Argentine Sea. *Scientia Marina* 69: 493–502.

Wakabara, Y., A.S. Tararam, and M.N. Flynn. 1993. Importance of the macrofauna for the feeding of young flsh species from infralittoral of Arrozal·Cananéia lagoon estuarine reglon (25°02'S-47°56'W) Brazil. *Boletim do Instituto Oceanográfico São Paulo* 41: 39–52.

Wakabara, Y., M.N. Flynn, and A.S. Tararam. 1996. Ingestion and selection of suprabenthic crustaceans by small-sized lishes in a lower saltmarsh system. *Revista Brasileira de Oceanografia* 44: 89–103.

Webb, P., and T.H. Wooldridge. 1990. Diel horizontal migration of *Mesopodopsis slabberi* (Crustacea, Mysidacea) in Algoa Bay, southern Africa. *Marine Ecology Progress Series* 62: 73–77.

Webber, M.K., and J.C. Roff. 1995. Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. *Marine Biology* 123: 481–495.

Wooldridge, T.H. 1986. Distribution, population dynamics and estimates of production for the estuarine mysid, *Rhopalophthalmus terranatalis*. *Estuarine, Coastal and Shelf Science* 23: 205–223.

Chapter 4. Species-specific and combined feeding rates and selectivity of dominant mysids from a subtropical estuary, Brazil

Abstract

We studied the influence of mysid species number on their feeding rates to test how the structure of the mysid assemblage may affect carbon fluxes in the Cananeia estuary. Three types of experiments were conducted at the laboratory in order to: (i) evaluate mysid feeding rates and selectivity on the natural zooplankton assemblage; (ii) determinate mysid functional responses to varying food density using *Artemia* sp. nauplii as food; and (iii) check inter- and intraspecific predation between mysids. For the former two experiments, three mysid species were incubated isolated or combined (2 species: *Metamysidopsis elongata atlantica* + *Mysidopsis coelhoi*; 3 species: *M. e. atlantica* + *M. coelhoi* + *Chlamydopleon dissimile*), comprising 5 treatments. The three mysid species had opportunistic feeding behavior on the natural zooplankton assemblage, but there was evidence of avoidance of medium-size prey (300-400 µm) mostly comprised of *Oithona* spp., probably due to a combination of small size and prey swimming patterns. Ingestion rates showed a non-linear increase with increasing food concentrations, suggesting a type II functional response for all mysid species and combination of species. There were both positive (complementarity effect) and negative effects of species combinations on the investigated response. Negative interactions were probably linked to intraguild predation as confirmed by experiment (iii), which resulted in a reduction of mysid predation over the zooplankton.

Keywords: biodiversity, feeding behavior, zooplankton, Mysidacea, trophodynamics, South Atlantic.

4.1. Introduction

Mysids are predominantly marine organisms (>90% species; Porter et al. 2008), and may occur from subpolar to tropical estuarine, neritic and oceanic waters (Mauchline 1980). They are omnivorous and prey mainly upon detritus, algae and small invertebrates (Wooldridge & Webb 1988; Fockedey & Mees 1999; Lehtiniemi et al. 2009). Because of their diverse diet and numerical dominance in coastal areas, mysids play a major role as intermediate consumers in coastal marine food webs (Rodríguez-Graña et al. 2008), serving as food for several fish, large invertebrates, birds and mammals (Mauchline 1980). Moreover, because most of the species are benthopelagic (>75%; Heard et al. 2006) and have strong diel migratory behavior (Almeida Prado 1973; Kouassi et al. 2006), mysids have an important role in the benthic-pelagic coupling (Jumars 2007).

Biodiversity alteration can affect the stability of ecosystem functions and the capacity of communities to use resources, produce biomass, decompose and recycle nutrients (Cardinale et al. 2012). A more diverse ecosystem is generally more stable and productive because it has higher probability of including key species of outstanding performance (sampling effect); and because diverse assemblages ensure colonization by species with different niches, whose interaction can lead to higher efficiency in the use of available resources (complementarity) (Loreau & Hector 2001). Despite the higher taxonomic and functional diversity in marine compared to terrestrial systems, relatively few works concerning the biodiversity-ecosystem functioning problem has emphasized the oceans, especially the pelagic ecosystem (Duffy & Stachowicz 2006).

Three types of experiments were conducted here: (i) to determinate mysid feeding rates and selectivity on the natural zooplankton assemblage; (ii) to evaluate their functional responses to varying food density using *Artemia* sp. nauplii as food; and (iii) to test inter- and intraspecific predation between mysids. For these experiments, we used the three dominant mysid species from the Cananeia estuary: *Metamysidopsis elongata atlantica*, *Mysidopsis coelhoi* and *Chlamydopleon dissimile*. These species co-occur and are the main intermediate consumers in the Cananeia estuary (Tararam et al. 1996). Among the three species, *M. e. atlantica* is the most abundant and that with widest distribution along the estuary (Tararam et al. 1996; Chapter 3), whereas *M. coelhoi* and *C. dissimile* are preferentially found in regions of stronger marine influence (Almeida Prado 1973). For experiments (i) and (ii), each of these species was incubated isolated or combined according to their *in situ* distribution pattern (2 species: *M. e. atlantica* + *M. coelhoi*; 3 species: *M. e. atlantica* + *M. coelhoi* + *C. dissimile*), totalizing 5 treatments.

Here, we studied the influence of mysid species number on predation rates and prey selectivity to explore how the structure of the mysid assemblage may affect carbon fluxes in the Cananeia environment. We hypothesized that species richness positively modulates feeding rates (resource use effectiveness), thus influencing carbon fluxes through the mysid compartment.

4.2. Materials and Methods

4.2.1. Study site

The Cananeia-Iguape Coastal System (Cananeia estuary, 24°35’- 25°10’S, 47°30’ - 48°05’W) is located in the south coast of the state of São Paulo, southeast Brazil. Annual mean air temperature and precipitation are 23.8°C and 2269 mm, respectively (Miyao et al. 1986; Silva 1989). This system is surrounded by a coastal plain area, salt marshes, mangroves and the Atlantic rainforest. It comprises a complex system of meandering channels delimited by four main islands (Cardoso, Cananeia, Comprida and Iguape), with two main connections to the Atlantic Ocean. The estuary is classified as partially mixed and weakly stratified (Type 2a; Miranda et al. 1995). Freshwater discharge is provided by several small rivers, whereas circulation along the estuary is forced mainly by semidiurnal tidal currents, with amplitudes of 0.83 m and 0.13 m during spring and neap tides, respectively (Miyao & Harari 1989).

4.2.2. Mysid sampling

For all experiments, mysids were collected using an epibenthic sledge fitted with a 500-µm pore size mesh towed during daytime at depths of 0.3 to 1.5 m. After the tows, samples were immediately poured into 12 L buckets and brought to the laboratory, usually within 40 min after collection. *In situ* temperature and salinity were measured with a multiparameter sensor (Oakton, 600 series). At the laboratory, adult/subadult mysids were individually picked from the buckets using small beakers, sorted by species and left for acclimatization to laboratory conditions for at least 3 h.

4.2.3. Feeding selectivity

Experiments were carried out between November 16 and 21, 2011 to estimate mysid clearance and consumption rates according to the classical setup used in plankton ecology studies (Båmstedt et al. 2000). Zooplankton was collected by horizontal subsurface tows with a conical plankton net fitted with a 90-µm mesh size. The sample was diluted in 12 L buckets and brought to the laboratory. At the laboratory, the sample was gently sieved through a 1 mm mesh to eliminate larger predators (e.g., jellyfish, fish larvae) and obtain a “prey sample pool” to be used during experiments. The density of plankton in the prey sample pool was estimated by taking and rapidly counting several 10 mL subsamples after gentle and thorough mixing. The resulting density was used to estimate the volume of the prey sample pool needed to attain a nominal prey density of 40 individuals L^{-1} in the experimental bottles, a typical density of mesozooplankton in the Cananeia estuary (Ara 2004). For the experiment, six mysids (single species or combination of species) were incubated in 9 L of filtered *in situ* seawater (5 µm). The experiment thus considered a constant predator density of 0.67 mysids L^{-1} for all treatments (Table 4.1), and four replicates in all cases. Four replicate samples of the prey sample pool of exactly the same volume as that added to the experimental bottles were established to estimate initial prey numbers. Bottles were incubated in darkness and at constant temperature (mean of 20.8 ± 0.2ºC), similar to those of the sampling site on the day of mysid collection. After 24h of incubation, contents of the bottles were sieved (90 µm), and the status of the mysids checked and recorded (live/dead, anomalous swimming behavior was also noted) and each individual was measured (body length, from the tip of the rostrum to the end of the telson). Remaining preys were fixed in 4% formaldehyde-seawater buffered solution, identified to the lowest taxon possible (usually species or genus for copepods), counted and measured (total length for nauplii or prosome length for copepods, 20 individuals per taxon) by digital image analysis using public domain Image-J software (Schneider et al. 2012). Dry weight (DW), ash-free dry weight (AFDW) or carbon weight (C) was estimated based on length-weight regressions (Uye 1982; Berggreen et al. 1988; Hansen & Ockelmann 1991; Webber & Roff 1995; Fotel et al. 1999; Hansen 1999; Ara 2001; Turner et al. 2001; Uye et al. 2002; Almeda et al. 2010). For copepods, we applied a conversion factor from AFDW to DW of 1.12 (Båmstedt 1986), and from DW to C of 0.46 (Ara 2001).

Clearance (mL $mysid^{-1}$ d^{-1}) and ingestion (ind. $mysid^{-1}$ d^{-1} and µgC $mysid^{-1}$ d^{-1}) rates were calculated according to Frost (1972). Mysids feeding preferences were evaluated through the electivity index (E*) of Vanderploeg & Scavia (1979):

$W = (Ri/Pi)/\sum(Ri/Pi);$

$E^* = [Wi - (1/N)]/[Wi + (1/N)],$

where Ri is the proportion of each food item in the diet; Pi is the relative abundance of the food item; and N is the number of prey available. E* values range from +1 to -1: values >+0.3 indicate positive selectivity, <-0.3 negative selectivity, and values in-between indicate neutral selection.

Table 4.1. Design of the feeding selectivity experiments: species composition, number of organisms per bottle, mysid mean body length (± SD), salinity, and date of experiments.

Treatment	Individuals per species	Body length (mm)	Salinity	Date (day/month/year)
Metamysidopsis elongata atlantica	6 *M. e. atlantica*	4.2 ± 0.5	23.9	17/11/2011
Mysidopsis coelhoi	6 *M. coelhoi*	5.0 ± 0.2	21.6	18/11/2011
Chlamydopleon dissimile	6 *C. dissimile*	7.7 ± 0.5	24.2	20/11/2011
2 species combined	3 *M. e. atlantica*	4.7 ± 0.1	23.9	19/11/2011
	3 *M. coelhoi*	4.9 ± 0.4		
3 species combined	2 *M. e. atlantica*	5.0 ± 0.1	24.2	20/11/2011
	2 *M. coelhoi*	4.5 ± 0.4		
	2 *C. dissimile*	7.7 ± 0.3		

4.2.4. Functional response

Experiments were carried out on March and May 2012. Six mysids (same species combination design as described above) were incubated in 6 L filtered seawater (5 µm) during 1-2 h with newly-hatched *Artemia* nauplii as food. Six different nauplii concentrations were supplied: 2, 5, 10, 50, 200 and 500 nauplii L^{-1}. Concentrations of 2 to 50 nauplii L^{-1} were prepared by individually picking batches of nauplii in numbers required to attain the desired concentration in each bottle. The number of nauplii was double-checked before the addition to the experimental bottle. The concentrations of 200 and 500 nauplii L^{-1} were prepared by an analogous procedure than that used for the "Feeding selectivity" experiment: the density of nauplii in the nauplii pool was first estimated and subsamples of the proper volume added to the experimental bottles to obtain a final concentration of 200 or 500 nauplii L^{-1}. At least three replicates and three control replicates (containing only *Artemia* nauplii and no mysid) were established for treatment. Control replicates were done only for concentrations of 200 and 500 nauplii L^{-1}. Bottles were incubated during daytime, in darkness and at controlled temperature (mean of 27.5 ± 0.3ºC), similar to that of the sampling site during mysid collection. At the end of the incubation, contents of the bottles were sieved (90 µm), and the status of the mysids checked and recorded (live/dead) and each individual was measured. Remaining prey were fixed in 4% formaldehyde-seawater buffered solution or in acid

Lugol's solution, and counted. The total length (µm) of 20 *Artemia* nauplii per bottle was measured by digital image analysis (Image-J). Clearance and ingestion rates were calculated according to Frost (1972). The functional response type was determined by the fitting of the ingestion rate data to three different models: rectilinear, curvilinear, and sigmoidal (Holling 1959).

4.2.5. Intraguild predation

Experiments to verify inter- and intraspecific predation between the three mysid species were done in January 24-25, 2013. One adult mysid of each species was incubated in 300 mL of filtered seawater (5 µm) with five juveniles of the same or other species. Three replicates were carried out for each treatment. Bottles were incubated in darkness, at controlled temperature (mean of 26.1 ± 0.3ºC) and constant salinity (30). After 2 h of incubation, the number of juveniles was counted, and the status of all mysids was checked and recorded (live/dead).

4.3. Results

4.3.1. Feeding rates and selectivity

The mean initial and final zooplankton densities were 41 ± 6 ind. L^{-1} and 22 ± 4 ind. L^{-1}, respectively. The natural zooplankton offered as food was composed mainly of nauplii and/or copepodites of *Oithona* spp. (*Oithona hebes* and *Oithona oswaldocruzi*), *Acartia lilljeborgii*, *Parvocalanus crassirostris*, *Temora turbinata* and *Pseudodiaptomus acutus* (Figs. 4.1 and 4.2). Copepod nauplii were the smallest prey, whereas copepodites of *A. lilljeborgii* and *P. acutus* were the largest prey.

Higher ingestion rates were related to the most abundant prey, regardless of the number of prey species available (Fig. 4.1). This fact was corroborated by the electivity index (E*) of Vanderploeg & Scavia (1979), which indicated neutral selection for most prey, with values ranging between -0.36 and 0.25 (Table 4.2). Conversely, clearance rates were not related to prey abundance (Fig. 4.2). Clearance rates were apparently more influenced by prey size, usually being higher in the smallest size class of 200-300 µm (Fig. 4.3), whereas higher ingestion rates occurred for prey in the medium-sized prey between 300-400 µm (Fig. 4.4). In general, E* was also neutral considering prey by size class, except for prey between 300-400 µm in the *M. e. atlantica* isolated experiment, which were negatively selected (Table 4.2).

Regarding the influence of the composition of mysid species on clearance and ingestion rates, the experiment with two species combined showed higher values compared with the other experiments (Table 4.3; $p < 0.05$, ANOVA), being significantly higher in relation to *M. e. atlantica* (clearance and ingestion rates; $p < 0.05$, Tukey HSD). In terms of carbon (µgC mysid^{-1} d^{-1}), differences occurred between *M. e. atlantica* and *M. coelhoi* ($p < 0.01$; Tukey HSD), and between *M. e. atlantica* and *C. dissimile* ($p < 0.05$; Tukey HSD).

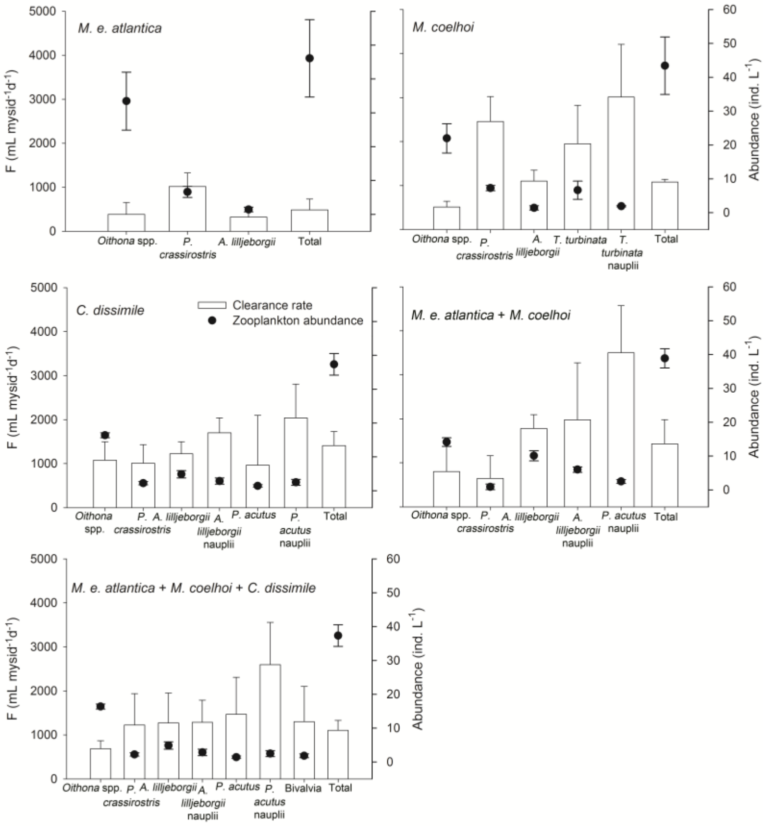


Fig. 4.1. Ingestion rate of each mysid species and combination of species, and biomass of the dominant zooplankton offered as food. Error bars represent the standard deviation.

Mysid mortality was observed only when species were combined. Death of one individual of *M. e. atlantica* was observed in two bottles of the two combined species experiment, whereas in the treatment with three species combined mortality occurred in three cases: in two cases one individual was found dead (*C. dissimile* in one bottle and *M. e. atlantica* in another), and in a third case two individuals died in one bottle (*M. coelhoi* and *M. e. atlantica*).

4.3.2. Functional response

In all cases, single species or combination of species, the ingestion rate increased asymptotically with increasing food concentrations, suggesting a type II functional response (Fig. 4.5). Maximum ingestion rate (I_{max}) was higher for *M. coelhoi* followed by *C. dissimile*, whereas *M. e. atlantica* and the species combinations showed lower values (Table 4.4). Conversely, the *a* parameter (hunting success; Jeschke et al., 2002) estimated by the Ivlev model (1961) was highest in *M. coelhoi* for single-species treatments, but increased in the two- and (increased further) in the three-species treatment (Table 4.4). Clearance rate was higher at lower food concentrations, decreasing as food availability increased (Fig. 4.5). Higher maximum clearance rate (F_{max}) was observed for *C. dissimile* and the combination of *M. e. atlantica* and *M. coelhoi* (Table 4.4). Mysid mortality did not occur in any occasion.

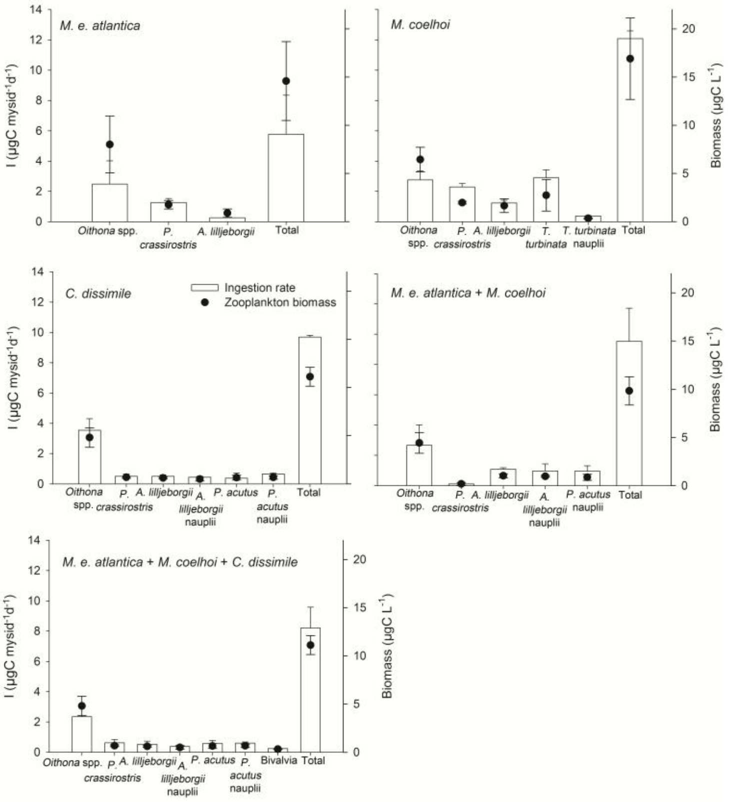


Fig. 4.2. Clearance rate of each mysid species and combination of species, and abundance of the dominant zooplankton offered as food. Error bars represent the standard deviation.

4.3.3. Intraguild predation

Predation was observed for *C. dissimile* and *M. coelhoi* over *M. e. atlantica*, only in one of the three replicate bottles (Table 4.5). Mortality of adults or juveniles not related to predation did not occur.

Table 4.2. Electivity index (E*) of Vanderploeg & Scavia (1979) for the most abundant prey, and separated by prey size class for each mysid species and combination of species.

	M.e. atlantica	*M. coelhoi*	*C. dissimile*	2 spp.	3 spp.
Oithona spp.	-0.21 ± 0.12	-0.36 ± 0.10	-0.04 ± 0.12	-0.23 ± 0.14	-0.26 ± 0.11
P. crassirostris	0.25 ± 0.17	0.12 ± 0.05	-0.05 ± 0.17	-0.24 ± 0.45	0.06 ± 0.14
A lilljeborgii	-0.34 ± 0.31	-0.10 ± 0.08	0.01 ± 0.10	0.08 ± 0.08	0.01 ± 0.14
A. lilljeborgii nauplii	-	-	0.05 ± 0.07	0.01 ± 0.18	-0.04 ± 0.09
T. turbinata	-	0.08 ± 0.08	-	-	-
T. turbinata nauplii	-	0.10 ± 0.01	-	-	-
P. acutus	-	-	-0.25 ± 0.35	-	0.04 ± 0.12
P. acutus nauplii	-	-	0.11 ± 0.05	0.08 ± 0.27	0.06 ± 0.13
Bivalvia larvae	-	-	-	-	-0.05 ± 0.25
200 - 300 µm	-	0.29 ± 0.15	0.08 ± 0.07	0.31 ± 0.22	0.10 ± 0.15
300 - 400 µm	-0.71 ± 0.03	0.06 ± 0.16	0.01 ± 0.06	0.25 ± 0.25	-0.20 ± 0.09
400 - 500 µm	-	-	-0.18 ± 0.41	-	0.01 ± 0.14
500 - 600 µm	0.20 ± 0.32	-	-	-	-
600 - 700 µm	-	0.10 ± 0.11	-	-	-

Table 4.3. Clearance (F) and ingestion (I) rates of the feeding selectivity experiments for each mysid species and combination of species.

	Feeding rates		
Species	F (mL $mysid^{-1}d^{-1}$)	I (ind. $mysid^{-1}d^{-1}$)	I (µgC $mysid^{-1}d^{-1}$)
M. e. atlantica	485.4 ± 248.0	18.6 ± 8.1	5.8 ± 2.6
M. coelhoi	1081.5 ± 59.7	32.6 ± 1.2	12.1 ± 0.5
C. dissimile	1410.9 ± 318.8	31.9 ± 3.5	9.7 ± 0.1
2 species combined	1532.1 ± 628.7	38.1 ± 9.9	10.2 ± 2.4
3 species combined	1243.3 ± 370.2	32.3 ± 8.1	9.2 ± 2.2

4.4. Discussion

4.4.1. Feeding rates and selectivity

Mysids are omnivorous and their feeding selectivity may vary according to species size, ontogenetically, and due to prey quantity and identity (Mauchline 1980;

Fockedey & Mees 1999; Kouassi et al. 2006; Lehtiniemi et al. 2009). The natural zooplankton offered as food was dominated by copepods, which usually are the main food source of several mysid species (Fockedey & Mees 1999; Lehtiniemi et al. 2009). The dominant copepods were *Oithona* spp., *P. crassirostris*, *A. lilljeborgii*, *T. turbinata* and *P. acutus*, as commonly observed during the entire year in the Cananeia estuary (Ara 2004; Chapter 3).

For the three mysid species studied here, ingestion rate was higher for the most abundant prey, as observed elsewhere (Wooldridge & Webb 1988; Viherluoto & Viitasalo 2001; Kouassi et al. 2006), and E* was neutral for most prey types, which indicates no preference or avoidance. However, the dominant prey *Oithona* spp. had negative E* values in all treatments, and in the single *M. e. atlantica* treatment, E* indicated rejection for medium-size prey between 300 and 400 µm (*Oithona* spp. size class). A certain degree of avoidance for these small copepods probably occurred because of mysid preference for larger and slowly moving prey (e.g., *Mysis mixta*; Viitasalo et al. 2001) and *Oithona* swimming behavior: *Oithona* are stationary ambush feeders, which turns them difficult to detect as they yield lower hydrodynamic signals than cruisers and suspension feeders (Svensen & Kiørboe 2000; Paffenhöfer & Mazzocchi 2002).

Table 4.4. Maximum clearance (Fmax) and ingestion (Imax) rates for each mysid species and combination of species. Parameters were estimated by the exponential decay equation [F = Fmax × exp(-bC)] and the Ivlev model {I = Imax × [1 – exp(-aC)]}, where C is the food concentration. Parameter a of Ivlev's model is a measure of hunting efficiency.

	Clearance rates			Ingestion rates		
Species	F_{max}	b	r^2	I_{max}	a	r^2
M. e. atlantica	6087.8	0.0125	0.61	321.2	0.0068	0.73
M. coelhoi	9913.7	0.0293	0.58	619.6	0.0025	0.80
C. dissimile	15390.7	0.0799	0.79	364.1	0.0076	0.77
2 species combined	14963.4	0.1288	0.67	247.2	0.0100	0.86
3 species combined	11269.7	0.0148	0.63	240.7	0.0266	0.76

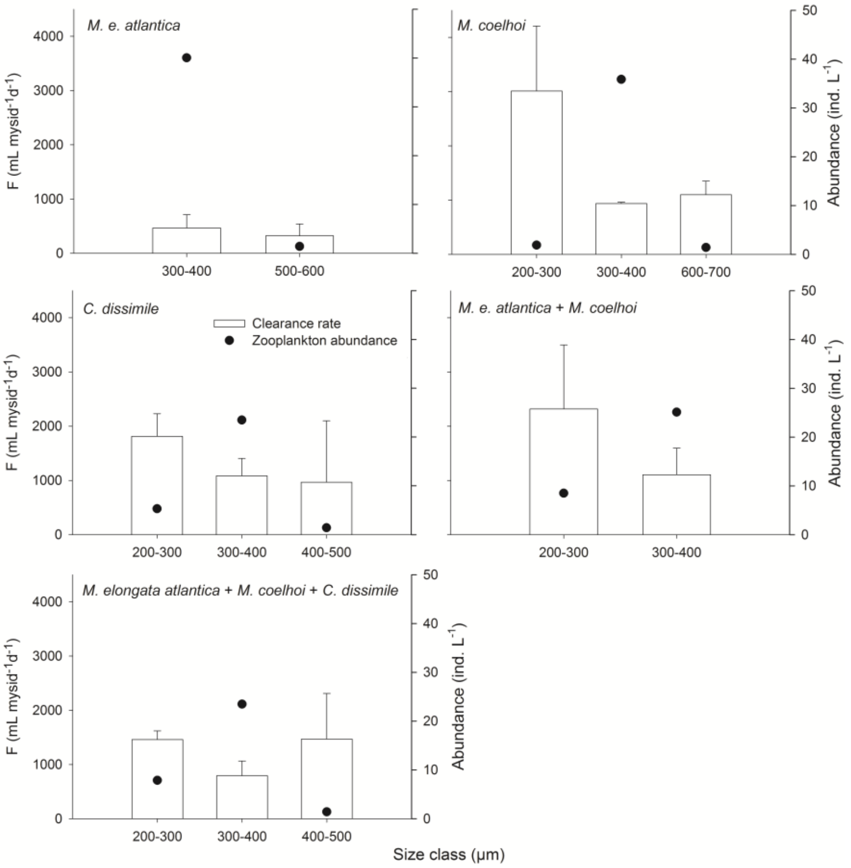


Fig. 4.3. Zooplankton abundance, and clearance rate of each mysid species and combination of species separated by prey size class. Error bars represent the standard deviation.

4.4.2. Functional response

Ingestion rates showed a curvilinear increase with food concentration, which generally is the most commonly observed functional response in mysids (Folt et al. 1982; Fulton 1982; Mohammadian et al. 1997; Bergström & Englund 2004) and other zooplankters (Hansen & Ockelmann 1991; Jeschke et al. 2002; Isari and Saiz 2011). Functional responses of types I and III are less common, but may also occur in mysids (Viitasalo & Rautio 1998; Viherluoto & Viitasalo 2001) and other zooplankters (Jeschke et al. 2004; Almeda et al. 2010; Morozov 2010).

Metamysidopsis e. atlantica reached saturation at lower food concentration compared with the two other mysid species, and reached a lower maximum ingestion rate. *Metamysidopsis e. atlantica* is the smallest of the three mysid species, thus it probably has lower metabolic requirements (Ikeda 2013), which may be related to its lower feeding rates and *in situ* numerical dominance (Tararam et al. 1996; Chapter 3) in relation to other mysid species.

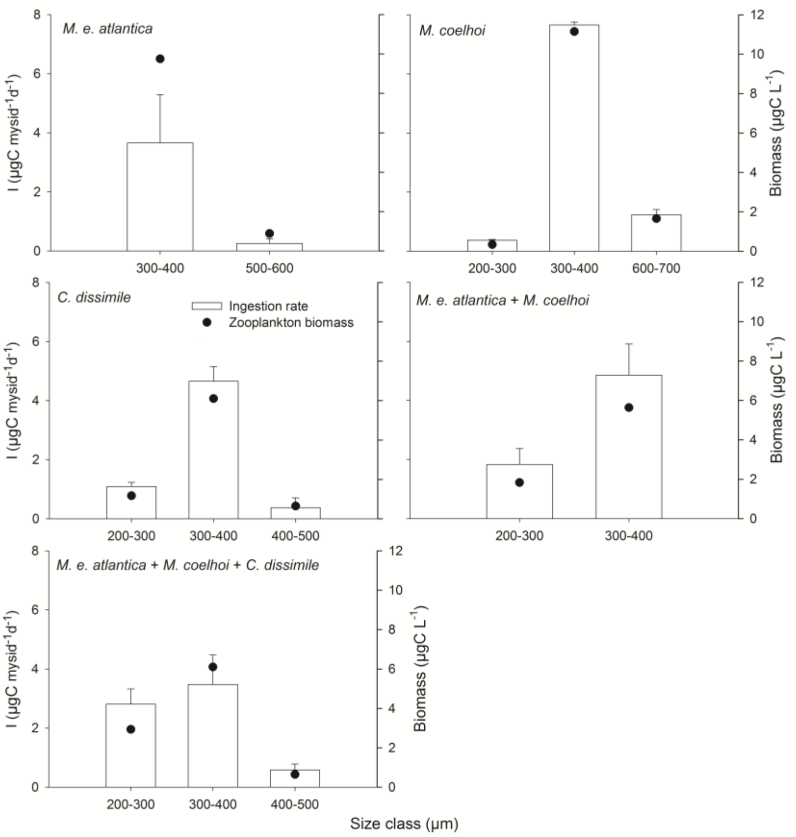


Fig. 4.4. Zooplankton biomass, and ingestion rate of each mysid species and combination of species separated by prey size class. Error bars represent the standard deviation.

Chlamydopleon dissimile and *M. coelhoi* showed opposite patterns: the former was the most effective predator (highest hunting success) and had higher ingestion rates at all food concentrations, except for the 500 nauplii L^{-1} food level, in which *M. coelhoi* developed higher rates. *Mysidopsis coelhoi* attained its maximum ingestion at higher food concentrations, suggesting that it is adapted to higher food conditions than *C. dissimile* and *M. e. atlantica*.

4.4.3. Mysid species interaction

There was a clear effect of species number on the feeding rates of the mysid assemblage, and both positive and negative interactions were observed. The ingestion rate of *M. e. atlantica* and *M. coelhoi* combined was significantly higher than that of *M. e. atlantica* and *C. dissimile* isolated. Hunting success was also higher in combinations compared with isolated species, and was highest in the three-species treatment. Higher ingestion rates and hunting success could be related to the complementarity effect (Loreau & Hector 2001) for those particular species combinations, i.e. mysid performance was better in the combined experiments likely because of resource partitioning or facilitation.

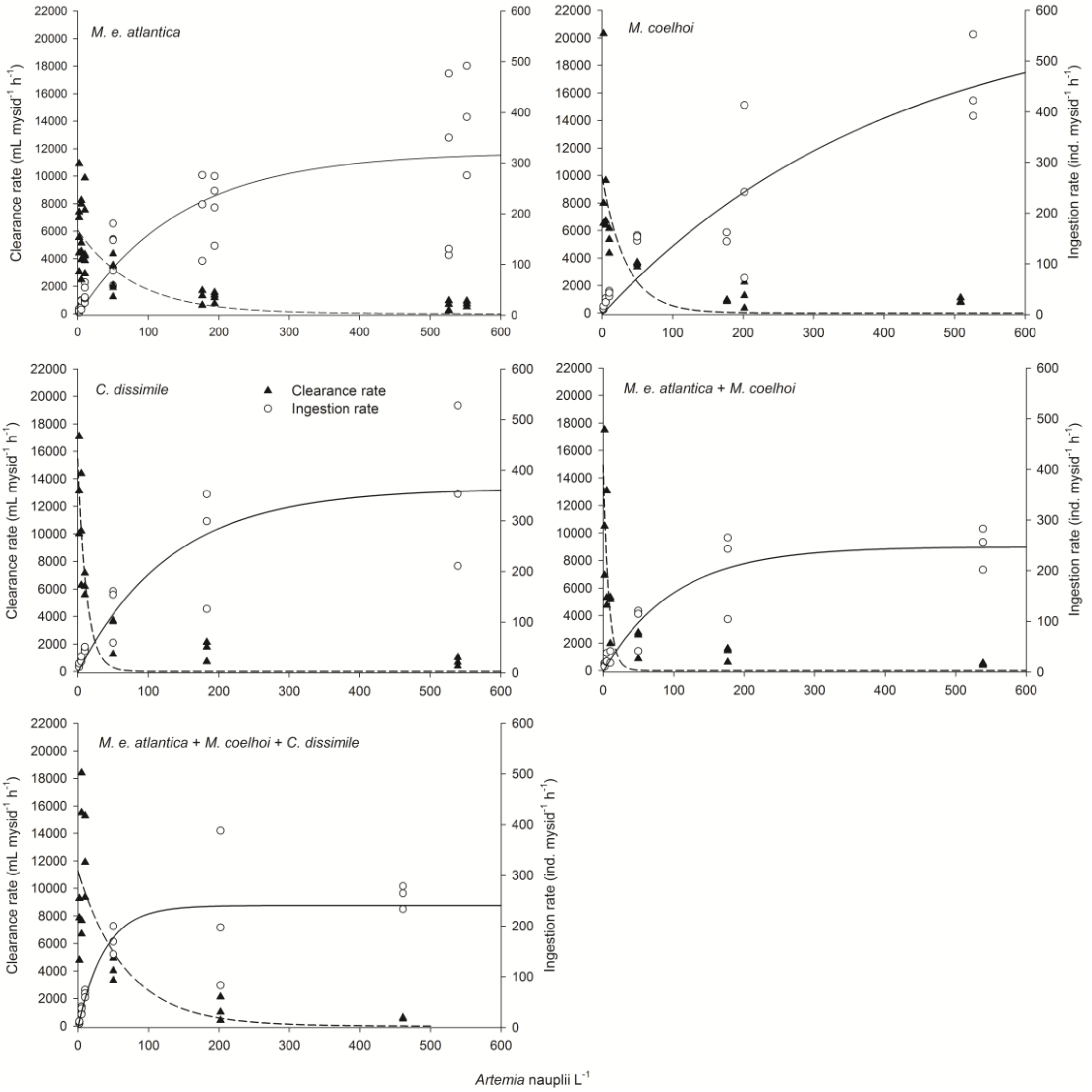


Fig. 4.5. Functional response of each mysid species and combination of species. Dotted (clearance rates) and continuous lines (ingestion rates) represent the model fitted to the respective data (see Table 4.4).

Table 4.5. Number of juveniles predated when maintained with adults of the same or other mysid species.

		Juveniles		
Adult	Replicate	*M. e. atlantica*	*M. coelhoi*	*C. dissimile*
M. e. atlantica	1	0	0	0
	2	0	0	0
	3	0	0	0
M. coelhoi	1	4	0	0
	2	0	0	0
	3	0	0	0
C. dissimile	1	2	0	0
	2	0	0	0
	3	0	0	0

Conversely, lowest maximum ingestion rates (functional response) and high frequency of mortality were observed when the three species were combined suggesting that co-occurrence of those three species was negative for the feeding performance of the mysid assemblage. Such negative interactions likely arose from intraguild predation (e.g., Finke & Denno 2004). Results of the intraguild predation experiment confirmed that such mechanism actually occurs for both *C. dissimile* and *M. coelhoi* over *M. e. atlantica*. Even when no direct intraguild predation takes place, an indirect effect of the presence of a potential top predator may involve deterrence or diminishing of feeding activity by the intermediate consumer linked to behavioral changes (Lima & Dill 1990; Trussell et al. 2003). However, that extreme was not evaluated in the present study.

Current results clearly indicated that mysid community structure is a relevant factor for the regulation of consumption rates and energy flows through this important ecosystem compartment, thus providing partial support for the working hypothesis. However, the relationship between species richness and mysid predation rates was not straightforward, depending both on species identity and prey availability as indicated by functional response patterns with highest predation efficiency, but lower maximum feeding rates for the three-species combination compared to single-species performance.

4.5. Conclusions

Ingestion rates of either single mysid species or in combinations, showed a curvilinear increase suggesting a type II functional response. The functional response curves suggested that *C. dissimile* and *M. e. atlantica* are more adapted to low food concentration conditions than *M. coelhoi*. The three mysid species tended to develop an overall opportunistic (i.e., non-selective) feeding behavior on the natural zooplankton assemblage, but there was evidence of avoidance of medium-size prey (300-400 µm), mostly comprised by *Oithona* spp. This pattern probably arose from a combination of small prey size and swimming patterns. There were both positive interactions of species combinations on community feeding response (complementarity effect between *M. e. atlantica* and *M. coelhoi*) and negative ones when the three mysid species were present. Negative interactions were probably linked to intraguild predation, resulting in a reduction of mysid predation over the zooplankton.

4.6. References

Almeda R., Augustin C.B., Alcaraz M., Calbet A., Saiz E., 2010. Feeding rates and gross growth efficiencies of larval developmental stages of *Oithona davisae* (Copepoda, Cyclopoida). J. Exp. Mar. Biol. Ecol. 387, 24–35.

Almeida Prado M.S., 1973. Distribution of Mysidacea (Crustacea) in the Cananéia region. Bol. Zool. Biol. Mar. N.S. 30, 395–417.

Ara, K., 2001. Length-weight relationships and chemical content of the planktonic copepods in the Cananéia Lagoon estuarine system, São Paulo, Brazil. Plankton Biol. Ecol. 48, 121–127.

Ara, K., 2004. Temporal variability and production of the planktonic copepod community in the Cananéia Lagoon estuarine system, São Paulo, Brazil. Zool. Stud. 43, 179–186.

Båmstedt, U., 1986. Chemical composition and energy content, in: Corner, E.D.S., O´Hara, S.C.M. (Eds.), The biological chemistry of marine copepods. Oxford University Press, New York, pp. 1–58.

Båmstedt, U., Gifford, D.J., Irigoien, X., Atkinson, A., Roman, M.R., 2000. Feeding, in: Harris, R.P., Wiebe, P., Lenz, J., Skjoldal, H.R., Huntley, M. (Eds.), ICES zooplankton methodology manual. Academic Press, London, pp. 297–400.

Berggreen, U., Hansen, B., Kiørboe, T., 1988. Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. Mar. Biol. 99, 341–352.

Bergström, U., Englund, G., 2004. Spatial scale, heterogeneity and functional responses. J. Anim. Ecol. 73, 487–493.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67.

Duffy, J.E., Stachowicz, J.J., 2006. Why biodiversity is important to oceanography: potential roles of genetic, species, and trophic diversity in pelagic ecosystem processes. Mar. Ecol. Prog. Ser. 311, 179–189.

Finke, D.L., Denno, R.F., 2004. Predator diversity dampens trophic cascades. Nature 429, 407–410.

Fockedey, N., Mees, J., 1999. Feeding of the hyperbenthic mysid *Neomysis integer* in the maximum turbidity zone of the Elbe, Westerschelde and Gironde estuaries. J. Mar. Syst. 22, 207–228.

Folt, C.L., Rybock, J.T., Goldman, C.R., 1982. The effect of prey composition and abundance on the predation rate and selectivity of *Mysis relicta*. Hydrobiologia 93, 133–143.

Fotel, F.L., Jensen, N.J., Wittrup, L., Hansen, B.W., 1999. *In situ* and laboratory growth by a population of blue mussel larvae (*Mytilus edulis* L.) from a Danish embayment, Knebel Vig. J. Exp. Mar. Biol. Ecol. 233, 213–230.

Frost, B.W., 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. 17, 805–815.

Fulton, R.S., 1982. Predatory feeding of two marine mysids. Mar. Biol. 72, 183–191.

Hansen, B., Ockelmann, K.W., 1991. Feeding behaviour in larvae of the opistobranch *Philine aperta* I. Growth and functional response at different developmental stages. Mar. Biol. 111, 255–261.

Hansen, B.W., 1999. Cohort growth of planktotrophic polychaete larvae—are they food limited? Mar. Ecol. Prog. Ser. 178, 109–119.

Heard, R.W., Price, W.W., Knott, D.M., King, R.A., Allen, D.M., 2006. A taxonomic guide to the mysids of the South Atlantic Bight. NOAA Professional Paper NMFS 4, 1–37.

Holling, C.S., 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Entomol. 91, 293–320.

Ikeda, T. 2013. Synthesis towards a global-bathymetric model of metabolism and chemical composition of mysid crustaceans. J. Exp. Mar. Biol. Ecol. 445, 79–87.

Isari, S., Saiz, E., 2011. Feeding performance of the copepod *Clausocalanus lividus* (Frost and Fleminger, 1968). J. Plankton Res. 33, 715–728.

Ivlev, V.S., 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven.

Jeschke, J.M., Kopp, M., Tollrian, R., 2002. Predator functional responses: discriminating between handling and digesting prey. Ecol. Monogr. 72, 95–112.

Jeschke, J.M., Kopp, M., Tollrian, R., 2004. Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biol. Rev. 79, 337–349.

Jumars, P.A., 2007. Habitat coupling by mid-latitude, subtidal, marine mysids: import-subsidised omnivores. Oceanogr. Mar. Biol. Annu. Rev. 45, 89–138.

Kouassi, E., Pagano, M., Saint-Jean, L., Sorbe, J.C., 2006. Diel vertical migrations and feeding behavior of the mysid *Rhopalophthalmus africana* (Crustacea: Mysidacea) in a tropical lagoon (Ebrié, Côte d'Ivoire). Estuar. Coast. Shelf Sci. 67, 355–368.

Lehtiniemi, M., Kiljunen, M., Jones, R.I., 2009. Winter food utilisation by sympatric mysids in the Baltic Sea, studied by combined gut content and stable isotope analyses. Mar. Biol. 156, 619–628.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412, 72–76.

Mauchline, J., 1980. The biology of mysids and euphausiids. Adv. Mar. Biol. 18, 1–681.

Miranda, L.B., Mesquita, A.R., França, C.A.S., 1995. Estudo da circulação e dos processos de mistura no extremo sul do mar de Cananéia: condições de dezembro de 1991. Bol. Inst. Oceanogr. S. Paulo 43, 153–164.

Miyao, S.Y., Harari, J., 1989. Estudo preliminar da maré e das correntes de maré da região estuarina de Cananéia (25°S-48°W). Bol. Inst. Oceanogr. S. Paulo 37, 107–123.

Miyao, S.Y., Nishihara, L., Sarti, C.C., 1986. Características físicas e químicas do sistema estuarino-lagunar de Cananéia-Iguape. Bol. Inst. Oceanogr. S. Paulo 34, 23–36.

Mohammadian, M.A., Hansson, S., De Stasio, B.T., 1997. Are marine planktonic invertebrates food limited? The functional response of *Mysis mixta* (Crustacea, Mysidacea) in the Baltic Sea. Mar. Ecol. Prog. Ser. 150, 113–119.

Morozov, A.Y., 2010. Emergence of Holling type III zooplankton functional response: Bringing together field evidence and mathematical modeling. J. Theor. Biol. 265, 45–54.

Paffenhöfer, G.-A., Mazzocchi, M.G., 2002. On some aspects of the behaviour of *Oithona plumifera* (Copepoda: Cyclopoida). J. Plankton Res. 24, 129–135.

Porter, M.L., Meland, K., Price, W., 2008. Global diversity of mysids (Crustacea-Mysida) in freshwater. Hydrobiologia 595, 213–218.

Rodríguez-Graña, L., Calliari, D., Conde, D., Sellanes, J., Urrutia, R., 2008. Food web of a SW Atlantic shallow coastal lagoon: spatial environmental variability does not impose substantial changes in the trophic structure. Mar. Ecol. Prog. Ser. 362, 69–83.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671–675.

Silva, J.F., 1989. Dados climatológicos de Cananéia e Ubatuba (Estado de São Paulo). Bol. Climatol. Inst. Oceanogr. 6, 1–21.

Svensen, C., Kiørboe, T., 2000. Remote prey detection in *Oithona similis*: hydromechanical versus chemical cues. J. Plankton Res. 22, 1155–1166.

Tararam, A.S., Wakabara, Y., Flynn, M.N., 1996. Suprabenthic community of the Cananeia lagoon estuarine region, Southeastern Brazil. Cah. Biol. Mar. 37, 295–308.

Trussell, G.C., Ewanchuk, P.J., Bertness, M.D., 2003. Trait-mediated effects in rocky intertidal food chains: Predator risk cues alter prey feeding rates. Ecology 84, 629–640.

Turner, J.T., Levinsen, H., Nielsen, T.G., Hansen, B.W., 2001. Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay, West Greenland. Mar. Ecol. Prog. Ser. 221, 209–219.

Uye, S., 1982. Length-weight relationships of important zooplankton from the Inland Sea of Japan. J. Oceanogr. Soc. Jpn. 38, 149–158.

Uye, S., Aoto, I., Onbé, T., 2002. Seasonal population dynamics and production of *Microsetella norvegica*, a widely distributed but little-studied marine planktonic harpacticoid copepod. J. Plankton Res. 24, 143–153.

Vanderploeg, H.A., Scavia, D., 1979. Two electivity indices for feeding with special reference to zooplankton grazing. J. Fish. Res. Board Can. 36, 362–365.

Viherluoto, M., Viitasalo, M., 2001. Temporal variability in functional responses and prey selectivity of the pelagic mysid, *Mysis mixta,* in natural prey assemblages. Mar. Biol. 138, 575–583.

Viitasalo, M., Rautio, M., 1998. Zooplanktivory by *Praunus flexuosus* (Crustacea: Mysidacea): functional responses and prey selection in relation to prey escape responses. Mar. Ecol. Prog. Ser. 174, 77–87.

Viitasalo, M., Flinkman, J., Viherluoto, M., 2001. Zooplanktivory in the Baltic Sea: a comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions. Mar. Ecol. Prog. Ser. 216, 191–200.

Webber, M.K., Roff, J.C., 1995. Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. Mar. Biol. 123, 481–495.

Wooldridge, T.H., Webb, P., 1988. Predator–prey interactions between two species of estuarine mysid shrimps. Mar. Ecol. Prog. Ser. 50, 21–28.

Chapter 5. Effects of predator species number and spatial heterogeneity on prey suppression

Abstract

We carried out two independent mesocosm experiments manipulating the number of top predator species and spatial heterogeneity to test their influence on resource use effectiveness, competition among predators and trophic cascades. Our hypothesis was that an increase in top predator species richness induces higher intermediate prey suppression because of complementarity effects, which consequently reduces their grazing over algae (basal prey assemblage). We used mysids as intermediate prey, whereas the predator treatments consisted of three monocultures of different top predator species, and one polyculture containing the three species of predators. Heterogeneity was manipulated by the introduction of oyster shells and the macroalgae *Gracilaria* sp. Top predator richness enhanced intermediate prey suppression relative to the mean performance of monocultures, but not in comparison to the most effective top predator. Positive effects of diversity increased with spatial heterogeneity, as it allowed interspecific complementarity effects between top predators to be better expressed. Moreover, mortality was reduced in treatments with higher spatial heterogeinity, probably because it dampened intraguild predation and/or negative behavioral interactions between predators. Finally, trophic cascades were not observed because mysids are generalist consumers, i.e. their grazing over algae was not significant as they might have explored other food sources.

Keywords: biodiversity, ecosystem functioning, habitat heterogeneity, carnivores, trophic cascade, marine, food webs.

5.1. Introduction

Biodiversity can be defined as the variety of species, genes, or functional traits in an ecosystem, having a major role on the ecosystem functions and services (Cardinale et al. 2012). The loss of biodiversity reduces the stability of ecosystem functions and the capacity of communities to use resources, produce biomass, decompose and recycle nutrients (Hooper et al. 2012). A more diverse ecosystem generally is more stable and productive because it has a higher probability of having key species with dominant effects (sampling effect); and because more diverse assemblages ensure colonization by species with different niches, whose interaction can lead to a more efficient capture of available resources (complementarity) (Loreau and Hector 2001).

Experimental evidence available shows that diversity effects are generally consistent across taxa and ecosystems (Cardinale et al. 2006, 2007; Stachowicz et al. 2007), but the responses may vary considerably according to spatiotemporal scale (Cardinale et al. 2004, 2011), spatial heterogeneity (Griffin et al. 2009; Godbold et al. 2011), and food chain length and complexity (Bruno and O’Connor 2005; Duffy et al. 2005, 2007; Bruno et al. 2008). An increase of these variables strengthens diversity effects because they allow resource partitioning to be better expressed, i.e. complementarity effects among species to be manifested (Cardinale et al. 2007; Stachowicz et al. 2008; Duffy 2009).

Most studies concerning biodiversity and ecosystem functioning (BEF) focused on lower trophic levels (Cardinale et al. 2006, 2011), i.e. producers and primary consumers, mainly because they are easier to manipulate than consumers in higher trophic levels. Moreover, predators usually have complex behavior and present complex trophic interactions, such as intraguild predation (Polis and Holt 1992; Finke and Denno 2004). On the other hand, there are recent evidences that the relationship between species richness effects and ecosystem functioning is stronger for predators than for producers and detritivores (Griffin et al. 2013). Thus, an alteration in predator species identity and diversity may alter top-down controls and cascade through consumers to the base of the food webs (Duffy et al. 2007; O’Connor et al. 2013).

Here, we carried out two independent mesocosm experiments manipulating the number of predator species and spatial heterogeneity to test their influence on resource use effectiveness, competition among predators and on trophic cascades. We hypothesized that predator species richness positively modulates intermediate prey suppression (higher predation because of complementarity effects), thus reducing their grazing on algae through cascading effects.

5.2. Methods

5.2.1. Experimental design

We carried out two mesocosm experiments in outdoor tanks supplied with water from the York River estuary, Virginia, USA, location where the organisms were collected. Flowing water was filtered through 150 µm mesh bags to avoid invasion of large organisms, but allowing the colonization by microalgae. Water was distributed to the mesocosms through a dump-buckets system. The first experiment was conducted in 50 mesocosms of 140 L, from July 18 to 23, 2013 (5 days), and included 10 treatments (5 replicates each): prey (intermediate prey), monocultures of each of the three predators with and without prey, predator polyculture with and without prey, and a control containing neither predators nor prey. The second experiment was implemented in 70 mesocosms of 15 L, from 22 October to 5 November, 2013 (14 days), and included 14 treatments (5 replicates each): prey, monocultures of each of the three predators with prey, predator polyculture with and without prey, a control containing neither predators nor prey, and all these same treatments within a structured habitat. In both experiments the food chain was a three-level arrangement: microalgae (basal prey), mysids (intermediate prey) and predators (top consumers, variable composition, and experimental factor).

For acclimation, one week prior to the introduction of predators, 51 and 15 mysids (intermediate prey) were introduced in the mesocosms for the first and second experiments, respectively. We have chosen mysids as prey because they are one of the main intermediate consumers in coastal waters (Mauchline 1980), including the Chesapeake Bay (Markle and Grant 1970; Latour et al. 2008). Moreover, mysids have a major role in the benthic-pelagic coupling, as they stay close to the bottom during the day and migrate to the water column during nighttime (Mauchline 1980). We selected the numerically dominant species in the field at the time of the experiment: *Neomysis americana* in the first experiment and *Americamysis bahia* in the second experiment. Adults of *N. americana* and *A. bahia* reach a total length of approximately 1 and 0.6 cm, respectively. Mysids are omnivorous, they eat detritus, algae, and small invertebrates (Mauchline 1980).

We introduced three predator specimens in each mesocosm, being one of each species in the three species combined treatment (polyculture). The predators chosen were the sand shrimp *Crangon septemspinosa*, the grass shrimp *Palaemonetes pugio*, the killifish (mummichog) *Fundulus heteroclitus* (first experiment only), and the blue crab *Callinectes sapidus* (second experiment only). Mean length ± SD of each predator was 27.4 ± 6.5 mm, 30.1 ± 4.5 mm, 55.2 ± 5.4 mm, and 15.9 ± 6.2 mm, respectively. These predators are omnivorous (James-Pirri et al. 2001; Douglass et al. 2011; Seitz et al. 2011) and may consume mysids (Price 1962; Morgan 1980; personal observation). Although these predators are omnivorous, they were not expected to have apparent impact on algae in our system.

Structure in experiment two was composed by oyster shells and the macroalgae *Gracilaria* sp. We selected dry oyster shells of similar size in enough quantity to cover only the bottom of the mesocosms. *Gracilaria* was defaunated before its introduction to the mesocosms by soaking in freshwater for 2-3h, followed by careful visual inspection after rinsing in freshwater. We added approximately 10 g of algae wet mass in each mesocosm. *Gracilaria* was weighed after removing excess water using a salad spinner (70 revolutions).

At the end of experiments, all invertebrates (mysids and predators) from the mesocosms were fixed in 70% ethanol for posterior counting at the laboratory. Mummichogs were measured and released. To quantify microalgal biomass (chl *a*), microalgae was sampled from the wall of the mesocosms (20 cm^2) and analyzed spectrophotometrically (Jeffrey and Humphrey 1975). *Gracilaria* was weighed as described above.

In the first experiment, one-way analysis of variance (ANOVA) was used to verify differences in mysid number and microalgal biomass between the different treatments. In the second mesocosm, differences in mysid number, microalgal biomass, and predator mortality between treatments were analyzed with two-way ANOVA (predator composition and presence of structure); and *Gracilaria* weight was analyzed with one-way ANOVA. All data were log transformed prior the analyses. Significant treatment effects were clarified through post-hoc Tukey HSD tests. In both experiments, mysid suppression was the response variable to test predator's efficiency, whereas microalgae biomass was used to verify cascading effects.

5.3. Results

5.3.1. First experiment

Mysids were consumed significantly (Tukey HSD, $p < 0.001$) only in treatments that contained mummichogs (mummichogs + mysids, and polyculture + mysids; Fig. 5.1). There were no differences in chl *a* between the different treatments (ANOVA, $p > 0.05$). All sand shrimps disappeared or died in the polyculture (Fig. 5.2). Sand shrimp death or disappearance was also observed in two replicates of the sand shrimp monoculture without prey.

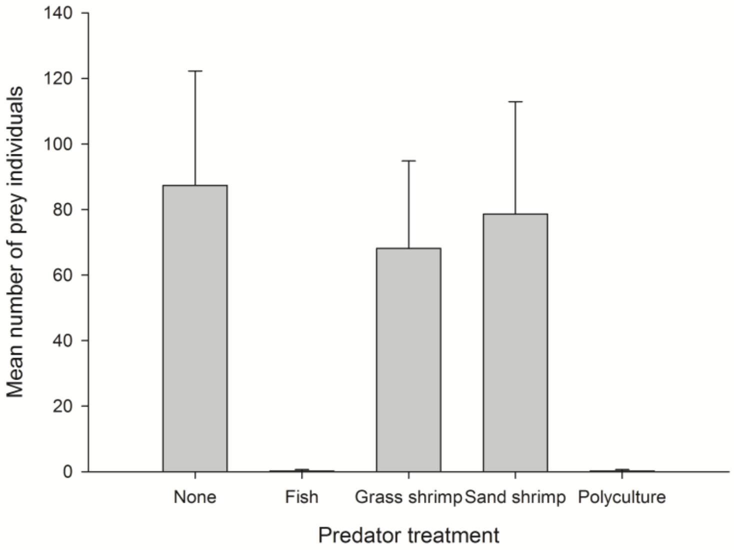


Fig. 5.1. Mysid final mean abundance in each predator treatment of the first mesocosm experiment. Error bars represent the standard deviation.

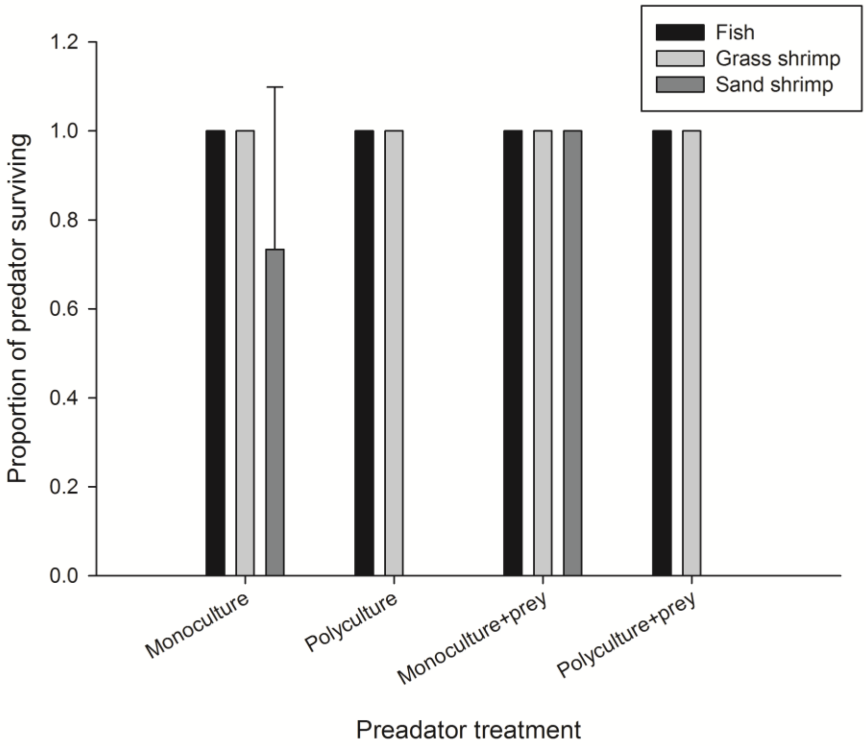


Fig. 5.2. Mean proportion of predator surviving at the end of the first experiment in each predator treatment.

5.3.2. Second experiment

Two-way ANOVA indicated that predator treatment and spatial heterogeneity influenced mysid suppression ($p < 0.001$), but their interaction was non-significant ($p > 0.05$). Monocultures of sand shrimp with and without structure, and the polyculture with structure were the most efficient treatments in reducing mysids abundance (Tukey HSD, $p < 0.001$; Fig. 5.3). Conversely, the interaction between predator treatment and spatial heterogeneity was significant for predator mortality (two-way ANOVA; $p < 0.001$), mainly for blue crab (Tukey HSD, $p < 0.05$). We observed mortality of blue crab in monocultures and polycultures, both without structure (Fig. 5.4). There were no differences in chl *a* between the different treatments (ANOVA, $p > 0.05$). *Gracilaria* weight increased along the experiment, being significantly higher (Tukey HSD, $p < 0.01$) in the three predators combined treatment in relation to the monocultures of grass shrimp and blue crab.

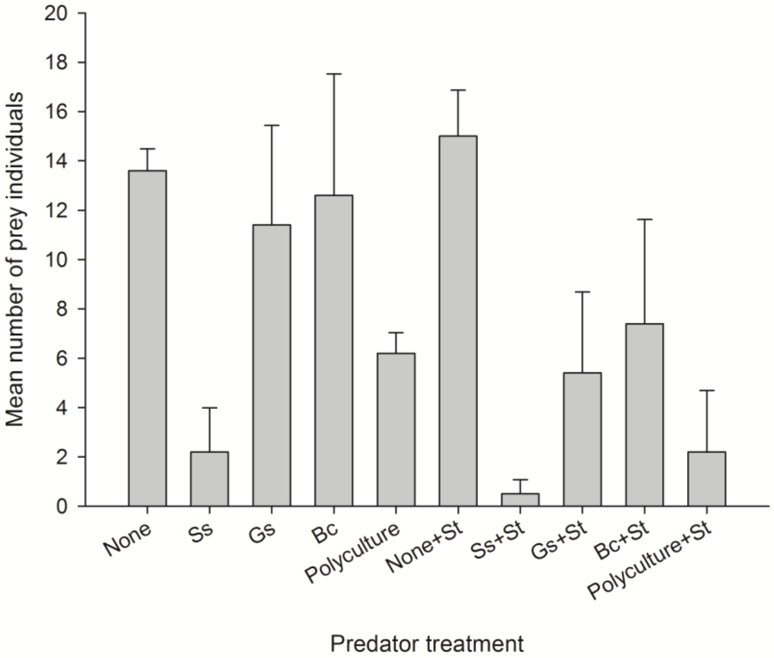


Fig. 5.3. Mysid final mean abundance in each predator treatment of the second mesocosm experiment. Error bars represent the standard deviation. Ss: sand shrimp; Gs: grass shrimp; Bc: blue crab; St: structure (*Gracilaria* + oyster shells).

5.4. Discussion

Mummichog and sand shrimp were the best-performing species in the first and second experiments, respectively, both followed by the combination of the three predator species combined. That result indicates that both predator identity and diversity influenced the efficiency of the assemblage to remove prey, as commonly observed (e.g. Bruno and O'Connor 2005). Our data are in agreement with a recent meta-analysis that showed that predator richness enhances prey suppression relative to the mean performance of predator monocultures, but not in comparison to the most effective predator (Griffin et al. 2013). This trend implies that maximum prey suppression (i.e., energy fluxes from prey to predator assemblages) would diminish with loss of predator diversity only if the most effective predator disappears (and assuming that predator density remains constant). However, in real world ecosystems predator diversity loss would affect other ecological properties and functions, as different species may maximize distinct ecosystem processes (Duffy 2009).

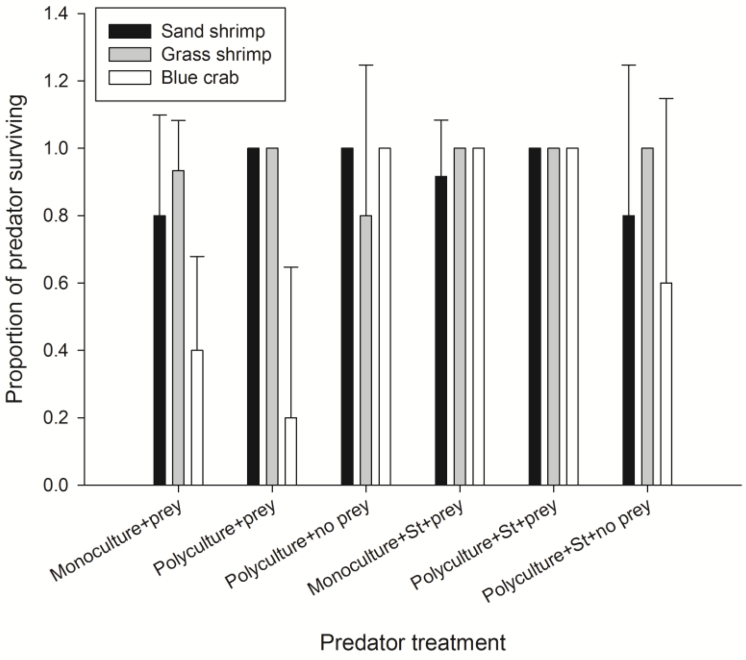


Fig. 5.4. Mean proportion of predator surviving at the end of the second experiment in each predator treatment. St: structure (*Gracilaria* + oyster shells).

Dominance in prey suppression by monocultures occurred as a result of the sampling effect. One of the main criticisms against BEF experiments is that positive effects of species richness occur because of species identity (sampling effect) and not because of diversity per se (Huston 1997). However, dominance of a given ecosystem function by a single species might result from a combination of positive complementarity and negative selection effects instead of the sampling effect (Duffy 2009). Moreover, the apparent predominance of the sampling effect may also be influenced by the experimental design, mainly the short temporal scale of experiments, and the quantification of only a single response (Stachowicz et al. 2008).

Despite being the best-performing species in the second experiment, sand shrimp was not effective to prey on mysids in the first experiment. This inconsistency in performance occurred because of differences in spatiotemporal scale and prey abundances between the two experiments. The first experiment lasted for five days, which was long enough time for the mummichog to remove all prey, but not for the sand and grass shrimps. In this case, more time would be necessary for interspecific complementarity effects to occur (Cardinale et al. 2007; Stachowicz et al. 2008). In relation to spatial scale, the first experiment was carried out in larger mesocosms, which were more appropriate for mysids to escape from predators, probably because mysids perform horizontal and vertical migrations to avoid predators (Mauchline 1980). Other works manipulating biodiversity effects have already emphasized the importance of organism dispersal in mesocosm experiments (France and Duffy 2006; Matthiessen and Hillebrand 2006).

We observed that predator species richness effects on mysid suppression were stronger in the presence of structure (*Gracilaria* and oyster shells), and that was irrespective of the predator species under consideration (i.e., non-significant interaction of predator species x habitat structure experimental factors). Interestingly, structure facilitated prey suppression by predators, instead of being beneficial for prey by providing a place to hide. This likely occurred because spatial heterogeneity allowed interspecific niche partitioning to be better expressed (Cardinale et al. 2004; Griffin et al. 2009). Without structure mortality of predators occurred, mainly of blue crab, suggesting that structure dampened intraguild predation and/or negative behavioral interactions between predators. Moreover, structure may have facilitated prey suppression because it aggregated predator and prey in space, proportioned an extension for predators to explore the water column, and provided a place for predators to hide and ambush the mysids. This result emphasizes the importance of bioengineering species that provide spatial structure for others to thrive (e.g., coral reefs and eelgrass) and for the function of ecosystems.

Differences in vertical and horizontal diversity modify the strength of trophic cascades along the food web (Duffy et al. 2007). We were expecting to observe differences in algal biomass between treatments in which mysids were present and absent or heavily preyed. However, we did not observe any sign of cascading effects, most likely because mysids did not eat algae to a significant extent. This occurred because mysids are omnivorous (Mauchline 1980), thus in addition to algae they probably ate detritus and small invertebrates (e.g., harpacticoid copepods) present in the mesocosms. In this respect, an improvement to the experimental design would imply either: exclusion of other potential prey for mysids (i.e., small crustaceans); or control and quantification of the whole prey assemblage to detect cascading effect to the microcrustaceans level.

In summary, we observed that predator richness enhanced prey suppression relative to the mean performance of predator monocultures, but not in comparison to the most effective predator. Positive effects of diversity increased in the presence of structure (spatial heterogeneity), as it allowed interspecific complementarity effects between predators to be expressed. Moreover, structure probably dampened intraguild predation and/or negative behavioral interactions between predators. Finally, trophic cascades did not occur probably because mysids are generalist consumers.

5.5. References

Bruno JF, O’Connor MI (2005) Cascading effects of predator diversity and omnivory in a marine food web. Ecol Lett 8:1048–1056

Bruno JF, Boyer KE, Duffy JE, Lee SC (2008) Relative and interactive effects of plant and grazer richness in a benthic marine community. Ecology 89:2518–2528

Cardinale BJ, Ives AR, Inchausti P (2004) Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. Oikos 104:437–450

Cardinale BJ, Srivastava DS, Duffy JE, Wright JP, Downing AL, Sankaran M, Jouseau C (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–992

Cardinale BJ, Wright JP, Cadotte MW, Carroll IT, Hector A, Srivastava DS, Loreau M, Weis JJ (2007) Impacts of plant diversity on biomass production increase through time because of species complementary. Proc Natl Acad Sci USA 104:18123–18128

Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE, Duffy E, Gamfeldt L, Balvanera P, O’Connor MI, Gonzalez A (2011) The functional role of producer diversity in ecosystems. Am J Bot 98:572–592

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67

Douglass JG, Duffy JE, Canuel EA (2011) Food web structure in a Chesapeake Bay eelgrass bed as determined through gut contents and ^{13}C and ^{15}N isotope analysis. Estuar Coast 34:701–711

Duffy JE (2009) Why biodiversity is important to the functioning of real-world ecosystems. Front Ecol Environ 7:437–444

Duffy JE, Richardson JP, France KE (2005) Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. Ecol Lett 8:301–309

Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thebault E, Loreau M (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. Ecol Lett 10:522–538

Finke DL, Denno RF(2004) Predator diversity dampens trophic cascades. Nature 429:407–410

France KE, Duffy JE (2006) Diversity and dispersal interactively affect predictability of ecosystem function. Nature 441:1139–1143

Godbold JA, Bulling MT, Solan M (2011) Habitat structure mediates biodiversity effects on ecosystem properties. Proc. R. Soc. B 278:2510–2518

Griffin JN, Jenkins SR, Gamfeldt L, Jones D, Hawkins SJ, Thompson RC (2009) Spatial heterogeneity increases the importance of species richness for an ecosystem process. Oikos 118:1335–1342

Griffin JN, Byrnes JEK, Cardinale BJ (2013) Effects of predator richness on prey suppression: a meta-analysis. Ecology 94:2180–2187

Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, Matulich KL, Gonzalez A, Duffy JE, Gamfeldt L, O'Connor MI (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–108

Huston MA (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110:449–460

James-Pirri MJ, Raposa KB, Catena JG (2001) Diet composition of mummichogs, *Fundulus heteroclitus*, from restoring and unrestricted regions of a New England (U.S.A.) salt marsh. Estuar Coast Shelf Sci 53:205–213

Jeffery SW, Humphrey GF (1975) New spectrophotometric equations for determining chlorophylls a, b, c1, and c2 in higher plants, algae and natural phytoplankton. Biochem Physiol Pflanz 167:191–194

Latour RJ, Gartland J, Bonzek CF, Johnson RA (2008) The trophic dynamics of summer flounder (*Paralichthys dentatus*) in Chesapeake Bay. Fish Bull 106:47–57

Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76

Markle DF, Grant GC (1970) The summer food habits of young-of-the year striped bass in three Virginia rivers. Chesap Sci 11:50–54

Matthiessen B, Hillebrand H (2006) Dispersal frequency affects local biomass production by controlling local diversity. Ecol Lett 9:652–662

Mauchline J (1980) The biology of mysids and euphausiids. Adv Mar Biol 18:1–681

Morgan MD (1980) Grazing and predation of the grass shrimp *Palaemonetes pugio*. Limnol Oceanogr 25:896–902

O'Connor NE, Emmerson MC, Crowe TP, Donohue T (2013) Distinguishing between direct and indirect effects of predators in complex ecosystems. J Anim Ecol 82:438–448

Polis GA, Holt RD (1992) Intraguild predation – the dynamics of complex trophic interactions. Trends Ecol Evol 7:151–154

Price Jr KS (1962) Biology of the sand shrimp, *Crangon septemspinosa*, in the shore zone of the Delaware Bay region. Chesap Sci 3:244–255

Seitz SD, Knick KE, Westphal M (2001) Diet selectivity of juvenile blue crabs (*Callinectes sapidus*) in Chesapeake Bay. Integr Comp Biol 51:598–607

Stachowicz JJ, Bruno JF, Duffy JE (2007) Consequences of biodiversity for marine communities and ecosystems. Annu Rev Ecol Evol Syst 38:739–766

Stachowicz JJ, Best RJ, Bracken MES, Graham MH (2008) Complementarity in marine biodiversity manipulations: reconciling divergent evidence from field and mesocosm experiments. Proc Natl Acad Sci USA 105:18842–18847

Chapter 6. Concluding remarks

The main objective of this thesis was to address the Biodiversity and Ecosystem Functioning (BEF) theme, emphasizing the trophic role of mysids in marine coastal food webs. Both positive and negative interactions were observed in experiments manipulating mysid species richness and evaluating their feeding response and interspecific behavior. When two mysid species were combined, their feeding rates increased in relation to monocultures, probably because of complementarity effects, i.e. as a result of resource partitioning and/or facilitation. However, higher mysid mortality occurred in polycultures (three mysid species combined), likely because of intraguild predation as confirmed by ad hoc experiments, and/or because of negative behavioral interactions between mysids.

Experiments that reconstructed more complex food webs with mysids as intermediate consumers indicated that their suppression was higher in treatments with multiple top predators relative to the mean performance of a single predator, but not in comparison to the most effective predator. Positive effects of predator species richness increased with spatial heterogeneity, as it allowed interspecific complementarity effects between predators to be better expressed. Moreover, habitat structure probably dampened intraguild predation and/or negative behavioral interactions between predators, as predator mortality was lower in the presence of structure. Top-down control was not observed, as microalgal concentration did not differ between treatments, which indicates that mysid did not consume algae to a significant extent. Mysids are generalist consumers (Mauchline 1980), thus in addition to algae they might also have eaten detritus and small invertebrates, resulting in the non-observance of a trophic cascade.

The BEF theory could also contribute to understand the implications of observed mysid spatiotemporal distribution on the energy fluxes in the Cananeia estuary (Chapter 3). For instance, *M. e. atlantica* was the most productive species and had wider spatial distribution in comparison to other mysid species. This dominance occurred because *M. e. atlantica* was the best adapted species for the particular environmental conditions observed, i.e. it was the single mysid species that effectively colonized low salinity areas in the estuary. The higher statistical probability of including species with a dominant effect, in this case *M. e. atlantica,* occurs when richness is higher, mechanism known as the sampling effect (Loreau and Hector 2001). The absence of *M. e. atlantica* in the Cananeia region would probably result in the non-occurrence of any mysid species in the low-salinity areas of the estuary, which would cause significant changes in the local food web. Conversely, a decrease in mysids species richness as we move from high to low salinity areas implies a decrease in consumption potential by mysids (Chapters 3 and 4); significant changes in the salinity regime of the Cananeia system (i.e., an overall decline in salinity) may thus affect organic matter and energy flows through that ecosystem compartment. Such results indicate that knowledge about regional biodiversity is crucial for a better understanding and management of ecosystems.

As summarized above, the results of the BEF experiments showed that species richness influenced mysid feeding and their suppression. However, it is difficult to foresee the consequences of biodiversity loss in real ecosystems, as the interaction between species is extremely complex, involving multiple trophic levels (horizontal and vertical), and inter- and intraspecific complex behavior. Because of that it is a major challenge to simulate and test the influence of biodiversity, especially for mobile and large animals. Despite these difficulties, future works should be capable to manipulate more complex systems, thus providing more empirical evidences of the influence of biodiversity loss on global environmental changes and ecosystem services.

6.1. References

Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76.

Mauchline J. 1980. The biology of mysids and euphausiids. Adv Mar Biol 18:1–681.