

# Biological Synopsis of the Japanese Skeleton Shrimp (*Caprella mutica*)

Christian Turcotte and Bernard Sainte-Marie

Regional Science Branch  
Fisheries and Oceans Canada  
Maurice Lamontagne Institute  
850, route de la Mer  
Mont-Joli (Quebec) G5H 3Z4

2009

**Canadian Manuscript Report of Fisheries and Aquatic  
Sciences 2903**



Pêches et Océans  
Canada

Fisheries and Oceans  
Canada

Canada

## **Canadian Manuscript Report of Fisheries and Aquatic Sciences**

Manuscript reports contain scientific and technical information that contributes to existing knowledge but which deals with national or regional problems. Distribution is restricted to institutions or individuals located in particular regions of Canada. However, no restriction is placed on subject matter, and the series reflects the broad interests and policies of Fisheries and Oceans Canada, namely, fisheries and aquatic sciences.

Manuscript reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in the data base *Aquatic Sciences and Fisheries Abstracts*.

Manuscript reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page.

Numbers 1-900 in this series were issued as Manuscript Reports (Biological Series) of the Biological Board of Canada, and subsequent to 1937 when the name of the Board was changed by Act of Parliament, as Manuscript Reports (Biological Series) of the Fisheries Research Board of Canada. Numbers 1426 - 1550 were issued as Department of Fisheries and Environment, Fisheries and Marine Service Manuscript Reports. The current series name was changed with report number 1551.

## **Rapport manuscrit canadien des sciences halieutiques et aquatiques**

Les rapports manuscrits contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui traitent de problèmes nationaux ou régionaux. La distribution en est limitée aux organismes et aux personnes de régions particulières du Canada. Il n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques de Pêches et Océans Canada, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports manuscrits peuvent être cités comme des publications à part entière. Le titre exact figure au-dessus du résumé de chaque rapport. Les rapports manuscrits sont résumés dans la base de données *Résumés des sciences aquatiques et halieutiques*.

Les rapports manuscrits sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre.

Les numéros 1 à 900 de cette série ont été publiés à titre de Manuscrits (série biologique) de l'Office de biologie du Canada, et après le changement de la désignation de cet organisme par décret du Parlement, en 1937, ont été classés comme Manuscrits (série biologique) de l'Office des recherches sur les pêcheries du Canada. Les numéros 901 à 1425 ont été publiés à titre de Rapports manuscrits de l'Office des recherches sur les pêcheries du Canada. Les numéros 1426 à 1550 sont parus à titre de Rapports manuscrits du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 1551.

Canadian Manuscript Report of Fisheries and Aquatic  
Sciences 2903

2009

BIOLOGICAL SYNOPSIS OF THE JAPANESE SKELETON SHRIMP  
(*Caprella mutica*)

by

Christian Turcotte<sup>1</sup> and Bernard Sainte-Marie

Regional Science Branch  
Fisheries and Oceans Canada  
Maurice Lamontagne Institute  
850, route de la Mer  
Mont-Joli (Quebec) G5H 3Z4

---

<sup>1</sup> Institut des sciences de la mer (ISMER), Université du Québec à Rimouski, 310 avenue des Ursulines, Rimouski (Quebec) G5L 3A1

© Her Majesty the Queen in Right of Canada, 2009.  
Cat. N° FS97-4/2903 ISSN 1488-5387

Correct citation for this publication:

Turcotte, C. and B. Sainte-Marie. 2009. Biological synopsis of the Japanese skeleton shrimp  
(*Caprella mutica*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2903 : vii + 26 p.

Cette publication est disponible en français.

# TABLE OF CONTENTS

LIST OF TABLES .....	iv
LIST OF FIGURES .....	iv
ABSTRACT .....	v
RÉSUMÉ .....	vi
PREFACE .....	vii
1.0 INTRODUCTION .....	1
2.0 NAME AND CLASSIFICATION .....	1
3.0 DESCRIPTION .....	2
3.1 Taxonomy of Caprellids and the Genus <i>Caprella</i> .....	2
3.2 Changes in Shape Related to Sexual Maturity in <i>C. Mutica</i> .....	4
3.3. Species Similar to <i>C. mutica</i> .....	5
4.0 DISTRIBUTION AND DISPERSAL .....	6
4.1 Native Distribution and Physiological Tolerance .....	6
4.2 Exotic Distribution Range .....	7
4.3 Pathways of Introduction and Small and Large Scale Dispersal Modes .....	9
5.0 ECOLOGY .....	12
5.1 Habitat .....	12
5.2 Caprellid Diet .....	12
5.3 Natural Predators .....	14
6.0 REPRODUCTION AND POPULATION DYNAMICS .....	15
6.1 Reproduction .....	15
6.2 Population Dynamics .....	16
7.0 IMPACTS FROM THE INTRODUCTION OF THE JAPANESE SKELETON SHRIMP ..	17
8.0 CONCLUSION .....	18
9.0 ACKNOWLEDGEMENTS .....	19
10.0 REFERENCES .....	19

## LIST OF TABLES

Table 1. Years and global locations where *Caprella mutica* was first found. ....8

## LIST OF FIGURES

Figure 1. Male (above) and female (below) *Caprella mutica*. From Ashelby (2005) with the author's permission. ....3

Figure 2. Photo showing a mature female *Caprella mutica* of around 9 mm total in length excluding the antennas. The marsupial chamber under the female is formed by the oostegites (author: Thierry Gosselin). ....5

Figure 3. Map showing the location where *Caprella mutica* was first described in 1935, and the years and locations where *Caprella mutica* was first introduced on other continents of the northern and southern hemispheres. ....10

## ABSTRACT

Turcotte, C. and B. Sainte-Marie. 2009. Biological synopsis of the Japanese skeleton shrimp (*Caprella mutica*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2903: vii + 26 p.

*Caprella mutica* is an amphipod crustacean that was first described in 1935 from the Siberian shores of the Japan Sea. In its indigenous habitat, *C. mutica* is mainly found in stands of eelgrass or macroalgae in the infralittoral zone where temperature varies from  $-1.8^{\circ}\text{C}$  in winter to  $25^{\circ}\text{C}$  in summer and salinity from 11 to 35. *C. mutica* has a high reproductive potential: there are two generations per year, females mature at a small size, are relatively fecund and reproduce more than once, and “direct” development of progeny ensures a good survival rate. *C. mutica* was introduced to North America first on the Pacific side in the early 1970s and on the Atlantic side in the late 1990s, as well as in Europe during the mid 1990s. The sites where *C. mutica* was introduced in the northern hemisphere are at temperate, boreal and subarctic latitudes between  $35$  and  $70^{\circ}\text{N}$ . Transoceanic introductions probably occurred by way of transport of aquaculture organisms and ballast waters. Secondary dispersal of the species along coasts may be due to commercial and recreational navigation, drifting on floatsam, and at a smaller spatial scale by swimming and creeping. In its new habitat in the northern hemisphere, *C. mutica* is found mainly or only on artificial structures such as nets, ropes and buoys that are used in aquaculture. Good environmental tolerance, rapid growth and a high reproductive rate, combined with a flexible diet, an aggressive nature and a high degree of commensalism with human activities, seem to contribute to make *C. mutica* a good invader. *C. mutica* apparently has a negative impact on some aquaculture activities but its effect on natural ecosystems remains unknown.

## RÉSUMÉ

Turcotte, C. et B. Sainte-Marie. 2009. Synthèse de la biologie de la caprelle japonaise (*Caprella mutica*). Rapp. manus. can. sci. halieut. aquat. 2903 : vii + 28 p.

*Caprella mutica* est un crustacé amphipode qui a été décrit pour la première fois en 1935 à partir de spécimens capturés sur les côtes sibériennes de la mer du Japon. Dans son habitat d'origine, *C. mutica* se retrouve principalement dans des halliers de zostères marines ou de macroalgues dans la zone infralittorale où la température varie entre  $-1,8$  °C l'hiver et  $25$  °C l'été et la salinité entre 11 et 35. *C. mutica* a un potentiel de reproduction élevé : il y a deux générations par année, les femelles sont matures à une petite taille, sont relativement fécondes, se reproduisent plus d'une fois et le développement « direct » de la progéniture assure un bon niveau de survie. *C. mutica* a été introduite en Amérique du Nord, d'abord du côté Pacifique vers le début des années 1970, puis du côté Atlantique vers la fin des années 1990, ainsi qu'en Europe vers le milieu des années 1990. Les sites d'introduction de *C. mutica* dans l'hémisphère nord sont aux latitudes tempérées, boréales et subarctiques comprises entre  $35$  et  $70$  °N. Le transport d'organismes pour l'aquaculture et les eaux de ballast pourraient expliquer ces introductions transocéaniques. La dispersion secondaire de l'espèce le long des côtes pourrait être assurée par la navigation commerciale et de plaisance, la dérive sur des macroalgues et des débris flottants et, à plus petite échelle spatiale, par la nage et la reptation. Dans ses eaux d'adoption de l'hémisphère nord, *C. mutica* est principalement ou uniquement retrouvée sur des structures artificielles comme des filets, des cordages et des bouées utilisés en aquaculture. Une bonne tolérance environnementale, une croissance rapide et un taux de reproduction élevé, conjugués à une diète flexible, un caractère agressif et un fort commensalisme avec les activités humaines semblent faire de *C. mutica* un bon envahisseur. *C. mutica* aurait un impact négatif sur certaines activités aquacoles mais son effet sur les écosystèmes naturels demeure inconnu.



## **PREFACE**

This document often refers to observations made by the authors which will be published eventually as reports, articles and as a Master's degree thesis. These observations stem from field and laboratory work, of which a portion was conducted with the cooperation of M. Fréchette (DFO, Mont-Joli) and R. Tremblay (Institut des sciences de la mer, Université du Québec à Rimouski). This work was carried out due to grants from the Société de développement de l'industrie maricole (SODIM), the Aquaculture Collaborative Research and Development Program (ACRDP) as well as from DFO's Aquatic Invasive Species (AIS) strategy.



## 1.0 INTRODUCTION

The caprellid *Caprella mutica* is an amphipod crustacean that was first described by Schurin (1935) from specimens captured on the Siberian shores of the Japan Sea. The species has since been introduced in waters along the coasts of North America, first on the Pacific side (Carlton 1979, Cohen and Carlton 1995), then on the Atlantic side (Locke *et al.* 2007). It has also been found in the north-eastern Atlantic Ocean bordering Europe (reported under the name *C. macho* by Platvoet *et al.* 1995, see Cook *et al.* 2007a) and, over the last few years, in New Zealand (Inglis *et al.* 2006). The transoceanic modes of introduction have not been specifically identified but the transport of organisms for aquaculture and ballast waters remain the most plausible hypotheses to date (Cohen and Carlton 1995).

*C. mutica* introduction sites are primarily located at temperate latitudes between 35 and 70 °N (Ashton 2006, Ashton *et al.* 2007a, Cook *et al.* 2007a). This species is likely to become established anywhere, except around the equator or the poles. In Canada, *C. mutica* was first reported in Prince Edward Island in 1998 (Locke *et al.* 2007), in Quebec in Chaleur Bay in 2003 (B. Sainte-Marie, pers. obs.) and just recently on the coasts of British Columbia (Frey *et al.* 2009). Although *C. mutica* has been introduced in several countries in the northern hemisphere, its impact on colonized marine ecosystems remains virtually unknown.

A significant concern pertaining to the introduction of an exotic species to an ecosystem is its potential effect on the structure of the food chain and on its upper trophic levels (Grosholz 2002). For example, *C. mutica* could cause a reduction in the richness and abundance of native invertebrate species on artificial structures, which appear to be its choice structure to colonize, and replace them in the diet of native predators (Page *et al.* 2007). In addition, mussel growers from Scotland and Quebec (Cascapedia Bay) have reported a drop in the collection and subsequent growth of *Mytilus* spp. spat since the appearance of *C. mutica* on their installations (Ashton 2006, B. Sainte-Marie and C. Turcotte, pers. obs.).

In light of the repeated observations and the apparent range expansion of *C. mutica* in Canada, this species has been targeted for an assessment of the risks it presents to Canadian marine ecosystems. In preparing for this assessment, a review of the literature on *C. mutica* was conducted in order to better understand its ecology, population dynamics, its modes of spread and its effective or potential impact on Canadian marine ecosystems.

## 2.0 NAME AND CLASSIFICATION

Classification of *C. mutica* according to the Integrated Taxonomic Information System (ITIS 2009) is as follows:

Kingdom: *Animalia*  
Phylum: *Arthropoda*  
Subphylum: *Crustacea*, Brünnich 1772  
Class: *Malacostraca*, Latreille 1802  
Subclass: *Eumalacostraca*, Grobben 1892  
Superorder: *Peracarida*, Calman 1904  
Order: *Amphipoda*, Latreille 1816  
Suborder: *Caprellidea*, Leach 1814  
Family: *Caprellidae*, Leach 1814  
Genus: *Caprella*, Lamarck 1801  
Species: *Caprella mutica* Schurin 1935

Common French name: no French name was found, but we propose the “*caprelle japonaise*”, a translation from the common English name.

Common English name: Japanese skeleton shrimp.

### 3.0 DESCRIPTION

#### 3.1 TAXONOMY OF CAPRELLIDS AND THE GENUS *Caprella*

Caprellids are filiform crustaceans with a skeleton-like appearance, as indicated by their generic English name “skeleton shrimp”. Caprellids live attached to various substrates using their hind legs (pereiopods) which are in the form of hooks (Figure 1).

Caprellid taxonomy is very complex, particularly due to the species’ resemblance and to their ontogenic changes in shape and body configuration related to development and maturation (see below). McCain (1968) divided caprellids into two large groups based on the occurrence or absence of a molar process on the mandible. The Caprellidae family belongs to the first group (with molar process), as do the Caprogammaridae and Aeginellidae families. Genus determination is based on five criteria revised by Arimoto (1976):

- 1) Number of flagellar segments on antenna II (second pair of antennas, see Figure 1),
- 2) Position and number of pereiopod segments (legs on the thorax, called pereion, Figure 1). Note: gnathopods I and II (Figure 1) are in fact pereiopods modified into gathering legs,
- 3) Number of gills (Figure 1),
- 4) Occurrence or not of a mandibular palp and its number of segments,
- 5) Position and number of abdominal appendage segments. Note: the abdomen or pleon in caprellids is usually very atrophic or vestigial.

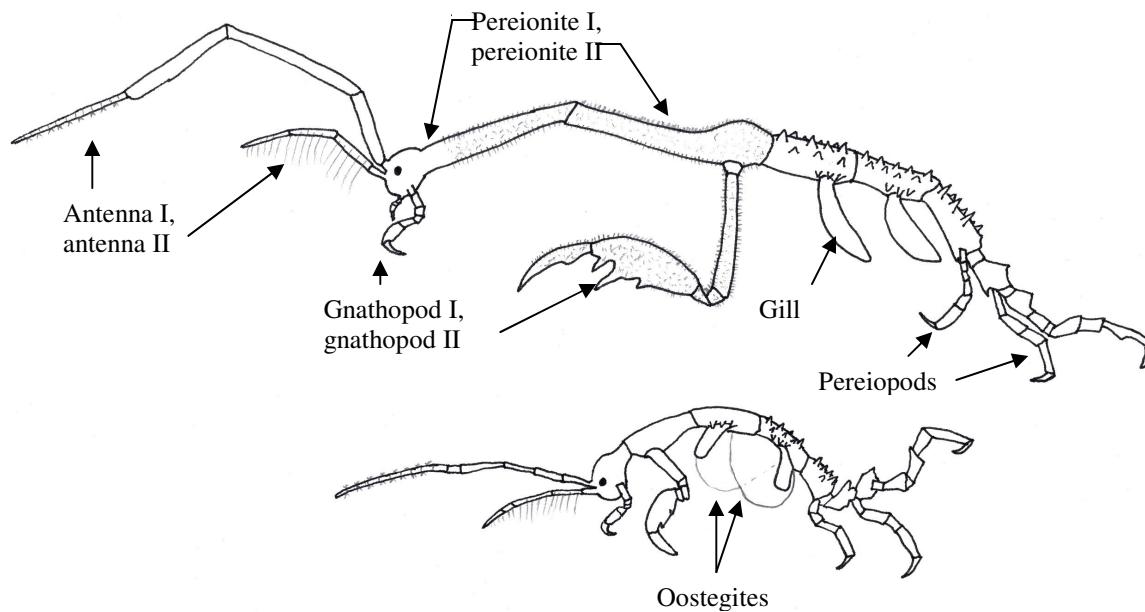


Figure 1. Male (above) and female (below) *Caprella mutica*. From Ashelby (2005) with the author's permission.

The genus *Caprella* is divided into three sub-genera based on the shape of the head. The sub-genus to which *C. mutica* belongs is *Caprella sensu stricto* in which the species have a spherical or oval shaped head free of tubercles or spines (Arimoto 1976). Species identification also involves many elements with the principal criteria being relative length of the pereionites (body segments forming the thorax, or pereion), the occurrence and distribution of spines or tubercles on the pereionites, the length of antenna I, the occurrence of natatory setae on antenna II (also called antennula), and the occurrence and size of spines on the palmar side of gnathopod II (Arimoto 1976, Laubitz 1972). The shape of the second gnathopod and the distribution of the spines and tubercles are especially important for identifying caprellids, but can also vary considerably between sexes of the same species, as well as among males of the same species depending on their size, their degree of maturity or their locality of origin (Arimoto 1976, Laubitz 1972, Riedlecker *et al.* 2009). These factors make the identification of caprellids difficult, in particular younger specimens.

The *C. mutica* species was first described by Schurin (1935) from juvenile specimens collected on the Siberian shores of the Japan Sea. The male *C. mutica* has an exoskeleton with several tubercles on pereionites III to VII, and the head and pereionites I and II are exempt of protuberances (Figure 1). The female also has tubercles on pereionites III to VII but may also have some small protrusions or projections on the head and pereionites I and II (Takeuchi 1995, Figure 2). As reported above, caprellids undergo significant changes in shape during their

development and it is not uncommon that young and adults of the same species are attributed to two separate species (Arimoto 1976). The publication by Platvoet *et al.* (1995) is a good example: the authors thought they had discovered a new caprellid species, which they named *Caprella macho*, but in fact it was an adult *C. mutica* male with very dense “hair”; the ultimate characteristic of maturity which only occurs in very large males. The common identity of *C. mutica* and *C. macho* specimens and the synonymy of the two names have since been recognized (Krapp-Schickel and Takeuchi 2005). In our opinion, the *C. mutica* figures presented by Takeuchi (1995), Platvoet *et al.* (1995) and Hosono and Munehara (2001) are among the best representations of the species’ adult form, even though they differ in the size of the median spine on the palmar side of the male’s gnathopod II and in the occurrence or absence of protuberances on the female’s pereionites I and II. These two characteristics also vary a lot.

### 3.2 CHANGES IN SHAPE RELATED TO SEXUAL MATURITY IN *C. MUTICA*

For caprellids in general, sex is difficult or impossible to differentiate through external examination during the juvenile stage, but the differences between the sexes increase as individuals grow. Two principal external criteria are used to determine the sex of *C. mutica* individuals. The first criterion is the insertion position and angle of the second gnathopod on the pereion’s second segment (Figure 1). For the male, the second gnathopod is inserted in the posterior part of the second pereionite and at its insertion point forms a  $\pm 90$  degree angle with the long axis of the pereionite. For the female, the second gnathopod is inserted into the anterior part of the second pereionite and forms a  $\pm 45$  degree angle. The second criterion for determining sex is the occurrence of oostegites in females on the third and fourth pereionite, or an absence of these oostegites in males. Fully developed oostegites form the incubating chamber in which eggs are laid and develop and where the female progeny is protected after emergence. Sex determination is more difficult on smaller caprellids because the oostegites initially appear like minuscule buds which are almost undetectable and the difference between sexes in the gnathopod II insertion point and angle is difficult to see.

For females, sexual maturity can be easily spotted with the occurrence of fully developed oostegites (Figure 2) and of eggs or juveniles in the incubating chamber formed by the oostegites. The oostegites of living female *C. mutica* have conspicuous red circular spots, but they disappear after a prolonged storage in formalin or ethanol.

For males, the gradual maturation process is revealed by the modification of several secondary sexual characteristics: the elongation of the first and second pereionite, the appearance, followed by the development, of the notches and spines on the palmar side of the second gnathopod, and an over-development of the second gnathopod. The appearance of a dense cover of setae (“hair”) can also be observed on the gnathopods as well as on the first and second pereionite (Platvoet *et al.* 1995). However in Cascapedia Bay (eastern Quebec), dense setation is rarely observed, only in larger males and particularly in samples collected in the fall (*C. Turcotte, pers. obs.*). Based on current knowledge, males cannot be divided into mature and immature categories according to external morphological and morphometric criteria.



Figure 2. Photo showing a mature female *Caprella mutica* of around 9 mm total in length excluding the antennae. The marsupial chamber under the female is formed by the oostegites (author: Thierry Gosselin).

Upon completion of their development and sexual maturation, both *C. mutica* sexes are characterized by a highly characteristic shape and noticeable size dimorphism. Males are elongated and up to three times longer than females.

### 3.3. SPECIES SIMILAR TO *C. MUTICA*

Canada has many caprellid species. There are at least 23 native species of which 16 belong to the genus *Caprella* in Canadian coastal waters of the Pacific Ocean, compared to 25 species of which 15 are of the genus *Caprella* along the Canadian coastal waters of the Atlantic and Arctic Oceans (Laubitz 1970, 1972). Only one native species is common to all three oceans: *C. equilibra*.

Certain species of the genus *Caprella* that occur in North America can be confused with *C. mutica*. On the Pacific side, *C. laeviuscula* is the most wide-spread (Laubitz 1970) and its general morphology resembles that of *C. mutica*. *C. laeviuscula* can be distinguished primarily from *C. mutica* by the lack of tubercles on its body and the enormous size (for adult males) of the middle spine on gnathopod II. *C. acanthogaster* is a native species from the Asian Pacific coasts that is apparently now found also on the west coast of the United States (Hines and Ruiz 2000) and is even more similar to *C. mutica* (Buschbaum and Gutow 2005). It appears that the two

species are regularly confused, even by taxonomists, partly because of the poor original graphic illustrations provided by Schurin (1935) (see comments in Marelli 1981, Vassilenko 2006). When it was discovered in California by Martin (1977), *C. mutica* was first identified as a subspecies of *C. acanthogaster*, *C. a. humboldtiensis* (see analysis by Marelli 1981). However, differences in the shape of the palmar side of gnathopod II and in the location, pattern and density of the tubercles or spines on the pereion allow discrimination of the adult specimens of *C. mutica* and *C. acanthogaster* (Arimoto 1976, Marelli 1981, Vassilenko 2006). In addition, male *C. acanthogaster* generally have a small protuberance on the head and usually have no dense cover of setae on the anterior part of their body (Arimoto 1976, Marelli 1981, Platvoet *et al.* 1995).

On North America's Atlantic coast, *C. linearis* (see Laubitz 1972) is likely the species that is closest in appearance to *C. mutica*. The two species share several general characteristics such as very similar notches and spines on the palmar side of gnathopod II in males. However, the middle spine on the gnathopod II in males is smaller in *C. linearis* than in *C. mutica* and pereionites III and IV of male and female *C. linearis* are generally free of tubercles and spines or the density and size of these structures are clearly smaller. Furthermore, the maximum size of *C. linearis* males is around 22 mm in total length (Laubitz 1972), which is much smaller than *C. mutica* mature males that can reach or even exceed 50 mm in total length (Takeuchi 1995, Ashton 2006). It should be noted that the total length of caprellids is measured from the anterior end of the head up to the posterior end of the abdomen.

## 4.0 DISTRIBUTION AND DISPERSAL

### 4.1 NATIVE DISTRIBUTION AND PHYSIOLOGICAL TOLERANCE

*C. mutica* is naturally distributed in the coastal waters of the sub-boreal regions of the north-eastern part of the Asian continent (Arimoto 1976, Fedotov 1992, Vassilenko 2006). In its native environment, the annual recorded temperatures between 1996 and 1998 varied between  $-1.8^{\circ}\text{C}$  in winter and  $25^{\circ}\text{C}$  in summer ( $15\text{--}25^{\circ}\text{C}$  for July–August) and salinity varied between 11 and 35 within the year (Schevchenko *et al.* 2004). *C. mutica* survival at temperatures as low as  $-1.8^{\circ}\text{C}$  is also supported by the species' persistence in Chaleur Bay (Gaspé Peninsula, Quebec) during winter, when the bay is covered by ice and water is as cold or colder (B. Sainte-Marie, pers. obs.).

Temperature and salinity are the principal factors that limit the spatial distribution of caprellids (McCain 1968, Laubitz 1970). *C. mutica* is no different, as shown by a series of experiments conducted by Ashton *et al.* (2007b) who established lethal or disabling temperature and salinity for adult *C. mutica* collected on the fish rearing structures in Dunstaffnage in Scotland. Results indicated a high increase in mortality after a 48 h exposure to temperatures above  $26^{\circ}\text{C}$ , with 100% mortality at  $30^{\circ}\text{C}$ . Caprellids were lethargic at  $2^{\circ}\text{C}$ , which suggests that growth, reproduction and the avoidance of predators were compromised. A 48 h exposure to water with a



salinity of 18 caused lethargy and every caprellid specimen died with salinity below 15. *C. mutica* tolerance for a range of temperatures and salinity make it an ideal candidate for introduction and survival at temperate to subarctic latitudes, where only brackish water (e.g. head of an estuary) would be inhospitable (Ashton 2006, Ashton *et al.* 2007b).

Other factors, abiotic and biotic, can be important for the distribution and survival of species of the genus *Caprella*, such as: degree of exposure to waves (Takeuchi *et al.* 1987, Guerra-Garcia 2001, Vassilenko 2006), substrate properties (Caine 1978), interspecific competition (Caine 1980) and predation (Guerra-Garcia 2001). The significance of these factors for *C. mutica* should be the subject of specific studies.

#### 4.2 EXOTIC DISTRIBUTION RANGE

Over the last four decades, *C. mutica* has been found on three continents (Table 1, Figure 3) in addition to its native continent. The list provided in Table 1 is not comprehensive; we are only trying to single out some key events in the introduction and expansion of the *C. mutica* range and to identify the extent of its known distribution in Canada. More detailed chronologies up to 2006 can be found elsewhere (Ashton 2006, Ashton *et al.* 2007a, Cook *et al.* 2007a).

From its native distribution range, *C. mutica* appears to have first colonized the western side of the North American continent because it was discovered in the 1970s in California and in Puget Sound, in the north of Washington State near the Canadian border (Carlton 1979, Marelli 1981). The species was then found in Europe, first in the Netherlands in 1994 (reported under the name *C. macho* by Platvoet *et al.* 1995), then on the west coast of Scotland in association with aquaculture operations (Willis *et al.* 2004). During this time, *C. mutica* had begun to spread to the west coast of Canada (Frey *et al.* 2009) and east coast of North America, where it was reported in Prince Edward Island in 1998 (Locke *et al.* 2007). *C. mutica* appears to have spread considerably along the western coast of North America around 2000–2003, having been observed in Alaska (Ashton *et al.* 2008a), in Quebec, Maine, Massachusetts, Rhode Island and Connecticut (Pederson *et al.* 2003; Table 1). Only one introduction to the southern hemisphere has been reported to date, in New Zealand in 2002 (Inglis *et al.* 2006). This recent introduction could mean that *C. mutica* might spread to the same latitudes in South America and possibly the southern part of Africa, where the water isn't too warm.

The history of the *C. mutica* introduction and expansion in Canada is short and not very well documented (Table 1). On Canada's east coast, *C. mutica* was first observed in 1998 at Prince Edward Island (Locke *et al.* 2007). It spread from 1998 to 2003 through the eastern side of Prince Edward Island into a network of estuaries and small bays where mussel aquaculture is practiced (Locke *et al.* 2007), but it does not appear to have colonized the more exposed coasts on the northern side of the island. The species was found in Quebec first in 2003 in Caspédia Bay near Carleton in the Gaspé Peninsula (B. Sainte-Marie, pers. obs.) and the following year in the Magdalen Islands (F. Bourque, MAPAQ, Cap-aux-Meules, pers. comm.). *C. mutica* populations in Quebec are well established and are able to survive through the harsh winters. In

2005, *C. mutica* was found on navigation buoys offshore from Caribou in New Brunswick (P. Archambault, Institut des sciences de la mer, Rimouski, pers. comm.). In 2008, in Quebec, the species was observed for the first time in Pasbebiac, Newport and Chandler and a single specimen was found in the Gaspé Bay in Quebec (N. Simard, DFO, Mont-Joli, pers. comm.). On

Table 1. Years and global locations where *Caprella mutica* was first found.

Year	Country	Location	Source
1935	Russia	Peter the Great Bay, Sea of Japan (native)	Schurin 1935 First description of the species
1973	United States	California	Cohen and Carlton 1995
1983	United States	Oregon	Cohen and Carlton 1995
1994	Netherlands	Burghsluis	Platvoet <i>et al.</i> 1995
1998	Canada	Brudenell, Prince Edward Island	Locke <i>et al.</i> 2007
2000	Scotland	Lynne of Lorne	Willis <i>et al.</i> 2004
2000	Germany	Sylt and Helgoland Islands, North Sea	Buschbaum and Gutow 2005
2000–03	United States	Alaska south-east of Aleutian Islands	Ashton <i>et al.</i> 2008a
2002	New Zealand	Timaru	Inglis <i>et al.</i> 2006
2003	Ireland	Bertraghbouy Bay	Tierney <i>et al.</i> 2004
2003	United States	Connecticut to Maine	Pederson <i>et al.</i> 2003
2003	Canada	Passamaquoddy Bay, New Brunswick – Maine border	S. Robinson, cited by Ashton <i>et al.</i> 2007a
2003	Canada	Cascapedia Bay, Quebec	B. Sainte-Marie, pers. obs.
2004	Canada	Magdalen Islands, Quebec	F. Bourque, MAPAQ, Cap-aux- Meules, pers. comm.
2005	Canada	Northumberland Strait, Caribou, New Brunswick	P. Archambault, Institut des sciences de la mer, Rimouski, pers. comm.

the west coast of Canada, museum specimens helped to establish that *C. mutica* was present at Vancouver Island as early as 1995 (Frey *et al.* 2009). However, the species may have appeared earlier because it was present in Puget Sound, just south of the Canadian border, in the 1970s (Carlton 1979). Frey *et al.* (2009) reported the occurrence of *C. mutica* all along the coast of British Columbia, from Washington State to the south up to Alaska to the north, including Queen Charlotte Islands.

The appearance and expansion over a few decades of *C. mutica* around the northern hemisphere certainly reflects repeated introductions and high adaptability and survival rate (see below). The various regions of the northern hemisphere continents where *C. mutica* was introduced and developed could be compatible donor-receiver sites, by their abiotic and biotic characteristics, for other invasive marine species (Ashton 2006).

#### **4.3 PATHWAYS OF INTRODUCTION AND SMALL AND LARGE SCALE DISPERSAL MODES**

The transoceanic spreading mechanisms (spatial scale in the thousands of kilometres) of *C. mutica* remain uncertain, but likely candidates are the transfer of Japanese oysters (*Crassostrea gigas*) and ballast water or, to a lesser degree, the hull of vessels (Cohen and Carlton 1995, Ashton *et al.* 2007a, Cook *et al.* 2007a). Caprellid survival in ballast water has been demonstrated (Carlton 1985, also see Cook *et al.* 2007b). All the reported introductions of *C. mutica* have occurred in areas with human activities: marinas, ports or aquaculture sites (Ashton 2006, Ashton *et al.* 2007a). The latter authors indicated that 59% of the introductions were detected within a 10 km radius of an international port, which further supports the hypothesis of introduction by maritime transport.

Without excluding other possibilities, the transfer of Japanese oysters via maritime or air transport seems particularly credible for explaining the introduction of *C. mutica* on the American west coast. In its natural environment, *C. mutica* can be found in association with the brown alga *Sargassum muticum* (Sano *et al.* 2003). This alga can attach itself to the shell of *C. gigas* oysters and has also been used for packing oyster spat for exportation (Druehl 1973, Critchley *et al.* 1983, Rueness 1989). *S. muticum* has colonized some 4,000 km of the North American Pacific coast within a 30-year period (Setzer and Link 1971; Critchley 1983). In Europe, after the first discovery of *S. muticum* in England in 1973, this alga has been found in the Mediterranean and North Sea, on the coasts of Portugal, Spain, France, Germany, Denmark, Sweden, Norway, Belgium and the Netherlands (Critchley *et al.* 1983, Rueness 1989). It is possible that *C. mutica* was introduced on the west coast of North America and in Europe around the same time as *S. muticum*, but that detecting the caprellid took longer because of identification problems. However, Cook *et al.* (2007a) are of the opinion that commercial navigation (ballast water or hulls) is responsible for introducing *C. mutica* to Europe. It should be noted that *S. muticum* has not yet been found on the east coast of North America, which appears to suggest that the most likely vector for introduction there would also be commercial navigation.

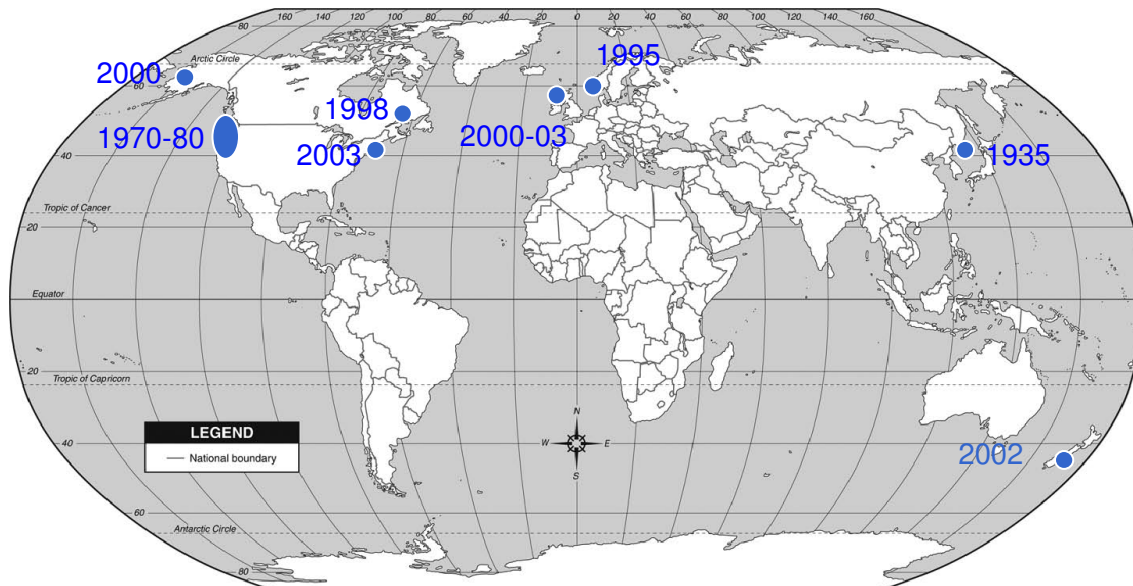


Figure 3. Map showing the location where *Caprella mutica* was first described in 1935, and the years and locations where *Caprella mutica* was first introduced on other continents of the northern and southern hemispheres.

The dispersal modes on a medium spatial scale (a few kilometres to a few hundred kilometers) that allow for secondary propagation of a species along a coastline following its initial introduction are also difficult to determine. However, the occurrence of *C. mutica* on temporary buoys offshore from the Canadian east coast suggests that these secondary propagation modes are effective (C. McKindsey, DFO, Mont-Joli, pers. comm.). These secondary dispersal modes can evidently also include transoceanic transportation modes as mentioned previously – transfer of organisms for aquaculture, ballast water and vessel hulls. The hulls of commercial vessels or pleasure crafts, if caprellids attach themselves directly or to other organisms already attached, represent a potentially important anthropic vector for the local transportation and secondary propagation of *C. mutica* (Ashton *et al.* 2006, Lewis *et al.* 2006, Vassilenko 2006, Frey *et al.* 2009). Attaching themselves to vessels could allow *C. mutica* to travel against the current and colonize areas upstream that are otherwise inaccessible by natural means. The human vector is probably the most important propagation and exotic distribution factor for *C. mutica* (Ashton 2006, Cook *et al.* 2007a).

Caprellids also have natural dispersal abilities which can contribute to their secondary propagation. All caprellid species live attached to a substrate and have no planktonic larval

phase, so it would appear that they are not very capable of dispersal. However, Caine (1980) concluded that *C. laeviuscula* can move actively by crawling or swimming and passively by drifting on floating algae.

Crawling and swimming are probably not effective natural modes of dispersal for caprellids on a medium spatial scale. Crawling is slow and has very short spatial limits and significant risks for predation. The swimming capacity of caprellids has not been documented much, but they do not have the streamlined body or the well-developed swimming appendages (pleopods) that characterize the powerful amphipod swimmers belonging to the suborder Gammaridea that are capable of traveling autonomously over several kilometres (Sainte-Marie and Brunel 1985, Sainte-Marie 1986). Caine (1978) indicated that a strong or directional swimming ability over a distance of more than 15 cm has never been observed in caprellids. Ashton (2006) reported anecdotally that *C. mutica* individuals, when disturbed in a laboratory, swim a short distance and then deploy their pereopods and slowly sink to the bottom. Our own laboratory and *in situ* observations showed that the swimming of *C. mutica* is relatively ineffective, resembling more a crawling motion in water, but suggested that downward oblique movements are possible with the current over distances of several meters to several dozen meters (or perhaps more) depending on the depth and current speed, but not against the current. Ashton (2006) showed that collectors positioned 6 m deep were colonized within eight weeks up to 1 km from an established *C. mutica* population. The dispersal mode was not determined, but the author did not rule out “free-swimming dispersal”, which appears to be unlikely.

It is more likely that the main dispersal mode of *C. mutica* on a medium spatial scale is passive and that it occurs by drifting (rafting) on natural floating objects, such as macro-algae and tree trunks, or on man-made waste (Ashton 2006; Cook *et al.* 2007a, Astudillo *et al.* 2009). These transportation vectors have the advantage of offering a structurally complex habitat protecting the caprellids from desiccation and predation and allowing them to continue their regular activities including reproduction (Highsmith 1985, Thiel and Gutow 2005a, 2005b). Sano *et al.* (2003) observed *C. mutica* individuals in drifting algae communities in the species’ natural habitat in Japan. *C. mutica* was also observed on *S. muticum* colonies floating on the surface near Helgoland Island in Germany and the drifting algae is considered the introduction and spreading mechanism of *C. mutica* in this area (Buschbaum and Gutow 2005). In Scotland, 29.6% (7/26) of the drifting algae samples collected within a radius of 25 m from a vessel over a distance of 40 km contained *C. mutica* at a density reaching as many as 71 individuals per sample (Ashton 2006). Passive transportation of *C. mutica* by drifting algae or debris could explain the rapid propagation of the species on the North American west coast and in Europe (e.g. Cook *et al.* 2007a).

Ashton *et al.* (2008b) attempted to retrace the introduction routes of *C. mutica* in North America by using mitochondrial DNA. They discovered a high genetic diversity in the species’ original natural environment (Sea of Japan) compared to that observed in its adoptive environments. They also discovered that North American introductions occurred by different means on the Atlantic and Pacific sides. Two different dominant haplotypes were observed on the east and west sides of the Atlantic, which would indicate the occurrence of several routes of dispersal in

this ocean (Ashton *et al.* 2008b). The introduced caprellids were not linked to any specific source population from the Sea of Japan and according to the authors, a more detailed sampling of intra and inter-populations in their native range would be required due to the high genetic diversity of the species.

## 5.0 ECOLOGY

### 5.1 HABITAT

Little is known about the ecology of *C. mutica*. Generally, caprellids are associated with littoral and infralittoral habitats, even though certain species have an extended bathymetric distribution range or are exclusively bathyal (e.g. Laubitz 1970). Caprellids are particularly well represented within biofouling epibenthic communities (Thiel *et al.* 2003), colonizing filamentous or branching structures such as algae, hydrozoans and bryozoans (e.g. McCain 1968, Caine 1998). In the Sea of Japan, *C. mutica* occurs naturally in the infralittoral (0.7–13 m deep) in eelgrass or algae beds (Fedotov 1992) and on drifting macroalgae (Sano *et al.* 2003). Hydrodynamics play an important part in the successful establishment of this species which is found primarily in bays shielded from waves in the Sea of Japan (Vassilenko 2006).

In its adoptive waters of the northern hemisphere, *C. mutica* is primarily or only found on artificial structures such as nets, ropes and cages used in aquaculture, docks in marinas and ports, oil rig platforms and navigation buoys (Willis *et al.* 2004; Buschbaum and Gutow 2005, Page *et al.* 2006, Ashton *et al.* 2007a, Cook *et al.* 2007a; Frey *et al.* 2009). *C. mutica* represented more than 50% of the amphipods found on the oil rig platforms off California, whereas there were almost no specimens on the neighbouring natural reefs (Page *et al.* 2007). In Europe, it seems that abundant numbers of *C. mutica* were observed only on artificial structures, along with other invasive species (Willis *et al.* 2004, Ashton 2006, Buschbaum and Gutow 2005, Cook *et al.* 2007a). Similarly, in eastern Canada, *C. mutica* has only been found so far on artificial structures. Buschbaum and Gutow (2005) hypothesized that this association with artificial structures could be due to the fact that these substrates represent a transitional habitat where *C. mutica* may acclimatize for a few years before spreading to natural habitats in its new environment.

### 5.2 CAPRELLID DIET

The morphology of caprellids may inform us about their diet. According to certain authors, the three characteristics that may determine or reveal a species' predominant diet are: the occurrence or not of a molar process on the mandible, of a mandibular palp and of natatory setae on antenna II (McCain 1968, Caine 1974, 1977). However, Guerra-García and De Figueroa (2009) did not find a good fit between the occurrence of these morphological characteristics and the diet of 26

*Caprella* species determined by stomach content analysis. The caprellid's position in relation to the substrate, either crouched or upright (Takeuchi and Hirano 1995), and the maximum reach of its antennas above the substrate, which is based on the size of the caprellid and the relative length of its antennas (Caine 1977), could also be significant dietary factors.

The caprellids of the genus *Caprella* can have a diversified diet and are considered as opportunistic feeders (e.g. Saunders 1966, Keith 1969) or primarily detritivores (Guerra-García and De Figueroa 2009). Saunders (1966) showed that the species of the genus *Caprella* on the American west coast fed on diatom algae, crustaceans and detritus. McCain (1968) and then Caine (1977) identified four possible feeding modes in the genus *Caprella*: browser, filter-feeder, scraper and scavenger. However, it appears that at least one *Caprella* species can be a predator at times on nematodes, polychaete worms, harpacticoid copepods, ostracods and gammaridean amphipods (McCain 1968). Based on personal communications describing an association between *Caprella* spp. and tunicates on mussel mainlines in Prince Edward Island, Paetzold *et al.* (2008) suggested that there may be some predation on tunicate larvae (note: due to the location where the study took place, the said caprellids may belong to the *C. mutica* species). Furthermore, a same species of caprellid could have different feeding modes according to certain circumstances (McCain 1968, Caine 1977). Finally, it should be noted that the frequent association between certain caprellid species and hydrozoans led to the hypothesis of a commensal or kleptocommensal relationship, with the caprellids feeding directly on particles or organisms captured by the hydrozoans (e.g. e.g. Krapp-Schickel 1993, Bavestrello *et al.* 1996, Camillo *et al.* 2008; but see below on the possibility that the hydrozoans may also be caprellid predators), or even a mutual relationship in which the hydrozoans benefit from a certain protection offered by the caprellids against nudibranchs (Caine 1998).

There is very little specific work concerning the diet of *C. mutica*. *C. mutica* is characterized by the occurrence of a molar process, the absence of a mandibular palp and the presence of natatory setae on the second pair of antennas, characteristics that qualify it for a filter-feeder feeding mode according to the Caine (1977) classification. In addition, *C. mutica* has various properties of a filter-feeding species, a large size, relatively long antennas and an upright position above the substrate (see Caine 1977, Takeuchi and Hirano 1995, B. Sainte-Marie and C. Turcotte, pers. obs.). A morphological, kinematic and biomechanical study revealed that the vertical range of the antennas, the position of the natatory setae as well as the antenna behaviour and balancing speed would in theory allow *C. mutica* to filter suspended particles, although more easily for adults than for juveniles (Michel *et al.* 2007, Nauwelaerts *et al.* 2007; S. Nauwelaerts, Mary Anne McPhail Equine Performance Center, Lansing, Michigan, pers. comm.). It is therefore possible that there are dietary differences between juveniles and adults, but also between females and males because of the considerable sexual size dimorphism that characterizes *C. mutica*.

The study of *C. mutica* stomach contents and laboratory experiments suggest that the species can have several feeding modes depending on the circumstances. Sano *et al.* (2003) concluded that *C. mutica* in its natural habitat was omnivorous and fed primarily on organisms related to its home substrate, for example small epibenthic crustaceans and periphyton such as pennate diatoms. Guerra-García and De Figueroa (2009) found that 98.4% of the stomach surface of 13

*C. mutica* specimens was occupied by detritus, and only 1.6% by copepod remains coming almost entirely or solely from harpacticoid forms. The analysis of stomach contents of *C. mutica* specimens sampled on mussel mainlines in Chaleurs Bay in the Gaspé Peninsula revealed only remains of small crustaceans and central (planktonic) and pennate diatom algae (B. Sainte-Marie and C. Turcotte, pers. obs.). In the laboratory, Cook *et al.* (2007b) found no significant survival difference after 18 days between groups of *C. mutica* fed only the macroalga *Fucus vesiculosus*, the central diatom *Cylindrotheca fusiformis* or salmon feed, although survival was lower with the feed possibly due to its overly high organic content or bacterial contamination. A second experiment showed a statistically equivalent survival after 20 days, from 43 to 57%, between groups of *C. mutica* fed *F. vesiculosus* or *C. fusiformis* and a group without any added food. One may wonder whether the cannibalistic necrophagia that Cook *et al.* (2007b) observed, or cannibalistic predation, may have played a key role in this longevity without food. Indeed, experiments carried out at the Centre Aquacole Marin de Grande-Rivière (CAMGR) in Quebec revealed that *C. mutica* individuals fed on dead congeners and the aggressive nature of the species towards living congeners (C. Turcotte, pers. obs.). Moreover, Nakajima and Takeuchi (2008) installed a *C. mutica* population in a public aquarium and it has survived and renewed itself for five years feeding only on the diatom *Phaeodactylum tricorutum* and recently hatched brine shrimp (*Artemia salina*). Therefore, it is likely that *C. mutica* is as flexible or perhaps more flexible than other *Caprella* species in its feeding habits and adopts a feeding mode based on the existing conditions, filterer, grazer, scavenger and perhaps even scraper and predator, which would make the species high adaptable to various nutritional conditions.

### 5.3 NATURAL PREDATORS

The known natural predators of caprellids are primarily fish (e.g. Caine 1989, 1991a, Page *et al.* 2007, O’Gorman *et al.* 2008), and to a lesser extent, invertebrates such as crabs (Dubiasiki-Silva and Masunari 2008), nudibranchs (Caine 1980), starfish (Lauerman 1998) and possibly hydrozoans (Genzano 2005). Caprellids can represent a significant link in the food chain between unicellular algae and some predatory fish (Caine 1989, Holbrook and Schmitt 1992, O’Gorman *et al.* 2008). In fact, it was recently proposed that caprellids could be used as fish feed in aquaculture operations (Woods 2009).

Fish are visual predators of caprellids and select their prey based on their behaviour (e.g. movement and degree of exposure) and size (Caine 1989). The passage of the migratory fish *Cymatogaster aggregata* was linked to a marked decrease of *C. laeviuscula* populations in Padilla Bay in Washington State, on the American west coast (Caine 1991a). Caprellids were not the preferred prey of *C. aggregata*, but rather a temporary diet option for a few weeks during a critical period of the fish life cycle (Caine 1991a). However, other fish species or sub-populations of a fish species can be specialized caprellid predators (Holbrook and Schmitt 1992). It is possible that male caprellids are more vulnerable to predation by fish because of their larger size (Ashton 2006).



## 6.0 REPRODUCTION AND POPULATION DYNAMICS

### 6.1 REPRODUCTION

The *C. mutica* populations that were studied in their natural environment in the Sea of Japan, as well as in Scotland, had a sex-ratio dominated by females except during the summer spawning period (Fedotov 1992, Ashton 2006). Caprellids are usually characterized by a considerable sexual size and shape dimorphism, with males being clearly larger, more robust and better armed (i.e. with much more developed second gnathopods) than females (see above). Sexual dimorphism, in particular the extreme development of gnathopod II and of spines on its palmar side, is most likely explained by strong sexual competition and the protective behaviour of males towards females (Caine 1991b, Conlan 1989, 1991). Sexual dimorphism is very evident in *C. mutica* and male aggressive behaviours towards other males and their protection of females have been observed in the laboratory (C. Turcotte, pers. obs.). The male caprellid protective behaviour may contribute to increase survival of females during and after the maturity moult that immediately precedes mating and egg-laying (Caine 1991b, Conlan 1991).

For caprellids, as for all other amphipods, eggs are laid and incubated in the marsupial chamber formed by the oostegites under the female's abdomen (Figure 2). Embryonic and larval development occurs inside the egg and, upon hatching, a juvenile quite similar in overall form to the adult appears. Juvenile caprellids remain in the marsupial chamber or near their mother for a period lasting between a few hours and 3–4 weeks after emerging, depending on the species (Arimoto 1976, Aoki and Kikuchi 1991, Aoki 1999; see below). Thus, there is no planktonic larval dispersal phase, which represents an advantage if juvenile caprellids are in appropriate habitat conditions after hatching or leaving their mother. The number of eggs per brood can vary from 15 to 363 per *C. mutica* female and there is a positive correlation between fecundity and female length (Vassilenko 1991, Fedotov 1992, Ashton 2006, Nakajima and Takeuchi 2008). *C. mutica* is no different than five other *Caprella* species in terms of fecundity and egg size (Vassilenko 1991). It should be noted that Caine (1991b) suggested the existence of nurse eggs in *C. laeviusculus*, which would contribute towards improving juvenile survival after emergence.

During laboratory experiments conducted by Cook *et al.* (2007b), female *C. mutica* showed a relatively high productivity at temperatures of 13–14°C by producing their first brood at a total length of 8.5 mm, corresponding to stage (instar) VII, which is reached around 44 days after hatching (according to their Table 1) and after releasing their first progeny around 53 days after hatching. The females produced on average two broods before dying, the second brood was released on average 20 days after the first. Juvenile *C. mutica* emerged from the marsupial chamber at a total length of around 1.3 mm (Cook *et al.* 2007b). The reproductive precocity and iteroparity of females, which are characteristics shared with other *Caprella* species (e.g. Takeuchi and Hirano 1991), provide for rapid demographic growth. It is also likely that male *C. mutica* are able to reproduce prior to full development of their secondary sexual characteristics,

as is the case with *C. gorgonia* (Lewbel 1978) and other amphipods with marked sexual dimorphism (Conlan 1989, 1991).

The reproductive characteristics of *C. mutica* could however be different in nature and vary within and among regions depending on their environmental conditions. Fedotov (1992) studied reproduction and population dynamics of *C. mutica* in Posyet Bay, in the Sea of Japan. Females that hatched in spring (May) reached sexual maturity at an average total length of 6 mm in June–July, around two months after hatching, whereas those hatched in July–August did not reach sexual maturity before January–February, around six months after hatching. Juveniles leaving their mother measured 1.8 mm in total length. Finally, Fedotov (1992) estimated that egg incubation lasted 30–40 days at temperatures varying between 13 and 17°C and 60 days at a temperature varying between 0 and 2°C. Generally, amphipods grow more slowly, sexual maturity occurs later and the length of incubation is longer as the latitude increases or as the temperature decreases within a species' distribution range (Sainte-Marie 1991).

Females of several species of the genus *Caprella* display maternal care after juveniles hatch (Lim and Alexander 1986, Thiel 1997, 2003, Aoki 1999). For the species most studied in this respect, i.e. *C. decipiens*, *C. monoceros* and *C. scaura*, juveniles remained on or around their mother for up to 26 days following their hatching (Aoki and Kikuchi 1991, Aoki 1997). The maternal care period could be necessary for recently hatched juveniles from many caprellid species because they are weak and unable to grab onto most substrate types except for their mother. Furthermore, in case of danger, the mother can provide spontaneous protection or carry to a shelter its older offspring that have remained near her (Aoki 1997). Direct development and maternal care likely provide a very high survival rate for the progeny. The occurrence of maternal care has not yet been demonstrated in *C. mutica*. According to Aoki (1999), maternal care is not very well developed or is non-existent in species from the genus *Caprella* that produce large juveniles (> 1.6 mm in total length after hatching) or that are associated to biogenic structures that provide protection to juveniles, such as branching hydrozoans.

## 6.2 POPULATION DYNAMICS

In the natural habitat of *C. mutica* in the Sea of Japan, there are apparently two generations per year providing for two reproductive periods per year, one in the spring, from March to May, and the other in the summer, from June to July. Juveniles appearing in May would be ready to spawn in June or July and those appearing at the end of summer likely hibernate, ensuring the renewal of the population the following spring (Fedotov 1992). Observations made on *C. mutica* in Cascapedia Bay (Chaleurs Bay, Quebec) also suggest the occurrence of two caprellid generations per year (B. Sainte-Marie and C. Turcotte, unpublished data). The fact that *C. mutica* have more than one generation per year increases its demographic growth potential. In Scotland, where the temperature is milder, berried females were reported throughout the year (K.J. Willis, Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, Oban, UK, pers. comm.).

In the Sea of Japan and in Scotland, seasonal abundance fluctuations of *C. mutica* appear to follow the annual primary production cycles (Fedotov 1992, Ashton 2006). In both cases, the population reaches an abundance peak in August–September and declines during the winter. The study by Buschbaum and Gutow (2005) conducted in the North Sea showed that *C. mutica* individuals measuring more than 10 mm in total length are almost absent from mid-November on, which indicates that the adults die after their last brood in late fall. This type of life cycle is typical for amphipods in temperate regions (Bynum 1978).

The density of *C. mutica* on artificial structures can be very high, but the density observed in Cascapedia Bay (Quebec) exceeds all previously published values. In particular, densities measured on mussel spat collectors in Cascapedia Bay were considerably higher than those reported in the natural *C. mutica* habitat in the Sea of Japan (see Fedotov 1992). In October 2005 for example, an average of 2,344 individuals per 10 linear cm of collector was observed in Cascapedia Bay, which is equivalent to 468,800 individuals per m<sup>2</sup> (B. Sainte-Marie and C. Turcotte, pers. obs.). The density reported that is closest to this value was in Dunstaffnage in Scotland by Ashton (2006) on plastic panels installed near artificial structures, such as marinas and pontoons, and totalled 319,000 individuals per m<sup>2</sup>. In comparison, the maximum density of *C. mutica* in its natural habitat is 1,220 or 2,600 individuals per m<sup>2</sup> depending on the location (Fedotov 1992, Vassilenko 2006).

## **7.0 IMPACTS FROM THE INTRODUCTION OF THE JAPANESE SKELETON SHRIMP**

Despite the introduction of *C. mutica* in several countries, few direct or indirect impacts have been reported. *C. mutica* population dynamics suggest that its impact is most likely to be felt during the summer because of its high abundance (Ashton 2006; B. Sainte-Marie and C. Turcotte, pers. obs.). Mussel farmers from Scotland and Quebec have reported a decrease in *Mytilus* spp. spat collection and growth since the appearance of *C. mutica* (Ashton 2006, B. Sainte-Marie and C. Turcotte, pers. obs.). A causal relationship could not be confirmed in Scotland (Ashton 2006). However, field and laboratory work conducted in Quebec confirmed there was a negative effect of *C. mutica* on mussel spat. The underlying mechanisms were documented and mitigation measures were recommended (B. Sainte-Marie and C. Turcotte, pers. obs.). According to Ashton (2006), the best period for attempting to control *C. mutica* populations is in late fall or in winter, following the intense reproduction period and when population abundance is at its lowest.

The potential effects on the food chain structure and on the upper trophic levels represent a major concern regarding the introduction of an exotic species in an ecosystem (Grosholz 2002). The introduction of *C. mutica* in California led to a noticeable change in the diet of the fish *Oxylebius pictus* on artificial reefs where this caprellid was abundant compared to the neighbouring natural reefs where it was not (Page *et al.* 2007). The transfer of predation effort from a native species

towards a more abundant and available invasive species can have significant consequences on the predator which may be advantaged or disadvantaged depending on the circumstances (Page *et al.* 2007). One of the advantages could be a high abundance of food, whereas one of the disadvantages could be that the invasive species has a lower nutritional value than the native prey. The fatty acids in *C. mutica*, described by Kawashima *et al.* (1999), appear however to make it a quality food for fish. It should be noted however that Takeuchi *et al.* (2001) noticed a sizeable bioaccumulation of the contaminant butyltin in *Caprella* spp. and so, by the way, this genus could be an excellent bio-indicator of pollution.

The introduction and development of *C. mutica* populations could however have other consequences on the native food web. *C. mutica* can no doubt represent an added food source for certain micro- or macro-predators and could improve their condition, but its abundance could also decrease the diversity and abundance of native invertebrate species, at least on artificial structures (Page *et al.* 2007). In its exotic distribution range, *C. mutica* does not appear to colonize natural substrates (see above). It is therefore difficult to establish the potential effects of *C. mutica* on natural ecosystems. However, a laboratory study demonstrated the aggressive nature of *C. mutica* towards a caprellid species that is native to eastern Canada, *C. linearis*, and its ability to exclude and kill it. At high densities, *C. mutica* could entirely exclude *C. linearis* from habitats, whether they had shelters or not (Shucksmith *et al.* 2009).

## 8.0 CONCLUSION

*Caprella mutica* appears to be well established in certain marine parts of Canada and is extending its range. Van der Velde *et al.* (2000) determined a list of characteristics that make a crustacean an effective invader. The following are a few of those characteristics that well describe *C. mutica*:

- Abundant and widely distributed in its home range,
- High genetic diversity in its home range,
- Tolerant to a wide range of environmental conditions,
- Diversified (opportunistic) diet,
- Commensal with human activities.

Other favourable characteristics identified by Van der Velde *et al.* (2000) determine a high biotic potential (“r” type strategy) and also characterize *C. mutica*:

- Short period between generations,
- Rapid growth,
- Early sexual maturity,
- High reproductive capacity.

However, these reproductive characteristics are very common among amphipods (Sainte-Marie 1991) and in particular among caprellid species sympatric to *C. mutica* in its home distribution range. The fact that none of these other of caprellid species has been a successful invader, except perhaps for *C. acanthogaster* (see Hines and Ruiz 2000, Guerra-García and Takeuchi 2004, Lewis *et al.* 2006), suggests that the biotic potential alone cannot explain the establishment and expansion of *C. mutica* in North America and Europe. For gammaridean amphipods, Devin and Beisel (2007) found that tolerance to a wide range of environmental conditions – specifically a euryhaline character – was one of the important factors for explaining a species’ potential for invading freshwater or brackish-water environments. Nevertheless, these authors, just as Grabowski *et al.* (2007), concluded that it is the combination of several characteristics that determines the success of an invasive amphipod.

The fact that *C. mutica* is only or almost only found on artificial structures in its exotic distribution range is intriguing, considering its biotic potential and its high dispersal capacity and the fact that it has been established in several North American and European locations for over 10–20 years. In comparison, the other amphipod invaders appear to establish themselves rather quickly in the natural environment and can cause severe damage to the ecosystem (e.g. Van der Velde *et al.* 2000, Devin and Beisel 2007, Bollache *et al.* 2008). The close relationship between *C. mutica* and artificial structures, should it continue, could suggest that the factor “commensal with human activities” is particularly important, both for their initial introduction and for the development of subsequent populations. The occurrence of *C. mutica* on rearing structures is likely due to the easy access of a constant and abundant source of organic particulate matter (plankton, feed or feces). Even though *C. mutica* does not appear to have caused noticeable damage to date in the natural ecosystems, it is certain that, as with all invasive species, its introduction represents a potential threat to biodiversity and economic activities.

## 9.0 ACKNOWLEDGEMENTS

We would like to thank Louise Gendron, Chris McKindsey, Nathalie Simard as well as Anne-Marie Clément for their comments on the manuscript and Diane Bélanger for her assistance for the page layout. A special thanks to Chris Ashelby for Figure 1 taken from Ashelby (2005) published in Essex Naturalist.

## 10.0 REFERENCES

Aoki, M. 1997. Comparative study of mother-young association in caprellid amphipods: Is maternal care effective? *J. Crustac. Biol.* 17: 447–458.

- Aoki, M. 1999. Morphological characteristics of young, maternal care behaviour and microhabitat use by caprellid amphipods. *J. Mar. Biol. Assoc. U.K.* 79: 629–638.
- Aoki, M. and T. Kikuchi. 1991. Two types of maternal care for juveniles observed in *Caprella monoceros* Mayer, 1980 and *Caprella decipiens* Mayer, 1890 (Amphipoda : Caprellidae). *Hydrobiologia* 223: 229–237.
- Arimoto, I. 1976. Taxonomic studies of caprellids (Crustacea, Amphipoda, Caprellidae) found in the Japanese and adjacent waters. *Spec. Publ. Seto Mar. Biol. Lab., Ser. III*, v + 229 p.
- Ashelby, C. 2005. The occurrence and distribution of non-native fauna in Harwich Harbour and the Stour and Orwell estuaries, including new records of *Caprella mutica* Schurin 1935 and *Bugula stolonifera* Ryland 1960. *Essex Natur.* 22: 103–116.
- Ashton, G.V. 2006. Distribution and dispersal of the non-native caprellid amphipod, *Caprella mutica* Schurin 1935. Ph.D. thesis, Univ. Wales, Swansea, Wales, 180 p.
- Ashton, G.V., K. Boos, R. Shucksmith and E. Cook. 2006. Risk assessment of hull fouling as a vector for marine non-natives in Scotland. *Aquat. Invas.* 1: 214–218.
- Ashton, G.V., E.I. Riedlecker and G.M. Ruiz. 2008a. First non-native crustacean established in coastal waters of Alaska. *Aquat. Biol.* 3: 133–137.
- Ashton, G.V., M.I. Stevens, M.C. Hart, D.H. Green, M.T. Burrows, E.J. Cook and K.J. Willis. 2008b. Mitochondrial DNA reveals multiple Northern Hemisphere introductions of *Caprella mutica* (Crustacea, Amphipoda). *Mol. Ecol.* 17: 1293–1303.
- Ashton, G.V., K.J. Willis, E.J. Cook and M. Burrows. 2007a. Distribution of the introduced amphipod, *Caprella mutica* Schurin, 1935 (Amphipoda: Caprellida: Caprellidae) on the west coast of Scotland and a review of its global distribution. *Hydrobiologia* 590: 31–41.
- Ashton, G.V., K.J. Willis, M.T. Burrows and E.J. Cook. 2007b. Environmental tolerance of *Caprella mutica*: Implications for its distribution as a marine non-native species. *Mar. Environ. Res.* 64: 305–312.
- Astudillo, J.C., M. Bravo, C.P. Dumont and M. Thiel. 2009. Detached aquaculture buoys in the SE Pacific: potential dispersal vehicles for associated organisms. *Aquat. Biol.* 5: 219–231.
- Bavestrello, G., C. Cerrano, R. Cattaneo-Vietti and M. Sarà. 1996. Relations between *Eudendrium glomeratum* (Cnidaria, Hydromedusae) and its associated vagile fauna. *Sci. Mar.* 60: 137–143.
- Bollache, L., J.T.A. Dick, K.D. Farnsworth and W.I. Montgomery. 2008. Comparison of the functional responses of invasive and native amphipods. *Biol. Lett.* 4: 166–169.
- Buschbaum, C. and L. Gutow. 2005. Mass occurrence of an introduced crustacean (*Caprella cf. mutica*) in the south-eastern North Sea. *Helgoland Mar. Res.* 59: 252–253.

- Bynum, K.H. 1978. Reproductive biology of *Caprella penantis* Leach, 1814 Amphipoda: Caprellidae) in North Carolina, USA. *Est. Coast. Mar. Sci.* 7: 473–485.
- Caine, E.A. 1974. Comparative functional morphology of feeding in three species of caprellids (Crustacea, Amphipoda) from the northwestern Florida Gulf coast. *J. Exp. Mar. Biol. Ecol.* 15: 81–96.
- Caine, E.A. 1977. Feeding mechanisms and possible resource partitioning of the Caprellidae (Crustacea: Amphipoda) from Puget Sound, USA. *Mar. Biol.* 42: 331–336.
- Caine, E.A. 1978. Habitat adaptations of North American caprellid Amphipoda (Crustacea). *Biol. Bull.* 155: 288–296.
- Caine, E.A. 1980. Ecology of two littoral species of caprellid amphipods (Crustacea). *Mar. Biol.* 56: 327–335.
- Caine, E.A. 1989. Relationship between wave activity and robustness of caprellid amphipods. *J. Crustac. Biol.* 9: 425–431.
- Caine, E.A. 1991a. Caprellid amphipods: Fast food for the reproductively active. *J. Exp. Mar. Biol. Ecol.* 148: 27–33.
- Caine, E.A. 1991b. Reproductive behaviour and sexual dimorphism of a caprellid amphipod. *J. Crustac. Biol.* 11: 56–63.
- Caine, E.A. 1998. First case of caprellid amphipod-hydrozoan mutualism. *J. Crustac. Biol.* 18: 317–320.
- Camillo, C.D., M. Bo., A. Lavorato, C. Morigi, M. Segre-Reinach, S. Puce and G. Bavestrello. 2008. Foraminifers epibiotic on *Eudendrium* (Cnidaria: Hydrozoa) from the Mediterranean Sea. *J. Mar. Biol. Assoc. U.K.* 88: 485–489.
- Carlton, J.T., 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Ph.D. thesis, University of California, Davis, 904 p.
- Carlton, J.T., 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. *Oceanogr. Mar. Biol. Ann. Rev.* 23: 313–371.
- Cohen, A.N. and J.T. Carlton. 1995. Nonindigenous aquatic species in a United States estuary: A case study of the biological invasions of the San Francisco Bay and delta. A report for the United States Fish and Wildlife Service, Washington, DC and the National Sea Grant College Program Connecticut Sea Grant Program, No. CONNT95002, 272 p.
- Conlan, K.E. 1989. Delayed reproduction and adult dimorphism in males of the amphipod genus *Jassa* (Corophioidea, Ischyroceridae) – an explanation for systematic confusion. *J. Crustac. Biol.* 9: 601–625.
- Conlan, K.E. 1991. Precopulatory mating behavior and sexual dimorphism in the amphipod Crustacea. *Hydrobiologia* 223: 255–282.

- Cook, E.J., M. Jahnke, F. Kerchof, D. Minchin, M. Faasse, K. Boos and G. Ashton. 2007a. European expansion of the introduced amphipod *Caprella mutica* Schurin 1935. *Aquat. Invas.* 2 : 411–421.
- Cook, E.J., K.J. Willis and M. Lozano-Fernandez. 2007b. Survivorship, growth and reproduction of the non-native *Caprella mutica* Schurin, 1935 (Crustacea: Amphipoda). *Hydrobiologia* 590: 55–64.
- Critchley, A.T. 1983. *Sargassum muticum*: a taxonomic history including world-wide and western Pacific distributions. *J. Mar. Biol. Ass. U.K.* 63: 617–625.
- Critchley, A.T., W.F. Farnham and S.L. Morrell. 1983. A chronology of new European sites of attachment for the invasive brown alga, *Sargassum muticum*, 1973–1981. *J. Mar. Biol. Ass. U.K.* 63: 799–811.
- Devin, S. and J.-N. Beisel. 2007. Biological and ecological characteristics of invasive species: a gammarid study. *Biol. Invas.* 9: 13–24.
- Druehl, L. 1973. Marine transplantations. *Science* 179: 12.
- Dubiaski-Silva, J. and S. Masunari. 2008. Natural diet of fish and crabs associated with the phytal community of *Sargassum cymosum* C. Agardh, 1820 (Phaeophyta, Fucales) at Ponta das Garoupas, Bombinhas, Santa Catarina State, Brazil. *J. Natur. Hist* 42: 1907–1922.
- Fedotov, P.A. 1992. Population and production biology of amphipod *Caprella mutica* in Poyset Bay, Sea of Japan. *Russ. J. Mar. Biol.* 17: 224–230.
- Frey, M.A., H.N. Gartner, C.C. Murray and T.W. Therriault. 2009. First confirmed records of the non-native amphipod *Caprella mutica* (Schurin 1935) along the coast of British Columbia, Canada, and the potential for secondary spread via hull fouling. *Aquat. Invas.* 4: 495–499.
- Genzano, G.N. 2005. Trophic ecology of a benthic intertidal hydroid, *Tubularia corcea*, at Mar del Plata, Argentina. *J. Mar. Biol. Assoc. U.K.* 85: 307–312.
- Grabowski, M., K. Bacela and A. Konopacka. 2007. How to be an invasive gammarid (Amphipoda: Gammaroidea) – comparison of life history traits. *Hydrobiologia* 590: 75–84.
- Grosholz, E. 2002. Ecological and evolutionary consequences of coastal invasions. *Tr. Ecol. Evol.* 117: 22–27.
- Guerra-García, J.M. 2001. Habitat use of the Caprellidea (Crustacea: Amphipoda) from Ceuta, North Africa. *Ophelia* 55 : 27–38.
- Guerra-García, J.M. and J.M.T. De Figueroa. 2009. What do caprellids (Crustacea: Amphipoda) feed on? *Mar. Biol.* 156: 1881–1890.



- Guerra-García, J.M. and I. Takeuchi. 2004. The Caprellidea (Crustacea: Amphipoda) from Tasmania. *J. Nat. Hist.* 38: 967–1044.
- Highsmith, R.C. 1985. Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. *Mar. Ecol. Prog. Ser.* 25 : 169–179.
- Hines A.H. and G.M. Ruiz. 2000. Biological invasions of cold-water ecosystems: ballast-mediated introductions in Port Valdez/Prince William Sound, Alaska. Report submitted to the Regional Citizens' Advisory Council of Prince William Sound. En ligne [www.pwsrcaac.org/docs/d0018502.pdf](http://www.pwsrcaac.org/docs/d0018502.pdf) (accessed February 2009)
- Holbrook, S.J. and R.J. Schmitt. 1992. Causes and consequences of dietary specialization in surfperches: Patch choice and intraspecific competition. *Ecology* 73: 402–412.
- Hosono, T. and H. Munehara. 2001. Caprellids (Crustacea, Amphipod, Caprellidea) from Usujiri, Pacific coast of southern Hokkaido. *Bull. Fish. Sci., Hokkaido Univ.* 52: 11–37.
- Inglis, G., N. Gust, I. Fitridge, O. Floerl, C. Woods, B. Hayden and G. Fenwick. 2006. Port of Timaru. Baseline survey for non-indigenous marine species (Research Project ZBS2000/04). Biosecurity N.Z. Tech. Pap. No 2005/06, 93 p.
- Kawashima, H., I. Takeuchi and M. Ohnishi. 1999. Fatty acid compositions in four of caprellid amphipod species (Crustacea) from Otsuchi and Mutsu Bays in northern Japan. *J. Jpn. Oil Chem. Soc.* 48: 595–599.
- Keith, D.E. 1969. Aspects of feeding in *Caprella californica* Stimpson and *Caprella equilibra* Say (Amphipoda). *Crustaceana* 16: 119–124.
- Krapp-Schickel, T. 1993. Do algal-dwelling amphipods react to the 'critical zones' of a coastal slope? *J. Natur. Hist.* 27: 883–900.
- Krapp-Schickel, T. and I. Takeuchi. 2005. A new species of *Caprella* (Amphipoda: Caprellidae) from the Cape Verde Islands (Atlantic), with note on Mediterranean *Caprella liparotensis*. *J. Mar. Biol. Assoc. U.K.* 85: 93–100.
- Laubitz, D.R. 1970. Studies on the Caprellidae (Crustacea, Amphipoda) in the American North Pacific. *Natl. Mus. Nat. Sci. Can., Publ. Biol. Oceanogr.* 1: 89 p.
- Laubitz, D.R. 1972. The Caprellidae (Crustacea, Amphipoda) of Atlantic and Arctic Canada. *Natl. Mus. Nat. Sci. Can., Publ. Biol. Oceanogr.* 4: 82 p.
- Lauerman, L.M.L. 1998. Diet and feeding behaviour of the deep-water sea star *Rathbunaster californicus* (Fisher) in the Monterey Submarine Canyon. *Bull. Mar. Sci.* 63: 523–530.
- Lewbel, G.S. 1978. Sexual dimorphism and intraspecific aggression, and their relationship to sex ratios in *Caprella gorgonia* Laubitz & Lewbel (Crustacea: Amphipoda: Caprellidae). *J. Exp. Mar. Biol. Ecol.* 33: 133–151.
- Lewis, P.N., D.M. Bergstrom and J. Whinam. 2006. Barging in: a temperate marine community travels to the subantarctic. *Biol. Invas.* 8: 787–795.

- Lim, S.T.A. and C.G. Alexander. 1986. Reproductive behaviour of the caprellid amphipod, *Caprella scaura typica*, Mayer 1890. *Mar. Behav. Physiol.* 12 : 217–230.
- Locke, A., J.M. Hanson, K.M. Ellis, J. Thompson and R. Rochette. 2007. Invasion of the southern Gulf of St. Lawrence by the clubbed tunicate (*Styela clava* Herdman): Potential mechanisms for invasions of Prince Edward Island estuaries. *J. Exp. Mar. Biol. Ecol.* 342: 69–77.
- Marelli, D.C. 1981. New records for Caprellidae in California, and notes on a morphological variant of *Caprella verrucosa* Boeck, 1871. *Proc. Biol. Soc. Wash.* 94: 654–662.
- Martin, D.M. 1977. A survey of the Family Caprellidae (Crustacea, Amphipoda) from selected sites along the Northern California coast. *Bull. South Calif. Acad. Sci.* 76: 146–167.
- McCain, J.C. 1968. The Caprellidae (Crustacea: Amphipoda) of the western North Atlantic. *Smithsonian Natl Mus. Bull.* 278. 147 p.
- Michel, K., S. Nauwelaerts, E. Stamhuis and K. Boos. 2007. Is the Japanese skeleton shrimp *Caprella mutica* a filter feeder? I. Head morphology and kinematics. *Comp. Bioch. Physiol. Part A* 146, S125 (abstract only).
- Nakajima, K. and I. Takeuchi. 2008. Rearing method for *Caprella mutica* (Malacostraca: Amphipoda) in an exhibition tank in the port of Nagoya Public Aquarium, with notes on reproductive biology. *J. Crustac. Biol.* 28: 171–174.
- Nauwelaerts, S., K. Michel, E. Stamhuis and K. Boos. 2007. Is the Japanese skeleton shrimp *Caprella mutica* a filter feeder? II. Mechanics. *Comp. Bioch. Physiol. Part A* 146, S126 (abstract only).
- O’Gorman, E., R. Enright and M. Emmerson. 2008. Predator diversity enhances secondary production and decreases the likelihood of trophic cascades. *Oecologia* 158: 557–567.
- Paetzold, S.C., J. Davidson and D. Giberson. 2008. Responses of *Mitrella lunata* and *Caprella* spp., potential tunicate micropredators, in Prince Edward Island estuaries to acetic acid anti-fouling treatments. *Aquaculture* 285 : 96–101.
- Page, H.M., J.E. Dugan, C.S. Culver and J.C. Hoesterey. 2006. Exotic invertebrate species on offshore oil platforms. *Mar. Ecol. Prog. Ser.* 325: 101–107.
- Page, H.M., J.E. Dugan, D.M. Schroeder, M.M. Nishimoto, M.S. Love and J.C. Hoesterey. 2007. Trophic links and condition of a temperate reef fish: Comparisons among offshore oil platform and natural reef habitats. *Mar. Ecol. Prog. Ser.* 344: 245–256.
- Pederson, J., R. Bullock, J. Carlton, J. Dijkstra, N. Dobroski, P. Dyrinda, R. Fisher, L. Harris, N. Hobbs, G. Lambert, E. Lazo-Wasem, A. Mathieson, M.-P. Miglietta, J. Smith, J. Smith III and M. Tyrrell. 2003. Marine invaders in the Northeast. Rapid assessment survey of non-native and native marine species of float floating dock communities. Massachusetts Institute of Technology Sea Grant College Program Publication No. 05-3, 40 p.

- Platvoet, D., R.H. De Bruyne and A.W. Gmelig Meyling. 1995. Description of a new Caprella-species from Netherlands: *Caprella macho* nov. spec. (Crustacea, Amphipoda, Caprellidea). Bull. Zool. Mus. 15: 1–4.
- Riedlecker, E.I., G.V. Ashton and G.M. Ruiz. 2009. Geometric morphometric analysis discriminates native and non-native species of Caprellidae in western North America. J. Mar. Biol. Assoc. U.K. 89: 535–542.
- Rueness, J. 1989. *Sargassum muticum* and other introduced Japanese macroalgae: biological pollution of European coasts. Mar. Poll. Bull. 20: 173–176.
- Sainte-Marie, B. 1986. Feeding and swimming of lysianassid amphipods in a shallow cold-water bay. Mar. Biol. 91: 219–229.
- Sainte-Marie, B. 1991. A review of the reproductive bionomics of aquatic gammaridean amphipods: variation of life history traits with latitude, depth, salinity and superfamily. Hydrobiologia 223: 189–227.
- Sainte-Marie, B. and P. Brunel. 1985. Suprabenthic gradients of swimming activity by cold-water gammaridean amphipod Crustacea over a muddy shelf in the Gulf of St. Lawrence. Mar. Ecol. Prog. Ser. 23: 57–69.
- Sano, M., M. Omori and K. Taniguchi. 2003. Predator-prey systems of drifting seaweed communities off the Tohoku coast, northern Japan, as determined by feeding habit analysis of phytal animals. Fish. Sci. 69: 260–268.
- Saunders, C.G. 1966. Dietary analysis of caprellids (Amphipoda). Crustaceana 10: 314–416.
- Shevchenko, O.G., T.Y. Orlova and S.I. Maslennikov. 2004. Seasonal dynamics of the diatoms of the genus *Chaetoceros* Ehrenberg in Amursky Bay (Sea of Japan). Russ. J. Mar. Biol. 30, 11–19.
- Schurin, A. 1935. Zur Fauna der Caprelliden der Bucht Peters des Grossen (Japanisches Meer). Zool. Anz. 122: 198–203.
- Setzer, R. and C. Link. 1971. The wandering of *Sargassum muticum* and other relations. Stomatopod 2: 5–6.
- Shucksmith, R., E.J. Cook, D.J. Hughes and M.T. Burrows. 2009. Competition between the non-native amphipod *Caprella mutica* and two native species of caprellids *Pseudoprotella phasma* and *Caprella linearis*. J. Mar. Biol. Assoc. U.K. 89: 1125–1132.
- ITIS (Integrated Taxonomic Information System). 2009. On line: [www.itis.gov](http://www.itis.gov). (accessed February 2009).
- Takeuchi, I. 1995. Suborder Caprellidea. In S. Nishimura (ed.), Guide to seashore animals of Japan with color pictures and keys. Vol. II, Hoikusha, Japon. pp 193–205.
- Takeuchi, I. and R. Hirano. 1991. Growth and reproduction of *Caprella danilevskii* (Crustacea: Amphipoda) reared in the laboratory. Mar. Biol. 110: 391–397.

- Takeuchi, I. and R. Hirano. 1995. Clinging behavior of the epifaunal caprellids (Amphipoda) inhabiting the Sargassum zone on the Pacific coast of Japan, with its evolutionary implications. *J. Crustac. Biol.* 15: 481–492.
- Takeuchi, I., R. Kuwabara, R. Hirano and H. Yamakawa. 1987. Species of the Caprellidea (Crustacea: Amphipoda) of the *Sargassum* zone on the Pacific coast of Japan. *Bull. Mar. Sci.* 41: 253–267.
- Takeuchi, I., S. Takahashi, S. Tanabe and N. Miyazaki. 2001. *Caprella* watch: a new approach for monitoring butyltin residues in the ocean. *Mar. Env. Res.* 52: 97–113.
- Thiel, M. 1997. Another caprellid amphipod with extended parental care: *Aeginina longicornis*. *J. Crustac. Biol.* 17: 275–278.
- Thiel, M. 2003. Extended parental care in crustaceans – an update. *Rev. Chil. Hist. Nat.* 76 : 205–218.
- Thiel, M., J.M. Guerra-Garcia, D.A. Lancelotti and N. Vasquez. 2003. The distribution of littoral caprellids (Crustacea: Amphipoda: Caprellidea) along the Pacific coast of continental Chile. *Rev. Chil. Hist. Nat.* 76: 297–312.
- Thiel, M. and L. Gutow. 2005a. The ecology of rafting in the marine environment. I. The floating substrata. *Oceanogr. Mar. Biol. Ann. Rev.* 42: 181–263.
- Thiel, M. and L. Gutow. 2005b. The ecology of rafting in the marine environment. II. The rafting organisms and community. *Oceanogr. Mar. Biol. Ann. Rev.* 43: 279–418.
- Tierney, T.D., F. Kane, O. Naughton, P. O’Donohoe, L. Copley and D. Jackson. 2004. On the occurrence of the caprellid amphipod, *Caprella mutica* Schurin 1935, in Ireland. *Ir. Nat. J.* 27: 437–439.
- Van der Velde, G., S. Rajagopal, B. Kelleher, I.B. Musko and A. Bij de Vaate. 2000. Ecological impact of crustaceans invaders: General considerations and examples from the Rhine River. *In* J.C. von Vaupel Klein and R. Schram (eds), *The Biodiversity Crisis and Crustacea, Crustacean Issues 12*, Balkema, Rotterdam. pp 3–33.
- Vassilenko, S.V. 1991. Ecophysiological characteristic of some common caprellids species in Possjet Bay (the Japan Sea). *Hydrobiologia* 223: 181–187.
- Vassilenko, S.V. 2006. Caprellids. *In*: Adrianov, E.V. (Ed.), *Biota for the Russian Waters of the Sea of Japan*. Vol. 4.
- Willis, K.J., E.J. Cook, M. Lozano-Fernandez and I. Takeuchi. 2004. First record of the alien caprellid amphipod, *Caprella mutica* for the UK. *J. Mar. Biol. Ass. U.K.* 84: 1027–1028.
- Woods, C.M.C. 2009. Caprellid amphipods: An overlooked marine finfish aquaculture resource? *Aquaculture* 289: 199–211.