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The biology and ecology of *Centropages typicus*: An introduction

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Abstract

We briefly introduce the different chapters of this special issue which review the current knowledge and understanding of the biology and ecology of *Centropages typicus* obtained over the last 30 years. The papers are grouped into two major theme areas: the first five papers review behaviour, feeding, metabolism, growth and development, and reproduction, and the four following papers have a regional focus dealing with temporal and spatial distribution in the Mediterranean Sea and in the North Atlantic shelf areas. The findings reviewed in the two groups of papers converge to explain why *C. typicus* is such a very successful copepod species in these coastal areas. In the different chapters, similarities and differences with congeneric species (*C. velificatus*, *C. hamatus*, *C. brachiatus*, *C. chierchiae*, *C. furcatus*, and *C. abdominalis*) have been explored where these are known.

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1. Introduction

Centropages typicus is one of the most abundant and best studied calanoid copepods, similar in this regard to Calanus finmarchicus and C. helgolandicus, or Acartia tonsa and A. clausi. During the last decades, most studies on the reproductive biology of copepods focused on Calanus species in the North Atlantic (TASC project, Tande and Miller, 2000), since these are considered to be important food sources for many larval stages of commercially important fish stocks.

The nine papers in this volume cover aspects of the biology and ecology of *C. typicus*. The first five papers review behaviour, feeding, metabolism, growth and development, and reproduction. The four following papers have a regional focus dealing with temporal and spatial distribution in the Mediterranean Sea and in the North Atlantic shelf areas. An overview of the main results is presented here, highlighting the complementarities in observations and explaining why *C. typicus* is such a very successful copepod species.

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2. Spatial distribution of C. typicus: its habitat in shelf areas

Centropages typicus is a temperate calanoid copepod with a wide range of distribution in the North Atlantic and adjacent shelf seas from 6°S to 66°N (Durbin and Kane, this issue; Beaugrand et al., this issue; Bonnet et al., this issue), as well as in the northern region of the Mediterranean Sea (Mazzocchi et al., this issue). It has a neritic-coastal distribution, being confined to inner regions of shelves or to shallow banks such as Georges Bank (Durbin and Kane, this issue), and it can also be found in shallow estuaries and embayments in areas with high salinity. It occurs in oceanic regions near continental slopes, infrequently in significant numbers, probably resulting from seasonal expatriation of individuals from populations living over the shelf-edge (Beaugrand et al., this issue).

C. typicus is among the most abundant copepod species on the North Atlantic shelves (Bonnet et al., this issue; Durbin and Kane, this issue) and even the most abundant identified by the monitoring of the CPR (Beaugrand et al., this issue). In the Mediterranean Sea, it is also a dominant copepod species (Mazzocchi et al., this issue). In shelf areas, it may account for 10–50% of total copepod numbers depending on the time of year (Mazzocchi et al., this issue; Bonnet et al., this issue). In general, its abundance increases with temperatures between 13 °C and 20 °C and decreases both below 13 °C and above 20 °C. Temperature appears to be the key factor explaining the variability in its spatial and temporal distribution on shelves where feeding is not food-limited, whereas offshore distribution is probably food-limited.

3. Behavioral and physiological processes: an adaptation to shelf conditions

The coastal distribution of *C. typicus* is probably driven by the flexibility of its behavioral and physiological processes, particularly adaptations for survival in the highly energetic coastal hydrodynamic conditions and for feeding on a large variety of prey.

Alcaraz et al. (this issue) provide an extensive review of the quite well documented behaviour patterns of *C. typicus*, which are tightly linked to all other aspects of its biology from feeding and searching for mates to avoiding predators. Adults and late developmental stages spend most of the time in slow swimming and resting breaks, with occasional and brief fast escape reactions and grooming events. The proportions of time allocated to the different swimming activities allow a high flexibility in behaviour and a rich repertoire of strategies to respond to biotic and abiotic factors of the coastal environment, such as type and concentration of food, presence of potential mates, light intensity, hydrodynamic flow and turbulence. Behaviour changes significantly during development. The nauplii do not produce feeding currents and swim continuously in a helicoidal pattern with escape jumps detected by hydrodynamic disturbances similar to those generated by predators, their escape distance increasing with age.

The variety of responses of *Centropages* to environmental changes seems to be controlled by the trade-off between energetic gains (food intake), losses (swimming energy expenditure), and predation risk.

C. typicus is mostly carnivorous or omnivorous, feeding on a wide spectrum of prey both phytoplankton, from small 3–4 µm equivalent spherical diameter *Isochrysis galbana* to large diatoms, and animal prey such as ciliates, appendicularia, eggs and nauplii of copepods, up to yolk-sac fish larvae larger than 3 mm length (Calbet et al., this issue). Its flexible swimming capacities allow it to use both suspension and ambush feeding strategies, depending on the characteristics of the prey, with a selective preference for large motile prey, such as ciliates or dinoflagellates, enhanced under moderate intensities of turbulence. It detects these large motile prey with mechanoreceptors and smaller prey with chemoreceptors.

Laboratory studies with mixed diets including animal prey result in higher growth and egg production rates compared with monospecifc diets (Carlotti et al., this issue; Ianora et al., this issue) suggesting that omnivory is the best feeding strategy for *C. typicus*. However, rates obtained in the laboratory are most often lower than those obtained from field studies (Ianora et al., this issue), underlining that the natural variety of prey is important for maximising the fitness of *C. typicus*. Field measurements of metabolic activities (O:N ratios) support its omnivorous–carnivorous role (Gaudy and Thibault-Botha, this issue). Therefore, *Centropages*, due to the flexibility of its physiological processes (Calbet et al., this issue; Gaudy and Thibault-Botha, this issue), is an important species in the mesozooplankton assemblage of the fluctuating neritic coastal marine environments.

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