

*Opinion*

# The Suspected Contradictory Role of Parental Care in the Adaption of Planktonic Calanoida to Temporary Freshwater

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**Abstract:** Calanoida have the highest number of species among Copepoda in marine plankton, but not in fresh water, where the greatest number are Cyclopoida. Freshwater Cyclopoida also live in more freshwater sites than Calanoida. This could be a consequence of an invasion of freshwater by marine Cyclopoida before Calanoida. Similar to Cyclopoida, but different from marine Calanoida, freshwater Calanoida females produce egg sacs and care for eggs. This strategy is common among all freshwater plankton, suggesting that the evolution of parental care is an obliged adaption to conquer fresh water. Calanoida, different from Cyclopoida, survive adverse conditions as resting eggs. This life-cycle constraint obliges eggs to survive their mother's death and wait in the benthos for a certain period. The necessity of completing embryonic development and the hatching of eggs far from the mother's protection may be responsible for the relatively lower evolutionary success of Calanoida in fresh water compared to Cyclopoida (which rest as juveniles, thus protecting eggs in any moment of their development). Therefore, the brooding of eggs appears to be the obliged solution for Calanoida's final establishment in fresh water, but the dispersion of eggs on the bottom after the mother's death and during the rest period is probably the weak point in Calanoida's competition with Cyclopoida.

**Keywords:** adaption; brooding; parental care; Calanoida; freshwater zooplankton

**Citation:** Belmonte, G. The Suspected Contradictory Role of Parental Care in the Adaption of Planktonic Calanoida to Temporary Freshwater. *2021*, *13*, 100. <https://doi.org/10.3390/w13010100>

Received: 27 November 2020

Accepted: 24 December 2020

Published: 4 January 2021

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## 1. Introduction

Calanoida are the most successful taxon of Copepoda in marine plankton in terms of number of species. This is not true in fresh water, where the greatest number of Copepoda species belong to Cyclopoida. Only one Calanoida family, Diaptomidae, is exclusive to fresh water, where it is represented by 530 species grouped in 63 genera [1]. Diaptomidae belong to the superfamily Diapomoidea, which contains six additional families. They are the only Calanoida represented in inland waters and estuaries at the sea-land border. Boxshall and Jaume [2] assumed that Copepoda evolved in marine waters and suggested that the time elapsed since the colonization of fresh water by a lineage of Copepoda is directly correlated with the species richness shown for that lineage in the new environment. In addition, the same authors suggest that one family could be considered as roughly corresponding to a single colonization wave from marine waters. Diaptomidae (quasi-absent from Australia) represent a colonization wave that gave origin to freshwater Calanoida after the separation of boreal landmasses from Gondwana, no more than about 160 million years ago. Accepting such an interpretation, the higher adaptive establishment of freshwater Cyclopoida, which has 924 species in all the continents, according to [1], all of which belong to the single family Cyclopidae, is

probably due to a preceding colonization wave from the marine environment in a period before the break-up of Pangea more than 190 million years ago. It is evident to the cited authors that the high number of Cyclopidae could be due to the longer evolutionary time available to them in fresh water.

Regarding the comparison with a marine environment, marine Calanoida represent a number of species about double that of Cyclopoida [3]. In addition, Cyclopoida inhabit more than 95% of inland waters, while Calanoida are reported in less than 50% of inland water sites (Table 1).

**Table 1.** Planktonic copepods. Some examples of species richness reported in marine and inland waters in areas of different geographic extension. (Data from references: [3]; [4]; [5]; [6]; [7]; [8]; and Walsh, personal communication).

Copepod	Number of Species							
	Marine Waters		Inland Waters					
	Western Mediterranean	Adriatic Sea	Europe	Italy	Mexico	Florida	Malaysia	Australia
Calanoida	310	181	95	31	15	3	11	41
Cyclopoida	124	90	210	100	48	41	28	120
References	[3]	[3]	[4]	[5]	[6]	[7]	[8]	Walsh

The scheme can be locally disregarded in the case of Canadian lakes, where Calanoida species are reported as more abundant than Cyclopoida [9] [10]. That situation, however, could correspond to a nonequilibrium state due to the relatively young age of the system (see [11] for a discussion of the role of time in the evolution of species numbers).

While both are Copepoda, planktonic Cyclopoida and Calanoida would likely not be perfectly similar in adaptive strategies, and differences in their evolutionary success could also derive from such differences rather than from a different adaption time.

## 2. Reproductive Traits Typical of Freshwater Calanoida

Diaptomidae can be considered to represent the Calanoida model of adaptive solutions to living in a freshwater environment. Diaptomidae, similar to other Diaptomoidea, but different from most other Calanoida, produce resting eggs, which allow species to survive adverse periods [12]. This life-cycle trait is fundamental for establishment in variable habitats (even temporary) as the freshwater ones. However, resting cannot represent the only solution because the rest capability is widespread in marine Calanoida, without allowing all lineages to successfully colonize fresh water. Resting among Calanoida could be typical of different life-cycle stages [13], but when considering only resting eggs, not all taxa with this feature successfully invaded freshwater.

On the other hand, the rest capability of freshwater Cyclopidae, which have been more successful than Diaptomidae, is not exhibited by eggs, but by the copepodite stage [14].

These facts suggest that the success of Diaptomidae in invading fresh waters relies not simply upon a resting stage, but also upon solving other problems, the most important in my opinion being the survival of the late embryo and the early life-cycle stage (the nauplius).

If we focus our attention on reproductive traits, we perceive an evident sexual dimorphism among Diaptomoidea, with adult males of each species sensibly smaller than females (compared to marine Calanoida), and equipped with a modified right antennule for grasping the female during mating.

The larger size of females in freshwater species could be imposed by the presence of a large egg sac, a trait absent in marine species. The egg sac is the evident common characteristic shared with planktonic Cyclopoida and with all freshwater zooplankton. In fact, Rotifera and Cladocera, which dominate the freshwater zooplankton together with Copepoda, both show extreme sexual dimorphism (with smaller or completely absent males), and enhancement of parental care by brooding few large eggs that hatch directly into juveniles. The investment in early-stage protection by Rotifera and Cladocera is a trade-off that results in a lower number of embryos per female. However, these invertebrates, balance the reduction of eggs per female with the ability to reproduce via parthenogenesis, thus maximizing the number of females in each population.

Diaptomidae are phylogenetically distant from Cladocera, and even more distant from Rotifera; they show populations with a sex ratio close to 1:1 and never engage in parthenogenesis. The presence of a large part of the population (males) that does not directly produce descendants is balanced by an enhancement of female fecundity. The high number of embryos produced by each female are brooded in an egg sac, thus requiring larger females that are able to actively avoid sinking due to the additional ballast of many eggs, which are negatively buoyant.

In general, among Calanoida, species with an egg sac have a lower egg-production rate per female [15]. A true egg sac is an exceptional feature in off-shore marine species, and it is common only in brackish water and lagoon species. An “apron” of unknown significance has been reported for fertilized mature females of some Acartiidae (Diaptomoidea typical of brackish water), although it does not have any involvement in egg protection [16] [17]. The production of a true egg sac in Diaptomidae, Temoridae, and Centropagidae—all of which successfully invaded fresh water—is a reliable indication of its value in the establishment of Calanoida in freshwater habitats.

Among Centropagidae, only freshwater species (e.g., those of the genera *Boeckella*, *Calamoecia*, *Limnocalanus*, and *Sinocalanus*) have an egg sac, and not the marine ones. The presence of an egg sac, which allows the eggs to remain in the water column together with the mother, could be interpreted as advantageous for species’ establishment in freshwater environments. Eggs laid free in a freshwater environment have a high probability of reaching the bottom before they hatch, and we suspect that problems for embryos inside eggs could be due to this interaction with the bottom. Hirst and Kjørboe [18], even without an interpretation of the data, demonstrated that broadcasted eggs have a mortality rate (excluding predation) that is significantly higher than those in egg sacs.

The female-biased sexual size dimorphism of Diaptomoidea justifies the presence of a more evident modification of the right antennule (A1) of the adult male, which allows it to powerfully grasp a larger and stronger female during mating in order to complete the transmission of the spermatophore. Given the likely presence of predators in the water column, the formation of a mating pair, or tandem, of individuals has to occur quickly, and a robust A1 ensures a prompt grasping and eliminates the need for repetitive attempts.

The fertilized female can be re-fertilized after the completion of a cycle of egg sac production and nauplii release (about 5–6 days in *Eudiaptomus gracilis*) [19]. The period of tandem holding during mating varies widely, ranging from 2–4 minutes in *Eudiaptomus* [19] to a period of days in *Eurytemora* [20], which is probably due to the result of sexual versus natural selection, reflecting trade-offs between enhancement of fertilization success and the reduction of vulnerability to visual predation [21]. The realization of tandems is a sort of evolutionary obligation because it is not suppressed (although it is reduced in order to optimize survival) when visual predators (e.g., fish) are present in the environment. The reduction of mating activities can be realized either by depressing the mating frequency (with sperm storage in females), or by shortening the time spent in tandem mating [21].

In marine pelagic environments, a lighter A1 geniculation (used to grasp females smaller than the freshwater ones) in non-Diaptomoidea Calanoida males has been

considered as an evolutionary solution to avoid mating for long durations in environments rich in predators [22], compensated by a smaller size dimorphism between sexes. This solution evidently did not involve the freshwater species.

Ali et al. [23] assessed the disadvantage, in terms of eggs produced, of multi-fertilized females. The larger body size of females should allow them to better impede males from attempting multiple mating. This has resulted in the amelioration of their fecundity in terms of eggs produced, and consequently, of their reproductive success.

The large size of Diaptomidae females, which is considered to be useful in the tuning of mating behavior, seems to be a pre-adaption resulting from the necessity to swim up in the water column while sustaining the additional weight of an egg sac.

The presence of an egg sac (absent in marine Calanoida), as in the case of the tandem composition, represents an obstacle for rapid escape behavior and increases individual visibility to predators. For this reason, the advantages deriving from an egg sac, which prevents the eggs from sinking to the bottom, have to largely exceed the disadvantages of interaction between broadcasted eggs and the bottom, the retarded mobility of egg-carrying females, and the visibility to predators of larger females and mating tandems.

In Cyclopidae, males have prehensile antennulae for grasping females during mating, and females produce eggs in paired lateral egg sacs. Additionally, sexual dimorphism in Cyclopidae is similar to that exhibited by Diaptomidae, with males sensibly smaller than females in each species. The general convergent adaption in these two taxa is the increase in body size in females, probably driven by the necessity to sustain egg sacs in the water column.

Notwithstanding all these similarities, Cyclopidae are the most successful family group of Copepoda in freshwater plankton, in terms of both number of species and number of inland water sites colonized. In fact, inland water sites without Cyclopoida species are very rare, while Calanoida generally are absent in more than 50% of the sites from which plankton have been collected (Table 2).

### 3. Conclusions

Planktonic populations of freshwater Copepoda are characterized by high numbers of nauplii, which derive from eggs when they are still in the sac attached to the mother's urosome. The rule of reduction/suppression of a free-swimming larva in freshwater invertebrates [24] appears to not be valid for freshwater Copepoda. Pennak [25] suggested that in freshwater organisms, the osmoregulation capabilities, which are necessary to cope with the highly diluted environment, require a certain level of physiological maturation during the first developmental stages (corresponding with the necessity for early stages to spend the larval stage time inside the egg envelope). Evidently, nauplii of planktonic Copepoda need not go through such a physiological maturation; they are able to avoid negative osmoregulation consequences in extremely diluted waters. At this point, the evolution of egg sacs in freshwater planktonic Copepoda seems to not be necessary for hatching advanced stages of progenies, but simply to keep the eggs from sinking to the bottom.

The predation pressure on females that carry egg sacs appears to be a risk of secondary importance, because females of freshwater Copepoda (similar to Cladocera and Rotifera) evolved protection of their eggs, irrespective of the increased visibility and retarded escape behavior that this condition could present. Conversely, the evolution of floating eggs (e.g., in *Artemia*), although favored by enhanced water density values (in hyperhaline ponds), can be viewed as an additional demonstration of the necessity for species to avoid the sinking of eggs to the bottom.

One explanation could be the negative effect of low temperatures and/or hypoxia/anoxia (relatively common—at least periodically—in freshwater bottoms, if compared with values in the water column) on the early embryonic stages of Copepoda eggs [26] [27]. In agreement with Kimmerer [28], who proposed that the vulnerability of individuals is inversely correlated with their developmental conditions, and that

invertebrate predation on nauplii is greater than fish predation on adults, I would like to suggest an extension of this rule to the egg stage. Karlson and Viitasalo-Frosen [29] demonstrated that invertebrates of infauna and epifauna actively subtract eggs from bottom sediments in the Baltic Sea. Only an extreme vulnerability of the eggs on the bottom can justify the energetic investment of planktonic mothers in realizing and carrying an egg sac. Gentleman and Head [30], similar to [18], on the other hand, gave their attention to the general weakness of early developmental stages of larva, which do not survive without suffering predation.

The occurrence of harsh conditions in the bottom layers of water habitats is common in shallow ponds. Among Copepoda, Harpacticoida are benthic and appear well-adapted to such conditions [31]. In the case of Harpacticoida, however, the presence of egg sacs in adult females can be interpreted as a device used to avoid the eggs becoming abandoned and immobile on the bottom.

When unfavorable conditions impact the entire water column, they are avoided by plankton through the use of resting stages, during which they stay immobile on the bottom and are largely immune to the unfavorable conditions that they can possibly encounter there. In addition, this benthic period occurs during a time when all the biota components (including predators and competitors) are impacted and obliged to rest, and any competitive and/or predatory pressure between species is suspended.

Finally, a common characteristic of resting eggs is a relative lack of sensitivity to predation due to the presence of a robust chorion that resists attacks [32], provides passive immunity to microbes [33], or even ensures an insensitivity to digestive fluids during their passage through the gut of larger predators [34].

Cyclopoida do not have resting eggs, and generally their eggs cannot pass long times in the benthos, even in the case of a free layering in the water column by respective mothers [35] [36]. In fact, Cyclopoida enter a resting period as copepodites (age CIV- CV) when no eggs are produced because the females are still immature.

In Calanoida, mature females produce successive egg sacs of subitaneous eggs. When resting eggs are produced by Calanoida, these reach the bottom together within the same egg sac, or with their mother when she dies, and they remain there until the return of favorable conditions to hatch a new generation. However, this phylogenetic constraint (present in Calanoida; absent in Cyclopoida) obliges the resting eggs of Calanoida to pass a certain time of their development in the benthos before they hatch. This is a sensible difference between the two Copepoda taxa, and could be involved in their different evolutionary success in terms of adaption and number of species.

Although the success could be simply due to a different evolutionary history of Copepoda coming from the marine environment in two waves (around 160 and 190 million years ago, according [2]), the obliged permanence of eggs when resting in the benthos probably plays an additional role in the competitive weakness of Calanoida in the colonization of fresh water. During the colonization of newly formed water bodies, Cyclopoida are still the winning colonizers [37] [38]. Finally, the percentage of water bodies occupied by Calanoida is very low (less than 50%), without any apparent correlation with the abiotic conditions (Table 2).

**Table 2.** The presence of Calanoida in freshwater bodies of different types and origins. In the same water bodies, Cyclopoida (not reported here) are present in more than 95% of sites.

Reference	Water Body Type Studied	Number of Sites	Number of Sites with Calanoida
[39]	alpine lakes	170	82
[40]	mountain lakes	30	9
[41]	island lakes	250	65
[42]	Artificial dams/reservoirs	51	21
[43]	lowlands lakes	121	55

[44]	medium-small ponds	60	18
[45]	soda ponds	110	91
[38]	endorheic ponds	36	19
[46]	Iceland ponds	12	1
<b>Total</b>		<b>881</b>	<b>402</b>

The successful colonization of Cyclopoida could be the result of the rapid appearance of reproductive individuals in just a few days, because resting copepodites reach advanced developmental stages, while Calanoida attain maturity only after weeks of complete development from nauplii born by resting eggs.

The existence of a brooding behavior (the protection of fertilized eggs in an ovisac attached to the mother) is the common element in all the freshwater plankton taxa, including Calanoida, which rarely show this character in marine environments. This suggests that the survival and persistence of species in an aquatic habitat is not determined by the presence of pelagic predators (which, on the contrary, can easily attack females with egg sacs), but by some intense negative selection pressure that explicitly acts on the bottom against broadcasted eggs (and the early embryos inside them) of all plankton taxa. All of the hypotheses regarding this widespread situation among taxa currently derive mainly from studies on coastal marine and/or brackish water species. Laboratory studies on separate or synergistic effects of bottom conditions (abiotic and biotic) on the embryonic development of freshwater plankton are lacking. These studies are necessary to understand the sensibility of embryos in eggs, which is the principal obstacle for the successful colonization of freshwater habitats by Calanoida.

**Funding:** This paper was written as part of the Fauna d'Italia project to create a monography on Copepoda Calanoida.

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** Please refer to suggested Data Availability Statements in section "MDPI Research Data Policies" at <https://www.mdpi.com/ethics>.

**Acknowledgments:** This paper was an invited contribution at the workshop "Temporary Wetlands Future in Drylands under the Projected Global Change Scenario" held in Baeza, Spain, on March 9–11, 2020. Here I thank Robert Walsh for his indications on Australian fauna; G. Boxshall (Natural History Museum, London, UK), who agreed to discuss some points in the paper; and M. Alcaraz (Institut de Ciències del Mar, CSIC, Spain), who helpfully criticized some logic constructions.

**Conflicts of Interest:** Author declare no conflict of interest.

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