

## **Chaetognaths feed primarily on dissolved and fine particulate organic matter, not on prey: implications for marine food webs**

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### **Abstract**

Chaetognaths are considered to be the dominant predators of small zooplankton and fish larvae. Therefore, it is thought that they play an influential role in marine pelagic food webs, transferring most of the zooplanktonic biomass to higher trophic levels. To date, their head armature (teeth and grasping hooks) and the results of laboratory feeding experiments have supported this view. However, analyses of gut contents and other aspects of their feeding behavior suggest that chaetognaths are primarily osmotrophic animals. They gulp seawater, taking in dissolved and thin particulate organic matter produced in abundance by viruses and bacteria. This diet explains the success of chaetognaths in number and biomass and the observed lack of relationship between chaetognaths and prey availability. The role of chaetognaths should be revisited in the global ocean ecological balance, particularly with respect to vertical carbon flux, and also in predicting fishery resources.

**Keywords:** chaetognaths, nutrition, osmotrophy, marine dissolved organic matter, planktonic food web shunt, marine viruses

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### **Introduction**

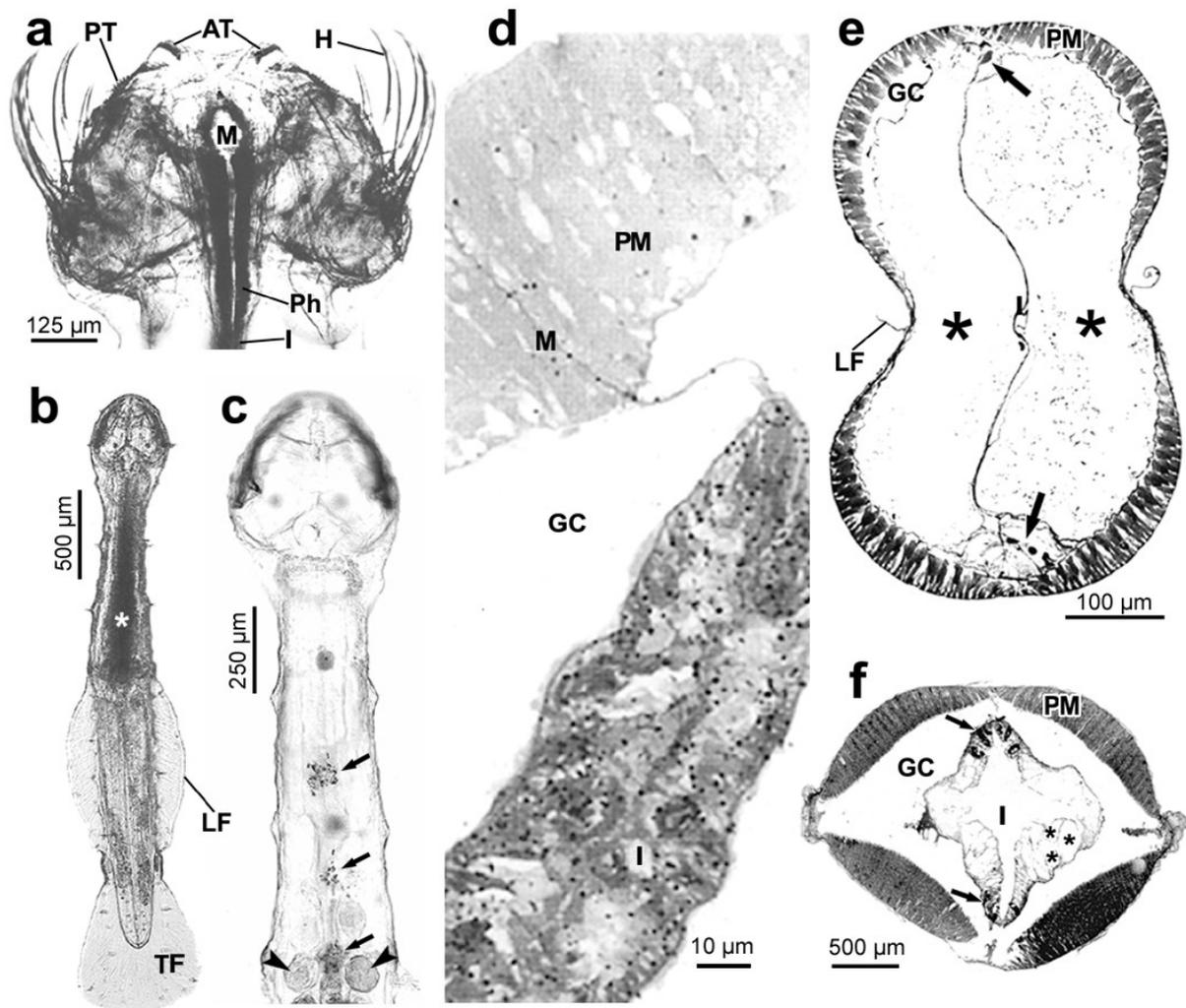
Chaetognaths are a primary constituent of marine zooplankton. Marine plankton include all drifting organisms (animals, plants or bacteria) that inhabit oceanic water masses and are a crucial source of food for larger aquatic organisms, such as fish and whales. In addition, through photosynthesis, phytoplankton convert mineral nutrients into organic matter and are responsible for much of the oxygen that is present in the Earth's atmosphere.

Chaetognaths are a small phylum of approximately 120 species, with representatives in almost all marine habitats: in open sea, on and near the sea bed, in dark submarine caves, in the interstitial milieu and around hydrothermal vent sites. They range in size between 2 and 120 mm. Planktonic chaetognaths are the most abundant and are believed to play a key role in pelagic food webs as the dominant predators of zooplankton and fish larvae [1]. Their global biomass is approximately 10-30 per cent that of copepod crustaceans (the major component of planktonic biomass). In numerical abundance, planktonic

chaetognaths are often second only to copepods; by weight, their contribution is even greater [2]. Therefore, they were believed to transfer most of this biomass to higher trophic levels [2]; to date, this view has been undisputed [3, 4].

Several observations support the status of chaetognaths as carnivores: the presence of one or two rows of teeth on each side of the head, the presence of one row of hooks (Fig. 1a), evidence of the injection of venom into prey [5], the presence of prey in the gut of some specimens in plankton hauls and experimental feedings.

However, many previous observations on different aspects of the feeding of chaetognaths in nature are inconsistent with their presumed voracity. One of the current authors (JPC) has examined several thousand chaetognaths over almost 40 years of studying plankton from oceanographic cruises, yet prey in the gut of these transparent animals has only rarely been observed. Similarly, Bone et al. [6] state that "*The gut lumen of Sagitta setosa is normally only virtual, since unless there is prey within it (which is rare)...*".



**Figure 1: Different aspects of chaetognath anatomy and physiology in relation to feeding.** a, *Sagitta lucida*: head in ventral view showing the cephalic armature, i.e., anterior teeth (AT), posterior teeth (PT) and hooks (H), the mouth (M), pharynx (Ph) and intestine (I). b, c, *Spadella cephaloptera*: photomicrographs of living specimens fed in the laboratory with *Artemia salina* nauplii; (b) entire animal 30 min. after feeding, showing the alimentary bolus completely filling the intestine (asterisk); (c) anterior part 24 h after feeding, showing the dark digestion-related granules in three areas of the intestine (arrows); note the seminal receptacles at the base of the ovaries flanking the intestine (arrowheads). d, *Sagitta friderici*: radioautographic study in transverse semi-thin section at the medioventral level (labelled with D2-deoxyglucose, stained with Unna's blue); note that silver grains are distributed densely throughout the entire intestine and are present along the mesentery (M) but are rare in or absent from the primary muscle (reprinted from Duvert et al. [25] with permission from the Journal of the Marine Biological Association of the UK). e, f, *Sagitta minima* and *S. zetesios*: transverse semi-thin sections of the trunk showing two degrees of vacuolation of gut A-cells, that are thus largely devoid of organelles involved in digestion. Note that the vacuoles (asterisks) of the former (e) are larger than those of the latter (f) such that there are only two vacuolar A-cells per section and that in the two cases there are normal A-cells in the dorsal and ventral ridges (arrows). Compare with the normal aspect of the gut of *S. friderici* devoid of vacuolation (d). GC, general cavity; I, intestine; LF, lateral fin; PM, primary muscle; TF, tail fin.

Two exceptions to predation in the chaetognaths have also been reported: a cave-living species attracted to decayed bait in traps [7] and deep-water benthoplanktonic species (i.e. living on or just above

the ocean bottom) that feed on organic matter and bacteria from sediments) [8].

We show here that the number of prey swallowed by chaetognaths in the wild cannot satisfy their

optimal daily food requirements, particularly during reproduction. We hypothesize that most of their food requirements are met through the intake of dissolved organic matter (DOM) by gut cells when ingesting seawater. Here we describe various aspects of the feeding biology of these animals, which support our hypothesis.

## 2 Chaetognath nutrition biology

### 2.1 Food requirements

There are hundreds of reports on the feeding of chaetognaths. A first synthesis was provided by Feigenbaum and Maris [9], who emphasised the striking differences in gut contents observed between laboratory and wild-caught specimens. They explained this "paradox" as arising from feeding differences: feeding is easier in the laboratory than in the wild because it requires the creation of higher prey densities for maximum consumption. Like other investigators, those authors believed that chaetognaths were carnivores and rejected as erroneous the report of gut emptiness by Heydorn [10], who himself considered chaetognaths to be carnivores and wrote "*In spite of this [absence of fish larvae in the gut of all the specimens of *Sagitta friderici*] it seems likely that chaetognaths can do extensive damage to stocks of larval fish, especially if they occur in large numbers, as *S. friderici* sometimes does.*" The many studies conducted since then provide conflicting results: some support the hypothesis of predation (e.g., experimental studies always demonstrating the consumption of many prey items per day per individual) whereas others describe little evidence of such predation in nature.

In describing the guts of hundreds of Mediterranean specimens of *Sagitta minima*, Ghirardelli [11] noted the consistent absence of alimentary remnant, which is a finding that is also reported for specimens near South Africa [10]. This absence could reflect the rapid action of digestive processes; however, this interpretation conflicts with the results of laboratory experiments and observations of specimens caught in the wild [4]. Alternatively, prey might be egested during capture, as suggested by Froneman and Pakhomov [12], who found that more than 90% of specimens of *Eukrohnia hamata* and *Sagitta gazellae* collected in the Southern Ocean had empty guts.

Øresland [13] studied the feeding of two chaetognath species in a Swedish fjord and concluded that "*The obtained FR [Food ratio] of 1.0 to 2.0 items  $d^{-1}$  for *Sagitta elegans* does not perhaps give the impression that the species should be particularly*

*important as a predator. ... However, the dominance in numbers of chaetognaths over other pelagic predators and the presence of *S. elegans* throughout the year indicate the importance of chaetognaths.*" As for *Pterosagitta draco* near Hawaii, a mean consumption rate of only one copepod/chaetognath/day was observed, leading to the conclusion that some large carnivorous copepods are more active predators in subtropical oceanic waters, in contrast to expectations [14].

Several authors have noticed the discrepancy between theory and data; they include Falkenhaus [15] who wrote the following about *Sagitta elegans* in the Barents Sea: "*Chaetognaths are supposed to be important predators in copepod communities... Generally, however, attempts to correlate feeding in nature with zooplankton availability have been unsuccessful ... and the results from the present data are no exception.*" This finding was confirmed more recently, e.g., in Antarctic waters [4]: "*In general, a low proportion of *Eukrohnia hamata* with food in their gut., with no significant difference among depths, stations or transects...*"

As for predation on fish larvae by chaetognaths, an examination of the gut contents of 6,817 specimens of numerous species from the South Atlantic Bight [16] found only one chaetognath that had consumed fish larva; in contrast, laboratory experiments on *Sagitta hispida* documented an average feeding rate of  $1.6 \pm 0.2$  to  $1.9 \pm 0.2$  larvae per day, depending on the prey fish species [1].

In summary, all reports of chaetognaths sampled in the wild note the scarcity of prey in their guts. How can the origin of this misunderstanding be explained? Reeve [17] was the first author to report the strong voracity of chaetognaths in laboratory experiments, indicating that 8.5 mm long adult *Sagitta hispida* consumed approximately 50 *Artemia* nauplii per day, representing up to 64 percent of their own dry weight. He later [2] hypothesised that chaetognaths were the major link between copepods and higher trophic levels, but with great caution since he noted: "*... if my estimation of the biomass of chaetognaths ... is accepted ... If copepods are the primary herbivores of the marine environment, chaetognaths may be considered as primary carnivores... if the two groups [copepods and chaetognaths] can approach the conversion efficiencies in natural populations which they demonstrate in the laboratory...*" Since then, these hypotheses have been accepted as fact, despite evidence to the contrary.

In the laboratory, food unequivocally affects growth and egg production, but this is not true in the wild [9]. This explains why, for example, size and fecundity depend on temperature but not food level

[18, 19]. This paradox also concerns benthic (i.e., bottom-dwelling) species. In our experiments on *Spadella cephaloptera*, adult specimens maintained in small tanks required a constant intake of prey (*Artemia nauplii*) (Fig. 1b) to mature their ova, whereas those directly sampled at sea almost always had empty guts. Moreover, if wild-caught specimens had ingested prey within the last day, their guts would have displayed intestinal cells containing dark granules in three areas, as a result of digestion [14, 20, 21] (Fig. 1c).

Previous studies on deep-living chaetognaths yield results that are consistent with these observations, for example, with benthoplanktonic species (genus *Heterokrohnia*) as said above [8] and with *Eukrohnia fowleri*, in the north-western Pacific [22]. *Eukrohnia fowleri* was dominant between 1,500 and 3,000 m and sometimes represented up to 60% of the total zooplankton biomass [22]. This dominance indicates that these animals are not predators because predators cannot be more numerous than their supposed prey. Perhaps they feed upon detritus (“planktonic snow”); this would be an adaptation to a milieu in which prey is scarce. However, such detritus should be evident in their guts. There are also numerous reports of dominance of planktonic species living at shallower depths where prey is not limited. This phenomenon elicited some unsupported explanations [23], such as sampling artifacts as well as reduced productivity of waters and, consequently, of the herbivorous/omnivorous plankters.

## 2.2 General metabolism

Previous experiments investigating the role of chaetognaths at all depths in ocean carbon flux (as representatives of higher carnivores occupying the entire water column) yielded unexpected results [24]. In contrast to studies of pelagic fish and crustaceans, no decline in metabolic rate or enzyme activity with depth was observed for planktonic chaetognaths (notwithstanding some variation among species). Even at great depths, chaetognath metabolism was comparable to that of deep-water fish and crustaceans known to be active swimmers. Other studies have also since reported a lack of relationship between oxygen consumption rate and depth. These observations indicate an unrestricted nutrient intake in spite of a scarcity of prey at depth.

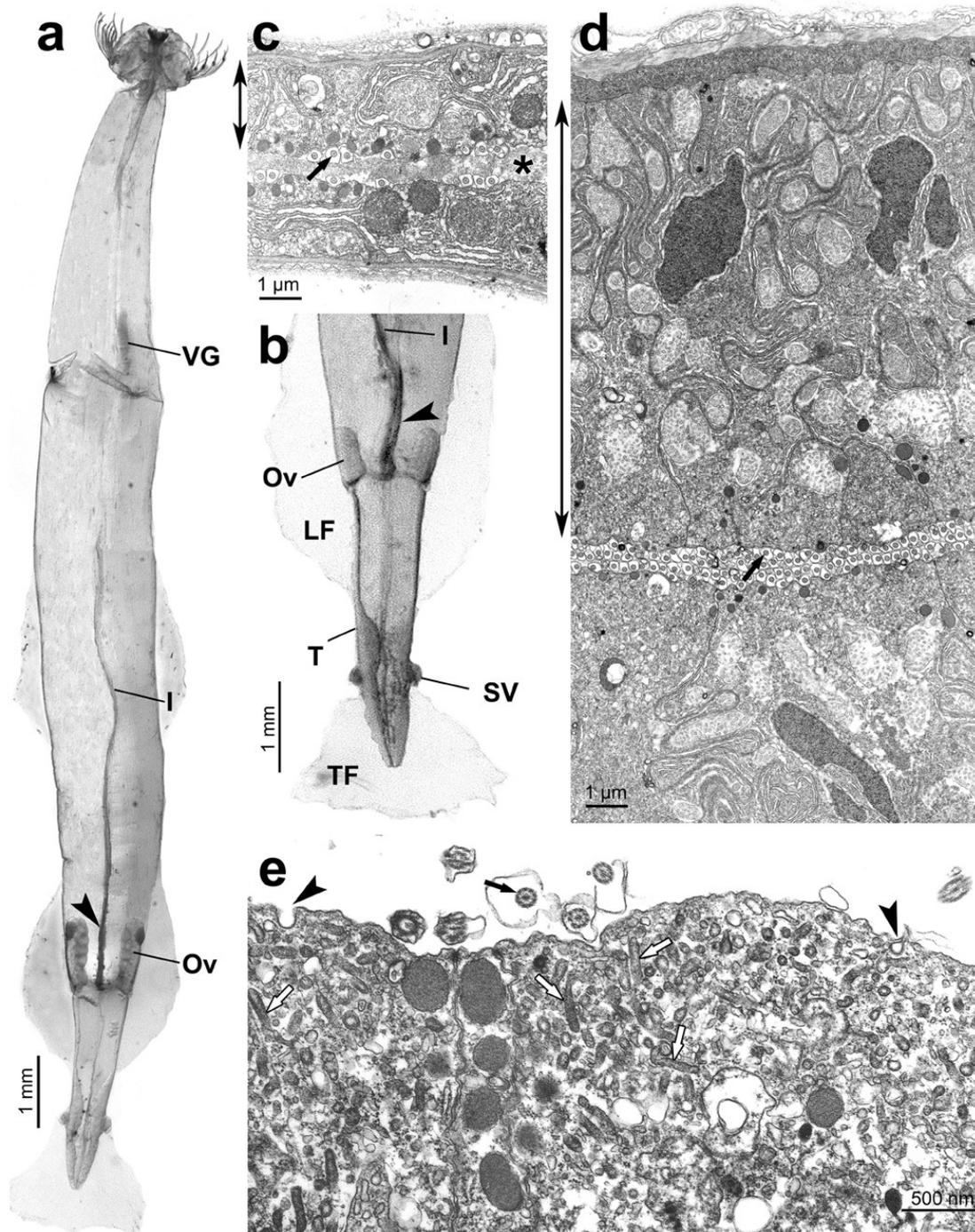
Two of the current authors (JPC, MD) have investigated osmotrophy in chaetognaths in the lab. One of our previous studies concerned the cytochemical and physiological aspects of the energetic metabolism of specimens of the planktonic species *Sagitta friderici* housed in seawater containing labelled molecules [25]. One of these

molecules, D2-deoxyglucose, was unevenly distributed throughout the body. The entire digestive system was heavily labelled from the mouth to the anus (Fig. 1d). Labelling also occurred in the gonads and in reproductive cells but less so in the epidermis and nerves. A second study showed that specimens of the benthic species *Spadella cephaloptera* can survive one month or more after decapitation [26]. Decapitated *Spadella cephaloptera* carrying ripe ova were able to lay them, to mature their spermatozoa once or twice, and to mate with intact mature specimens. These results indicate that chaetognaths can take in nutrients through the body wall like many other marine animals [27] because the gut is closed by wound healing. However, this mechanism is not sufficient to supply all their needs, as decapitated animals are unable to mature ova. These findings confirm that maximum dissolved nutrient supply occurs in the gut and, to a lesser extent, via the body wall, which is consistent with Ferguson’s report [28] that “*The gut tended to be highly labeled [tracer = free amino acids], and moderate uptake into ovaries also was noted... No food, however, could be detected in the digestive tracts... these pictures indicate that they are likely obtaining some of their nutrition directly from dissolved sources, both through the epidermis and by fluid ingestion*”, and later: “... *why should not most of these animals allow some sea water passage through their digestive tracks?*” This passage of sea water was first demonstrated by Doncaster [29] and successfully reproduced later [11]. There are other reports of chaetognaths ingesting water. Below, we provide evidence that the gut cells of chaetognaths display typical digestive processes in the absence of visible gut contents.

## 2.3 Morphology and ultrastructure of the gut

The gut displays three main zones: the pharynx, oesophagus, and intestine; the intestine accounts for approximately 90% of the total gut length and ends in a short rectum. Detailed ultrastructural studies of the gut of these organisms [20, 30, 31] have described the presence of secretory cells involved in mucous and enzyme secretions and a type of ciliated cell that specializes in the absorption of macromolecules and intracellular digestion (A-cells).

Some planktonic species exhibit a particular type of gut cell that is characterised by the presence of vacuoles of unusual size. They were first described in *Sagitta minima* [29] and were later accurately described in *S. elegans* [6]. Perez et al. [32] showed that vacuolation involves only the A-cells, which



**Figure 2: Ultrastructure of the gut during the reproductive period of the chaetognath *Sagitta enflata*.** **a, b,** specimens at different stages of ovary maturity in transmitted light. Note the absence of prey in the intestine and the enlargement of the hindgut (arrowheads) where nutrient intake occurs. **c-e,** Transmission electron microscopy photographs of the gut; **(c)** longitudinal section at the level of the ventral ganglion (see VG in a); note the thinness of the gut cells (same magnification as d, see double arrows), the dense material in the gut lumen (asterisk) and the small number of cilia (arrow); **(d)** longitudinal section at the level of the ovaries (see in b); note that the gut cells are considerably higher and that they exhibit strong activity despite gut emptiness (no lumen); note also that the cilia (arrow) are more numerous; **(e)** detail of the apical pole of A-cells with cilia (black arrow); note the large vesicular traffic indicated by organelles involved in endocytosis, i.e., coated pit and vesicle (arrowheads), and tubular vesicular system (white arrows); I, intestine; LF, lateral fins; Ov, ovaries; SV, seminal vesicles; T, testes; TF, tail fin.



nevertheless always contain the organelles involved in absorption and intracellular digestion. Transverse sections at different levels in the trunk of these species show that only the short posterior intestine contains "normal" A-cells, which are evidently too few to rapidly provide nutrients if they are involved in all the stages of the digestive process (Fig. 1e, f). In addition, chaetognaths lack the storage structures necessary to provide the high daily food requirements during reproduction [30]. Thus, via evolution, chaetognaths have likely acquired the ability to shunt the digestion of prey and to ingest DOM directly from seawater by means of periodic water intake. The presence of abundant cilia [30] are consistent with this feeding strategy; i.e., they may assist in water circulation.

#### 2.4 Diel feeding cycle during spawning

To understand the relationship between food availability and reproduction, we examined the diel cycle of the planktonic species *Sagitta enflata* during spawning at 3-hour intervals (unpublished data). Specimens require a greater amount of food during spawning [30], and we were able to observe aspects of the feeding process (i.e., gut contents and the ultrastructure of intestinal cells) (Fig. 2). Samples were collected off the marine station of Villefranche-sur-Mer (Mediterranean) where previous studies had shown that specimens of *S. setosa* lay eggs nightly both in the wild [33] and in the laboratory (when they consume a maximum amount of provided prey [34]. In our samples, *Sagitta enflata* was the most abundant chaetognath (63%) observed, with approximately 2,100 specimens collected. Among them, only 18.53 percent had prey (or remnants of prey) in the gut, corresponding to a daily ration of 0.19 prey items per individual.

During daylight hours (8 a.m. to 2 p.m.), the guts of most specimens were empty and had the appearance of transparent laminae; all the adults had short ovaries with small ova. After 5 p.m., the posterior part of the intestine at the level of the ovaries became slightly distended in most specimens (Fig. 2a, b). The two opposite lateral sides of the gut epithelia exhibited a pale brownish coloration, but the gut lumens were generally devoid of visible content. In the meantime, ova volumes increased gradually. Mature ova were observed from 8 p.m. to 5 a.m., indicating that spawning occurred at night.

The ultrastructural study of empty guts showed that the A-cells of the hindgut were strongly polarised (Fig. 2c-e). The entire apical pole of each A-cell was dominated by tubulo-vesicular and endosomal compartments, as well as a fluctuating set of dense bodies, suggesting strong activity related to vesicular

traffic and absorption such as endocytosis linked to the apical membrane. Beside, during starvation experiments, absorption processes were also observed [20]. Our observations also indicate DOM absorption.

#### 2.5 Diet markers

In recent decades, the position of organisms within different levels of marine food webs has often been determined by different markers, such as stable carbon and nitrogen isotopes and fatty acids. The  $\delta^{15}\text{N}$  isotope is the marker most often used. It is biomagnified by consumers, which are typically enriched in  $\delta^{15}\text{N}$  by 3-4‰ relative to their diet and is thus most abundant in animals of higher trophic positions. In most studies, chaetognaths have exhibited high  $\delta^{15}\text{N}$  values, in particular higher than those of copepods, a finding that is consistent with a supposed strict carnivorous diet.

However, numerous studies have found that  $\delta^{15}\text{N}$  ratios of chaetognaths were lower than those of carnivorous copepods, and in some cases, the ratios were lower than those of grazing copepods, placing the trophic level of chaetognaths at an unexpectedly low position. For example, around the Endeavour Ridge hydrothermal vent plume (off British Columbia), Burd et al. [35] reported that the ratios of *Eukrohnia fowleri* (8.7‰ to 15.1‰) were always lower than those of the predator copepod *Euchaeta rubra* (15.1‰ to 16.4‰) and were often similar to or lower than those of grazing copepods (5.8‰ to 15.3‰). According to these authors, grazing copepods are primarily herbivores but can also opportunistically filter detritus, bacteria and protozoans. It is unlikely, however, that *E. fowleri* could rely on similar sources of nitrogen as copepods because chaetognaths lack a filtering apparatus: they must ingest sea water containing dissolved and fine particulate organic matter. Attempts to provide plausible hypotheses explaining these findings have been unsuccessful. In a study of areas surrounding seamounts in the northeast Atlantic [36], the  $\delta^{15}\text{N}$  ratios recorded during April 2004 (approximately 6.5‰) were similar for *Sagitta* spp. and a carnivorous copepod, but always higher than those of grazing copepods (3.7‰ to 5.5‰). The author emphasised that "*in November the  $\delta^{15}\text{N}$  value of *Sagitta* spp. was lower ... this reflected more likely an isotopic shift of the baseline of the food web, rather than a more herbivorous feeding*". Hirsch favoured a hypothesis of diet shift of their potential prey (as reported for several copepod and euphausiid species) over that of the ingestion of phytoplankton. In a comparison of the  $\delta^{15}\text{N}$  contents of two particle-grazing copepods and two "carnivorous" chaetognaths in the California Current, Ohman et al. [37] found a weak association

between them, despite a positive correlation with abundance. They concluded that, owing to the longer life span of chaetognaths, nitrogen levels in their body tissue might be influenced by feeding earlier in development and that these “obligate predators” could feed on other prey than these copepods. Thus, the carnivory of chaetognaths was never questioned.

Off the coast of Western Australia, Philp [38] noted that chaetognaths displayed both the highest zooplankton biomass and the highest chlorophyll-to-phaeophyton ratio. Phaeophyton is the pigment produced when zooplankton feed on phytoplankton and digest chlorophyll a. As chaetognaths are supposed carnivores, Philp [38] suggested that the presence of the chlorophyll pigment reflected the consumption of copepods (which feed on phytoplankton) by chaetognaths. If so, why is this pigment not found in other carnivores? Our alternative hypothesis is that chaetognaths absorb DOM resulting from the lysis of phytoplankton.

Analyses of fatty acid markers also support an alternative view of the feeding position of chaetognaths. Kürten et al. [39] found that clusters comprised primarily of *Sagitta elegans* were distinguished from other zooplankton taxa by the presence of bacterial lipidic markers, indicating that they rely more heavily on the microbial food web than their bulk  $\delta^{15}N$  signature alone might indicate.

### 3 Discussion

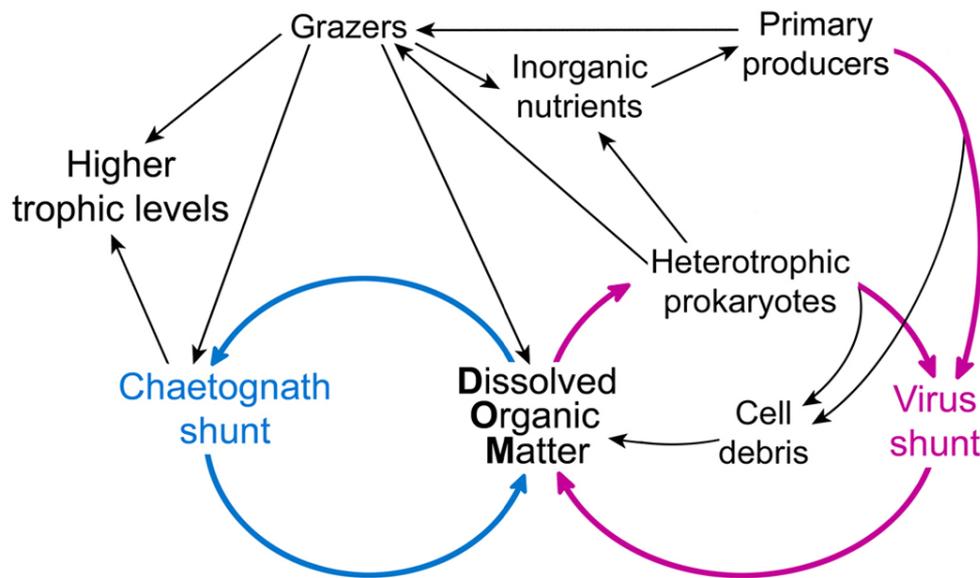
Bonnet et al. [3] noted the difficulties in correlating chaetognath feeding in the wild with zooplankton availability. We agree with this perspective, but argue that examination of chaetognath feeding can resolve the apparent discrepancies: data from the literature and our experimental results suggest that chaetognaths feed primarily on DOM, with predation being of minor importance.

The relationships between chaetognaths and microorganisms are now evident. In the mid-1980s, a community of chaetognaths of the benthoplanktonic family Heterokrohniidae, living a few meters above the sea bed, was discovered unexpectedly in the North-East Atlantic, occurring at -700 m and deeper to the abyssal plains [8, 40, 41]. They inhabit a homogeneous water mass of variable thickness that overlies the sea bed (up to 350 m), called the deep benthic boundary layer. This layer is characterised by a concentration of particulate matter greater than that of the water column above [42]. The resuspension of particles greatly increases bacterial abundance and biomass [43] and consequently, the presence of viruses and DOM. The observations of a greater abundance of chaetognaths near the sea bottom at

shallower depths for some species may reflect the greater abundance of bacteria, viruses and DOM in the water just above the bottom [44].

Other observations illustrate that chaetognath distribution is sometimes associated with that of microbial communities. In a study of the distribution and abundance of *Parasagitta* (= *Sagitta*) *elegans* in a lagoon in Northern Japan, Kotori et al. [45] unexpectedly found adults typical of deep waters living near the surface. They wrote “... the causes inducing the planktonic carnivore *P. elegans* to aggregate near the sea surface under the ice... are unknown”. An explanation was later provided by Maranger et al. [46], who studied the spring algal bloom at Resolute in the Canadian Arctic waters and stated that sea ice contains more viruses, and consequently more DOM, than the water beneath it. This observation was partly confirmed by Søreide et al. [47], who related that *Eukrohnia hamata* and *Sagitta elegans* primarily utilised mixed Pelagic and Ice POM (particulate organic matter) source pathways in European Arctic waters. Søreide et al. suggested that, for *S. elegans* “which is strictly carnivorous”, its dominant Ice-POM source pathway is in the spring because this species fed on *Pseudocalanus*, a species which grazes extensively on ice diatoms. In fact, organic matter is absorbed directly by *Sagitta elegans* and not via copepods based on the scarcity of prey in their guts; otherwise Kotori et al. [45] would not have underlined the unexpected position of the species.

The importance of viruses in all marine habitats is now undisputed [48-50] and sheds light on the availability of DOM in seawater. Their importance explains the success of chaetognaths in terms of abundance and biomass. Viral lytic infection contributes to bacterial and phytoplankton mortality, converting cells into newly produced viruses and cellular debris. The latter is made up of dissolved molecules, colloids and cell fragments [51], most of which constitute “operational DOM” [52]. It is assumed that most or all of these products are readily available to bacteria. Consequently, this viral shunt would make these products unavailable to grazers and all planktonic food webs through the transfer of this material from lysed phytoplankton to bacteria. Chaetognaths have apparently taken advantage of this shunt by changing their diet. This possibility explains the apparent “paradox” of the non-use by fauna of the high prokaryotic biomass in the benthic deep-sea realm [50], at least for chaetognaths. The chaetognath shunt of DOM likely functions per se next to the global marine ecosystem (Fig. 3). Chaetognaths do not reinject the majority of DOM they consume in the global ecosystem. Despite their great abundance - just



**Figure 3: The chaetognath shunt in a planktonic food web. The revised status of chaetognaths, removed from their former exclusively carnivore trophic level, in a schematic diagram of a planktonic food web: a chaetognath shunt is tightly connected to the viral shunt to take advantage of feeding on the DOM production of the latter (curved lines) (adapted from Fuhrman [52]).**

behind the copepods - they are never described as major prey items of other animals.

#### 4. Conclusion

Chaetognaths can no longer be regarded as "the tigers of the plankton" [53] nor as the carnivore standards in trophic levels analyses. Until now, this widely held notion induced many wrong statements regarding the conceptual view of food web analysis. Chaetognath predation on fish larvae must henceforth be removed from the modelization of fishery resource prediction. The functioning of food webs must now be revisited, due to the great abundance (number and biomass) of chaetognaths and their newly apparent role in the microbial shunt. We need to identify the predators converting the large amount of grazer biomass, which until now were thought to be primarily transferred by chaetognaths "... as major predators upon copepods ..." [1] to higher trophic levels. However, this large transfer is unlikely, as it is based on the strict carnivory of chaetognaths. All the true carnivore animals, and not just a particular group, play a role in the pelagic energy flow. All these considerations lead to another important consequence that requires investigation. Some authors have suggested that carnivorous zooplankton have little impact as predators on mesozooplankton and that these organisms would therefore have contributed little to the energy flow in particular areas, such as marine

fronts (e.g., the South Tropical Convergence limiting the Southern Ocean). More recently, Gieseke et al. [4] proposed that chaetognaths may act not only as a link between small zooplankton and top predators but can also contribute to carbon sequestration. Our hypothesis strengthens and enlarges this newly apparent role of chaetognaths. DOM resulting from the viral lysis of marine bacteria and microalgae, in addition to that resulting from the bacterial decay of dead plankton, constitute nutrients for both bacteria and chaetognaths. As chaetognaths play only a minor role in the vertical carbon flux and are a major component of the planktonic biomass, they comprise a large amount of carbon biologically sequestered in the world oceans.

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