Fluid Mechanics of Plankton

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These first lines of Hensen's article (Figure 1) in the "Fünfter Bericht" (1887) translate as follows.

"The material called "Auftrieb" has been investigated by zoologists and botanists since the groundbreaking contributions by Johannes Müller. It has been investigated and collected many times with fine, permeable nets. This material is—besides Müller's interest in its systematics and anatomy—without any doubt of great importance to the metabolism of the seas.

This contribution tries to get a closer look at this metabolism. It turns out that the name "Auftrieb" is not sufficiently comprehensive and descriptive, therefore, I have preferred to name this material "Halyplankton" (1). However, since we are only talking about the oceans here, the shorter term "Plankton" will be sufficient. It is defined as "everything that floats in water, regardless of whether it is high or low in it, and whether it is dead or alive."

A limitation of the expression to include only certain forms as plankton would not encompass the many embryonic forms that no longer occur in the plankton in their developed states. The decisive factor is whether the animals drift with the flow of the water, or whether they move with a certain degree of independence from the driving forces? Fish, therefore, belong only in the form of eggs and brood to plankton, but not as adult animals; whereas the copepods, though lively swimming, are carried away with the water flow, and must therefore be counted as part of the plankton . . . "

The change of words, from "Auftrieb" to "Plankton", was a big step in the perception of life in the oceans. "Auftrieb", the German word for buoyancy, defined anything floating in the water due to buoyancy. Scientists, like Johannes Müller mentioned in the article, were interested in the different animals floating within the material. They researched physiological and morphological questions, wondered about mating mechanics, but did not put the different species in context with each other. With naming this community of floating biology "Plankton" a first step toward recognizing an ecosystem was made.

Hensen continued these starting lines with a short discussion about how deep light might penetrate the upper water layer, and therefore, living entities may use it for living. He concluded that life in the oceans, and especially to produce fish, depends on plankton as the source of food (Figure 2).

With this step, Hensen accepted plankton as a lower level of the food pyramid and became the "grandfather of biological oceanography".

Life of the earth appeared roughly 3.8 billion years ago and spent nearly 3 billion years as single-cell organisms. Due to the limitation of molecular diffusion, a single cell can be no more than 1 mm scale, in which the viscosity dominates (the Kolmogorov scale). Under this condition, life stayed another nearly two billion years before multicell organisms emerged.

Citation: Yamazaki, H.; Strickler, J.R. Fluid Mechanics of Plankton. *Fluids* **2021**, *6*, 56. <https://doi.org/10.3390/fluids6020056>

Received: 21 January 2021

Accepted: 22 January 2021

Published: 27 January 2021

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At the present date, most phytoplankton cells are below the Kolmogorov scale. Even a large fraction of zooplankton is also not free from the viscosity of water. It would be unwise to assume that all microscale organisms do not pay attention to the immediate surrounding fluid motions. In fact, many microscale organisms swim more than 10 body-lengths per second, whereas most large-scale organisms swim an order of one body-length per second. Clearly, microorganisms have the ability to manipulate the properties of water. In order to maintain the population, phytoplankton require sunlight and nutrients; zooplankton pay attention to feeding, mating and escaping from predators.

Das mit dem Namen »Auftrieb« bezeichnete Material, welches von Zoologen und Botanikern, seit den bahnbrechenden Arbeiten von JOHANNES MÜLLER, so vielfach untersucht worden ist und mit feinem durchlässigen Netz gefischt wird, hat, neben seinem Interesse für Systematik und Anatomie, ohne Zweifel für den ganzen Stoffwechsel des Meeres eine grosse Bedeutung.

Diese Arbeit versucht es, dem bezüglichlichen Stoffwechsel näher zu treten. Es zeigt sich, dass der Name: Auftrieb nicht genügend umfassend und bequem ist, so dass ich es vorgezogen habe dies Material mit dem Namen Halyplankton¹⁾ zu belegen; da hier jedoch nur vom Meere die Rede ist genügt der kürzere Ausdruck Plankton. Ich verstehe darunter Alles was im Wasser treibt, einerlei ob hoch oder tief, ob todt oder lebendig.

Eine bestimmte Begrenzung des Ausdrucks auf bestimmte Formen lässt sich nicht gewinnen, denn es gehören zum Plankton viele Embryonal-Formen, die im entwickelten Zustand ihm Plankton nicht mehr vorkommen. Das Entscheidende ist der Umstand, ob die Thiere willenlos mit dem Wasser treiben oder ob sie einen gewissen Grad der Selbständigkeit dieser Triebkraft gegenüber bewahren? Die Fische gehören daher höchstens in der Form von Eiern und Brut zum Plankton, aber nicht als erwachsene Thiere; die *Copepoden*, obgleich lebhaft schwimmend, werden doch willenlos mit dem Wasser fortgerissen, und müssen daher zum Plankton gerechnet werden. Auf eine ganz genaue Abgrenzung des Begriffes kommt es durchaus nicht an; es knüpft sich dagegen,

¹⁾ Der Ausdruck ist nach einem Vorschlag meines Kollegen Professor FÖRSTER aus ἡ ἑλς und πλανᾶω gebildet. Der Ausdruck pelagisch bezeichnet nur das ganz allgemein zum Meere Gehörige.

Figure 1. First lines of Hensen, Victor. 1887. “Ueber die Bestimmung des Plankton’s oder des im Meere treibenden Materials an Pflanzen und Thieren”. *Bericht der Kommission zur wissenschaftlichen Untersuchungen der deutschen Meere, in Kiel* 5: 1–107, 6 pls.

erkläre mir dies Verhalten daraus, dass ein in fauliger Zersetzung begriffenes Material einer stärkeren Verdauungskraft bedarf, als diejenige ist, welche die Organisation der niederen Thiere hervorzubringen vermag.

Das Plankton kann im Allgemeinen wohl überall im Meere wachsen, es gewährt lebendige Nahrung, und scheint deshalb eine vorzügliche Quelle der Nahrungsstoffe zu sein.

Dieser Stoffquelle nachzugehen ist die Aufgabe, zu welcher ich im Verlauf meiner Untersuchungen geführt worden bin. Schon als ich 1867 im preussischen Landtag für die Herbeiziehung wissenschaftlicher Untersucher zur Erforschung des Meeres im Interesse der Fischerei eintrat, schwebte mir der Gedanke vor, dass man nur dann richtige Massnahmen im Interesse der Fischerei werde aufzufinden vermögen, wenn man in der Lage sei, sich ein Urtheil über die Ertragsfähigkeit des Meeres zu bilden. Als Mitglied der bezüglichlichen wissenschaftlichen

Figure 2. Excerpt from Hensen (1887). The small paragraph translates as: “Plankton can in principle grow all over in the oceans. It constitutes live food and therefore is a great source of nutrition”.

Our contribution here in this Special Issue focuses on some of the few words at the end of the text in Figure 1. It is the question about moving “with a certain degree of independence from the driving forces.” The perception that some animals just drift with the water flow is a scale-dependent question. Looking at the planet Earth from the star Sirius would not give the observer the impression that we human entities move around. Our contributions look at different scales to comprehend the importance of plankton to the life in the oceans as Hensen years ago was already contemplating.

Making use of a long observational data set, Tanaka [1] shows evidence of turbulence avoidance, and found that ambush feeders showed statistically significant changes in response to turbulence, whereas suspension feeders did not. Niimoto et al. [2] demonstrated the physical mechanisms of rotation for copepod nauplii about three principal axes of the body: yaw, roll, and pitch. Based on the results gained in experiments, they suggest the development of microscopic robots. Dabiri et al. [3] studied turning mechanisms of aquatic animals, e.g., jellyfish, and zebrafish. Turning requires torque while minimizing the resistance to the moment of inertia. These two are opposing mechanisms. Their results are

based on laboratory experiments and show how aquatic animals balance these mechanisms. Jiang [4] proposes a theoretical fluid mechanics model to estimate propulsion efficiencies of several planktonic species. For example, a tailed ciliate shows a high efficiency (~ 0.9). Copepods also show an unexpectedly high efficiency (>0.95), whereas in squid it is 0.44 and in small medusae 0.38.

Svetlichny et al. [5] provides scaling laws for swimming modes of calanoid copepods. Cruise swimming and short-lasting jumps are scaled with prosome length to a power between 2 and 3. The cost of transportation was higher for jumping than cruise swimming by a factor of 7 for large copepods but only a factor of 3 for small ones. These facts explain why small copepods can afford to more often jump than large copepods that are cruising swimmers. Suwaki et al. [6] studied the potential impacts of microplastics on zooplankton behavior. Microplastics are a recent hot topic because of human's interference with oceanic life. They found that the swimming behavior of calanoid copepod *Temora turbinata* is affected by microplastics. Selander et al. [7] discussed chemical cues that are used for resource acquisition, mate finding and assessing predation risk. They investigated how turbulence affects the distribution of chemical properties at a micro-scale using a numerical simulation model (DNS). They found that the chemical trail can be found under moderate turbulence conditions, but, when the rate of turbulent kinematic energy dissipation exceeds 10^{-7} ($\text{W}\cdot\text{kg}^{-1}$), the trails are shortened drastically.

Borazjani [8] reviewed numerical methods used to study (1) the force and flow generated by different part of body; (2) the relation between the small-scale flow around the body and the large-scale flow; and (3) flow and energetics. The author also discusses future prospects of numerical model developments. Schapira and Seuront [9] investigated how microscale nutrient patchiness is affected by turbulence. Based on a modeling approach, they found that phytoplankton exposed to high turbulence intensities are more efficient to uptake high concentration nitrogen pulses; on the other hand, uptake rates are higher for low concentration when turbulence is weak. Wagner et al. [10] investigated how scyphomedusae entrains and transports surrounding fluids and prey in order to catch calanoid copepods. The feeding currents generated by the medusa create a shear field that is well above the detection limit in copepods. However, only 58% of copepods reacted to the feeding currents. Hidden mechanisms in scale and flow fields may hinder the detection by copepods. Pécseli et al. [11] studied the encounter rate and the capture probabilities between cod larvae and prey (copepod) based on a field study under the different conditions of turbulence intensity.

Finally, it is essential to recognize and acknowledge the efforts provided by anonymous reviewers, which made it possible to maintain the high quality of all the contributions in this Special Issue.

Author Contributions: Both authors contributed equally to this article. All authors have read and agreed to the published version of the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

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