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Tumors (re)shape biotic interactions: evidence from the freshwater cnidarian Hydra

Justine BOUTRY¹, Juliette MISTRAL¹, Alexander KLIMOVICH², Jácint TÖKÖLYI³, Laura FONTENILLE⁴, Beata UJVARI⁵, Mathieu GIRAUDEAU¹,⁶* & Frédéric THOMAS¹*.

*equal contribution

1-CREEC/CANECEV (CREES), MIVEGEC, Unité Mixte de Recherches, IRD 224–CNRS 5290–Université de Montpellier, Montpellier, France
2-Zoological Institute, Christian-Albrechts University, Kiel, Germany
3-MTA-DE Behavioural Ecology Research Group, Department of Evolutionary Zoology, University of Debrecen, 4032 Debrecen, Hungary
4-AZELEAD, 377 Rue du Professeur Blayac, 34080 Montpellier, France
5-Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Waurn Ponds, Victoria, Australia
6-LIENSs, UMR 7266 CNRS-La Rochelle Université, 2 Rue Olympe de Gouges, 17000 La Rochelle, France
While it is often assumed that oncogenic process in metazoans can influence biotic interactions, empirical evidence for that is lacking. Here, we use the cnidarian Hydra oligactis to experimentally explore the consequences of tumor associated phenotypic alterations for the hydra’s predation efficiency, the relationship with commensal ciliates and the vulnerability to predators. Unexpectedly, the efficiency of hydra predation on prey was higher in tumorous polyps compared to non-tumorous ones. Commensal ciliates colonized preferentially tumorous hydras than non-tumorous ones, and had a higher replication rate on the former. Finally, in a choice experiment, tumorous hydra were preferentially eaten by a fish predator. This study, for the first time, provides evidence that neoplastic growth has the potential, through effect(s) on host phenotype, to alter biotic interactions within ecosystems and should thus be necessarily taken into account by ecologists.
Over the last few decades, great attention has been devoted by ecologists to understanding the relationships between biological community dynamics and the functioning of ecosystems. It is now clearly established that the outcome of species interactions and their ecosystem consequences are often strongly influenced by variation in the functional traits of the organisms. Factors influencing individual phenotypic variability are numerous, including genetic and epigenetic ones in interaction with external biotic and abiotic variables (e.g., predation, food availability), as well as internal biotic factors associated with the holobiont. For instance, host-microbe interactions are known to influence animal behavior and life-history traits. Besides, many manipulative parasites have the capacity to alter a broad range of phenotypic traits of their hosts, from color to morphological traits and behavior. Because alterations in the phenotype of parasitized hosts can be substantial, it has been argued that manipulated hosts can be ecologically equivalent as new organisms in the ecosystem, involved in novel direct and/or indirect interactions with other species.

In addition to microbiota and parasites, multicellular organisms also evolve with another category of living entity inside their body: the community of neoplastic cells. Neoplastic cell transformation affects most, if not all, multicellular organisms, from hydras to whales. Prior to being, in some cases, fatal for their hosts, tumor development often results in the alteration of phenotypic traits in their hosts, e.g., in morphology, physiology, body odors, reproductive activities, as well as social interactions. Despite this large range of phenotypic alterations and the omnipresence of neoplastic processes in the wild, the ecological consequences of neoplastic processes on ecosystems and animals’ life histories remain largely unexplored.

To fill this gap, we developed a novel model system, an artificial (tripartite) microcosm, which allows empirically testing whether bearing tumor may have implications for biotic dynamics within ecosystems. The freshwater cnidarian Hydra oligactis (further referred to as hydra) is naturally found in aquatic habitats attached to aquatic vegetation or
submerged rocks. Within its ecosystem, hydra are involved in a variety of interactions with invertebrates and vertebrates. For instance, they are predators of various zooplankton species or even fish spawn\cite{33,34}. They can also serve as host for commensal\cite{35} or parasite\cite{36} species. Finally, they can be a prey for fish or mollusks grazing on plants\cite{37,38}. Domazet-Lošo and co-authors \cite{39} have demonstrated that *H. oligactis* polyps can spontaneously develop tumors. These neoplasia not only severely alter the polyp's body shape, but tumor-bearing individuals also show a shift in their microbiota and display a higher number of tentacles (fig 1, see also \cite{39,40}). These tumors reduce the hosts' fitness but rarely kill them, and are vertically transmitted to the buds when polyps reproduce asexually \cite{39}. The prevalence of tumor-bearing individuals in the natural environment is unknown, but the observation of tumorous hydrams in strains derived from wild sampled individuals suggests that susceptibilities to tumor development exist in natural populations (unpublished data, Tökölyi J.). Given the substantial phenotypic differences between healthy and tumorous hydrams, we hypothesized that tumorigenesis might influence the biotic relationships involving hydrams. To test this hypothesis, we experimentally tested for the first time the consequences of tumor associated phenotypic alterations on three types of biotic interactions: hydrams' ability to catch prey, their capacity serving as a host for a commensal ciliate and their vulnerability to predators. Through this pioneer study, we aim to improve our understanding of the impact of tumorigenesis on ecosystem functioning.

**Material and methods**

Clonal non-tumorous and tumorous individuals *Hydra oligactis* strains (St. Petersburg strains, control and tumorous lineages from the laboratory of Thomas Bosch\footnote{1} ) were used for all experiments \cite{39}. Polyps were maintained at 18°C in Volvio© water and fed three times per week with freshly hatched *Artemia salina* nauplii according to standard protocols \cite{41}. Artemia nauplii were obtained by adding 0.5g of eggs microcyst (*Artemia salina*, Planktovie S.A.S.,

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\footnote{1} Zoological Institute, Christian-Albrechts-University Kiel, Am Botanischen Garten 1–9, D-24118 Kiel, Germany.
Marseille, France) in 400ml of seawater prepared with 36 g/L of sea salt (Reef Crystals, Aquarium systems, Sarrebourg, France) and oxygenated with an aquarium pump. After 24 to 48 hours of incubation at 30°C, nauplii hatched and were collected with a pipette, rinsed with a filter and suspended in a 200ml beaker of Volvic water.

(a) Hydra predation ability

For each trial, one hydra was placed in the experimental tank (20 ml well of a 6 well-plate (Thermo Scientific) and left for two minutes of habituation for allowing the polyp to reattach to the substrate. Prey were added at two different prey density levels: In *ad libitum* feeding (by adding 250 µl taken at the bottom of the Artemia beaker, representing more than hundred nauplii) or restricted feeding (by adding 250 µl of Volvic from the upper part of the beaker containing around 10 nauplii in total). The total number of nauplii added in restricted feeding was re-counted at each trial. The predation capacity of hydra was calculated by counting the number of preys captured in their tentacles in 10 minutes under the dissection microscope.

(b) Hydra colonization by commensals

The ciliates *Kerona pediculus* (named ciliate thereafter) are naturally present on hydra both in the lab and in the wild, and considered as commensals and hence were used here as a model to test commensal interactions. We collected *K. pediculus* individuals on polyps from an *H. oligactis* C2/7 strain previously sampled in Hungary and maintained in J. Tökőlyi’s laboratory. Ciliates were taken from C2/7 strain hydra using a one-millilitter pipette tip, under a binocular magnifier, by mildly aspirating the water around the hydra. In a first experiment (free-choice), we introduced one ciliate into the 1.5 ml well of a microplate (12 well-plate, Thermos Scientific) containing one tumorous and one non-tumorous hydra (both free from ciliates). After 4 hours, we recorded on which hydra the ciliate was present. A second experiment consisted in inoculating a single ciliate into a 1.5 ml well containing one hydra,

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2 Department of Evolutionary Zoology and Human Biology, University of Debrecen, Hungary.
tumorous or non-tumorous. We first verified the presence of the ciliate 15h after the inoculation. The number of ciliates on each individual was counted daily over six days. The trials for which ciliates failed to colonize the host were removed.

(c) Predation risk on hydra

To model the predation interactions, we used Siamese fighting fish (*Betta splendens*) as predator. In the aquarist circle, some fishes are well-known to consume Hydra efficiently but it is poorly documented in the litterature. Fifty adult females were obtained from pet shops (Oxyfish© Verlinghem and Botanic©, Clapiers, France). Each fish was introduced into 500ml plastic tanks (16*8,4*6,5cm) in Volvic© water at 25°C at least one hour before the test. A tumorous and a non-tumorous polyps were introduced together in the central hole (5ml) of a standard six well plastic plate for at least ten minutes of acclimation. The plate containing the two polyps was then introduced progressively in the container with the fish and pressed against the wall in front of the camera to allow recording and visualization of each hydra during the test. The upper and open part of the plate was turned inside to let the fish consume the polyps attached in the central well of the plate. Two observers identified precisely the position of each hydra during the test to recognize which one was consumed at each predation event. The trial stopped after the predation of the two hydras or after 45 minutes in any case (i.e., no predation or only one specimen predated). Each trial was recorded on a camera (GoPro©).

Statistical analysis

The effect of the tumorous phenotype on hydra predation was assessed by comparing the total number of Artemia nauplii captured by the two types of hydra (tumorous and non-tumorous). In *ad libitum* condition we used a Poisson generalized linear mixed model (glmm). In restricted feeding condition, we used a binomial glmm taking into account the proportion of artemias consumed over the number introduced initially since small variation can exist between trials. In both analyses we included the hydra type as a fixed effect and
the date as a random effect (see model choice in supplementary material). The number of tentacles per polyp of each group was compared using a Wilcoxon test.

The proportion of tumorous to non-tumorous hydras colonized by ciliates was compared to the number expected under a no preference hypothesis (50%, binomial test). The verification has been done that there is no effect of the day of measurement using a Fisher exact test and we checked the power of the analysis at a 0.01 alpha risk (see in supplementary material). We used a Poisson glmm to compare the number of ciliates in each group across time with the group as a fixed effect and the individual as a random effect.

The proportion of tumorous hydra captured by the predator was compared to the expected number under a random choice, using a binomial test. The verification has been done that there was no effect of the measurement day, using a Fisher exact test. We excluded from the analysis fish that attacked none of the hydras.

All analyses were performed using Rstudio (version 1.3). The power of all analyses was measured using the SimR or the MESS package (see supplementary material). When generalized linear random models were used, we specified each family, fixed, random effect choice in the analysis in the supplementary material.

**Results**

(a) Hydra predation ability

Besides carrying conspicuous tumorous buds, tumorous *H. oligactis* have been earlier reported to have substantially higher number of tentacles per polyp$^{40}$ (fig1.). The number of tentacles was significantly higher in the tumorous group (9.35 ± 1.14 for tumorous, 5.71 ± 0.75 for non-tumorous; W-value = 5969, p< 2.2e-16). Since the chief function of the tentacles is capturing prey, we hypothesized that the tumorous polyps might have a different predation capacity compared to the healthy polyps. We tested this hypothesis in two feeding experiments - using *ad libitum* and restricted amount of prey. In both feeding conditions,
tumorous hydersons captured significantly higher number of nauplii than non-tumorous ones (ad libitum: fig2a., Incidence ratio rates (IRR) = 1.31 ± 0.07; Z= 5.245; df= 81, p<0.001; restricted feeding conditions: fig2b., Odds ratio (OR) = 1.54 ± 0.14; Z=3.091; df=80; p=0.002). These results suggest that tumorous phenotype in hydra is associated with altered interactions with its prey.

(b) Hydra colonization by commensals

Because host surface serves as a habitat for epibiont species, and that the body of tumorous hydersons is severely modified in size and shape, we predicted that the tumorous phenotype may influence the colonization preference and/or dynamics of the commensal epibiont - the ciliate *K. pediculus*. When given the choice between a tumorous and a non-tumorous hydra, the ciliates colonized preferentially the tumorous one (fig3a., 81% ± 13%, p = 6.877e-05, alpha=0.01, binomial exact test, n=42), without any effect of the day of measurement (p = 0.1081, alpha=0.01, Fisher exact test, n=42). Of the 36 individuals inoculated with ciliates, 24 non-tumorous and 33 tumorous were colonized successfully by ciliates. Long-term observation of the colonization dynamics uncovered that the number of ciliates on hydra increased faster over time and reached higher densities on tumorous hydra than on the non-tumorous ones (fig3b., IRR=1.19; Z= 3.208; df= 337, p= 0.001). These results suggest that tumorous phenotype in hydra is associated with altered interactions with commensal species.

(c) Predation risk on hydra

Given that tumorous and non-tumorous hydersons do not have the same size/morphology, we predicted that they may experience a different predation risk by visually hunting predators. To test this hypothesis, we used Siamese fish as predators. They ate hydersons in 37 out of 51 trials and the first hydra consumed was significantly more often the tumorous one (fig4a., i.e. 73% of cases, 27 times over 37 trials, p = 0.008, binomial exact test). Nine fish preyed only on the tumorous hydra and none of them preyed only the non-tumorous one (fig4b.). There
was no influence of the measurement day (p= 0.650, Fisher exact test, n=37). When the first hydra consumed was a non-tumorous one, the time needed to observe the second predation event was significantly shorter than when the first hydra captured was the tumorous one (fig4c., 715 ± 738 seconds vs. 55 ± 98.3 seconds; Z=-4.632, p=3.62e-06, df=26). Although this shorter delay could indicate that satiation is more rapidly reached when the first prey was the tumorous individual, our findings are overall in accordance with the hypothesis that tumorous polyps are more detectable than non-tumorous ones.

Discussion

Ecological implications of oncogenic processes, while theoretically important in ecosystem functioning\textsuperscript{45}, have never been studied experimentally until now. This study provides empirical evidence for the first time for the hypothesis that the phenotypic consequences associated with the presence of tumor(s) in an organism reshape, qualitatively and/or quantitatively, various types of biotic interactions. We found that (i) the predation performance of tumorous hydras was increased compared to non-tumorous ones, (ii) the tumoral phenotype is more often colonized by a ciliate and with a faster colonization and (iii) tumorous hydras were preferentially eaten by predatory fish. Although tumorous and non-tumorous hydras used in our experiments differ in the presence of tumors and their phenotypic consequences, as well as their microbiota \textsuperscript{40}, they originate from the same ancestral polyp and are genetically identical (clonal). Therefore, the alterations of biotic interactions reported here are most likely caused by the phenotypic alterations induced by the tumors (i.e. non-tumorous hydra being here a perfect control).

The significantly higher ability of tumorous hydras to capture prey may first appear counterintuitive given that neoplasms are usually associated to reduced host performances \textsuperscript{46,47}. The most parsimonious explanation here is that this higher performance is due to the increased number of tentacles in tumor-bearing hydras compared to non-tumorous ones (see also \textsuperscript{39}). Precise causes behind this novel phenotype are unclear and could have
different origins since it could benefit the host (e.g. compensatory mechanisms, see for instance \textsuperscript{48}), the tumor (e.g. host manipulation, see for instance \textsuperscript{49}) or be beneficial for both the host and the tumor (see for instance \textsuperscript{50}). Deciphering the molecular cross-talk between the host and the tumor during the window when additional tentacles are growing could help to clarify this point (see for instance \textsuperscript{51}). Further experiments estimating fitness benefits for the host and the tumor would be required to distinguish between these possibilities. Also, given that microbiota is altered in the tumorous polyps, and that the microbiota alters the behavior of hydras\textsuperscript{52}, we cannot exclude that a modified neuronal activity and feeding behavior might be responsible for the more efficient predation of tumorous polyps. We particularly emphasize here that the effect of higher predation efficiency was observed in both feeding conditions, ad libitum and restricted feeding, whereby the limited food supply is likely the more natural condition for hydra\textsuperscript{54}. In any case, these results suggest that the level of resources could influence the coexistence between tumorous and non-tumorous individuals in a non-expected manner. Indeed, while it is intuitively logic that tumorous individuals, already weakened by the presence of tumor, would suffer more from a lack or from scarcity of prey than non-tumorous ones, our results conversely suggest that their persistence could be facilitated in poor habitats.

The higher preference of ciliates for tumor-bearing individuals, as well as their faster replication rate on them compared to non-tumorous ones, may indicate that the formers offer a larger living surface and/or more resources for epibiont organisms. Precise mechanisms operating here remain however to be determined, at least four hypotheses could be tested. (i) Ciliates prefer chemical cues specifically produced by tumor-bearing individuals, (ii) tumor-bearing individuals might be more easily detected or encountered by actively searching ciliates because of their bigger size, their higher number of tentacles and/or a different behavior associated with tumors, (iii) tumorous hydras might lack some defenses against ciliates and are then more vulnerable to the opportunistic colonization, (iv) tumorous hydras might harbor more bacteria and/or release more feeding byproducts useful for ciliates
due to their altered feeding behavior. The commensal role itself of this ciliate remains however to be explored\textsuperscript{35,53,55–57}. For instance, the presence of a high number of ciliates seems to be associated with an increased budding rate in \textit{H. oligactis}, but the causes of this phenomenon are not well understood\textsuperscript{35}. Thus, we cannot exclude that the commensal nature of the interaction between this ciliate and the hydra is not stable and varies with different parameters including the density on hydra. Further explorations of the impact of ciliates’ density on the fitness (e.g. budding rate, survival) of tumorous and non-tumorous hydras could help us to understand the costs and/or the benefits of these commensals for tumorous and non-tumorous hydras.

The higher predation risk of tumor-bearing hydra could be ascribed to both visual and chemical cues, since the fish species used here is able to exploit both, at least in sexual selection and competition contexts\textsuperscript{58–60}. However, given that this fish is mostly a visually hunting predator\textsuperscript{61,62} and from our observations during the experiments, we favor the first hypothesis, i.e. that they detect and capture in priority bigger (tumorous) preys. The respective role of the abnormal neoplastic mass and/or of the higher number of tentacles in enhancing the hydra detectability could be tested in the future by removing some tentacles from tumor-bearing individuals, and/or by grafting the upper part of tumorous hydras on non-tumorous ones and vice versa (see for instance\textsuperscript{63}). In addition, further experiments should also focus on the possible role of the behavioral differences between tumorous and non-tumorous hydras. For instance, tumorous polyps do not contract spontaneously and their induced contractility is compromised. Therefore, they potentially could not retract themselves in case of attack and/or have a lower ability to detect predators (hydras are light sensitive and can detect shadows from the fish\textsuperscript{64}).

Because this study was experimental and the prevalence of tumor-bearing individuals is unknown in the field, the extent to which these findings illustrate processes occurring in the wild remains to be determined. We have developed here a unique
experimental pattern, with tripartite microcosm composed of two interacting organism with, one containing tumoral cells considered as a third living entity impacting the interaction. It allows assessing the impact of tumor burden onto multiple biotic interactions within an ecosystem. Moreover, it can provide new insights for a mechanistic understanding of these dynamics. The simplicity of the system and its accessibility offers unlimited perspective for ecological, behavioral or even biochemical studies.

Beyond the present demonstration that the tumorigenesis has the potential to alter biotic interactions, further experiments manipulating in microcosms the frequency of tumor-bearing individuals in *Hydra oligactis* populations would be necessary to simulate the possible cascade effects on the whole aquatic community. As suggested above, these experiments should also test if the influence of tumors in biotic interactions depends on the phenotypic variation already existing in tumor-free individuals, especially natural size variability of non-tumorous hydra. Our experiments also uncovered a truly surprising phenomenon: bearing tumor may appear advantageous in particular conditions. The evolutionary significance of this principle and its impact onto the species' life history may be also studied in long-term experiments.

The results we presented here suggests that neoplastic processes in biological communities should be fully considered by ecologists to understand and predict the evolutionary ecology of species interactions, as well as their consequences on ecosystem functioning. This research direction is likely to become crucial in the future given that ecosystems are increasingly exposed to oncogenic pollution resulting from anthropic activities\(^{32}\).

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Ethic statement:
All experimental animals were treated in accordance with French and European Union regulations (directive 2010/63/UE). All the behavioural observations were included in the project authorization APAFIS: 29961. No fishes were injured or killed during the experiments.

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Legend of figures

Figure 1: Phenotypic differences of non-tumorous and tumorous hydras
The non-tumorous hydra is on the left and the tumorous one on the right. We can notice an increased body size and number of tentacles.

Figure 2: Tumorous hydras have higher predation abilities
The number of prey captured per hydra (a.) in *ad libitum* and in restricted feeding (b.). The proportion of prey captured per hydra in restricted feeding were counted during ten minutes. Boxplots represent the first, median and third quartiles on the 95% extent. A point represents each measurement with the non-tumorous group in green and the tumorous in red. (c.) Pictures of tumorous and non-tumorous hydras capturing prey.

Figure 3: Ciliates established easier on tumorous hydras than on non-tumorous ones.
(a.) Five hours after the introduction of a ciliate into an experimental tank containing both hydra type, we found 81% of the ciliates attaches to the tumoral host instead of the non-tumoral one. (b.) After the introductions of one ciliate into the well of a tumoral or a non-tumoral individual, we counted daily the number of ciliates per hydra. Each point represents the number of ciliates measured on a given day; the size of the point depends on the number of hydras recorded at this measurement. The black line represents the average value predicted by the model and the colored areas the confidence interval at 95% predicted by the model. In green, on the left, the non-tumorous group on the left and in red, on the right, the tumorous group on the right in red. (c.) Pictures of eleven ciliates attached to a hydra at x20 and zoomed picture of one ciliate on a hydra.

Figure 4: Tumorous hydras have a higher predation risk by fish than non-tumorous ones
(a.) The histogram represents the number of fish that consumed first the tumoral (in red), the non-tumoral (in green) or none of the hydra during the test (in grey). Among the 37 trials which fish consume a first hydra, the pie plots represent the proportion of fish that consumed the second one. The color of the section corresponds the type of the remaining hydra; in grey if the second hydra consumed is non-tumoral, in red if the second hydra consumed is tumoral and in grey if the fish did not consume the second hydra. (c.) A point represents the time required to the fish to consume the second hydra after the first one, on the left when the remaining prey is non-tumorous (in green), on the right when it is a tumorous (in red). (d.) Pictures of two hydras, a tumoral and a non-tumoral in a plastic well plate. The fish consumed the tumoral, and then, only the non-tumoral remain visible on the last picture. These illustrative pictures were taken during a session separate from the experiments.
**Figures**

**Figure 1.** Phenotypic differences of non-tumorous and tumorous hydas

**Figure 2.** Tumorous hydas have higher predation abilities
Figure 3. Ciliates established easier on tumorous hydas than on non-tumorous ones.

Figure 4. Tumorous hydas have a higher predation risk by fish than non-tumorous ones.