

# Summary of Professional Accomplishments

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Summary of Professional Accomplishments provides a description of academic achievement under Article 16 Paragraph 2 of the Act of 14 March 2003, on scientific degrees and academic titles and on degrees and titles in the field of art (Journal of Laws of the Republic of Poland, no. 65, Item 595 as amended) as well as other interests and academic achievements.

1. *First and Last Name:*

Anita Kaliszewicz

2. *Awarded diplomas and Academic/Artistic Degrees – with the name, place, and year of attainment, as well as the titles of doctoral dissertations:*

- 1995-2000: studies at Faculty of Biology, Warsaw University (specialization: environmental biology).

- 2000: Master of Science, title of dissertation "Reaction of *Stylaria lacustris* (Oligochaeta) to damages caused by predators", supervising prof. dr hab. Ewa Pieczyńska.

- 2006: PhD in the field of Biology, Faculty of Biology, Warsaw University, title of doctoral dissertation „Predation effect on life-history strategies of prey – growth, division and regeneration in an aquatic oligochaete” supervising prof. dr hab. Janusz Uchmański at Centre for Ecological Research, Polish Academy of Sciences.

3. *Employment in the scientific field:*

- 15.01.2001- 14.11.2002: Biologist, Institute of Ecology, Polish Academy of Sciences, Dziekanów Leśny

- 15.11.2002- 30.06.2006: Assistant, Centre for Ecological Research, Polish Academy of Sciences, Dziekanów Leśny

- 01.07.2006- 31.12.2012: Assistant Professor, Centre for Ecological Research, Polish Academy of Sciences, Dziekanów Leśny

- 01.10.2008-30.09.2009: Assistant Professor, Institute of Ecology and Bioethics, Cardinal Stefan Wyszyński University in Warsaw

- od 01.10.2009: Assistant Professor, Faculty of Biology and Environmental Sciences, Cardinal Stefan Wyszyński University in Warsaw

4. *Indication of achievements under Article 16 Paragraph 2 of the Act of 14 March 2003, on scientific degrees and titles and on degrees and titles in the field of art (Journal of Laws of the Republic of Poland, no. 65, Item 595 as amended):*

4.1. *Titles of the scientific achievement:*

**Mechanisms affecting the variability in the reproductive strategies of hydras (Cnidaria: Hydridae)**

A series of 6 publications thematically related to each other and published in the years 2011-2019 in journals from Journal Citation Reports. Copies of publications included in the scientific achievements can be found in the Attachment 4. Statements of co-authors are included in the Attachment 5.

4.2. *List of publications included in the scientific achievement:*

1. **Kaliszewicz A.** 2011. Interference of asexual and sexual reproduction in the green hydra. *Ecological Research* 26:147–152.  
IF<sub>2011</sub> =1,565; 5-year IF<sub>2011</sub> = 1,477;
2. **Kaliszewicz A.,** Lipińska A. 2012. Maturation costs affect maturation timing: sexual reproduction in a heterogonic hydra. *Hydrobiologia* 679: 19-25.  
IF<sub>2012</sub> =1,985; 5- year IF<sub>2012</sub> = 2,270;
3. **Kaliszewicz, A.,** Lipińska A. 2013. Environmental condition related reproductive strategies and sex ratio in hydras. *Acta Zoologica* 94: 177–183.  
IF<sub>2013</sub> =1,296; 5- year IF<sub>2013</sub> = 1,280;
4. **Kaliszewicz A.** 2015. Intensity-dependent response to temperature in *Hydra* clones. *Zoological Science* 32: 72-76.  
IF<sub>2015</sub> =0,814; 5- year IF<sub>2015</sub> =0,861;
5. **Kaliszewicz A.** 2018. Sex ratio patterns and trade-off between sexual and asexual reproduction in the brown hydra. *Freshwater Science* 37: 551–561.  
IF<sub>2017</sub> =2,489; 5- year IF<sub>2017</sub> = 2,951;
6. **Kaliszewicz A.** 2019. Variations of hydra reproductive strategies arising from its modular structure. Two aspects of the modular reproductive effect. *Ecological Modelling* 393: 52–60. IF<sub>2017</sub> =2,507; 5-year IF<sub>2017</sub> = 2,697;

Total IF = 10,656; total 5-year IF: 11,536

4.3. Discussion of the scientific purpose and results achieved, along with discussing scientific and research achievements:

## INTRODUCTION

Closely related species, which individuals reproduce in different modes, can be model organisms to study reproductive strategies and factors that affect them. Organisms, that reproduce both sexually and asexually, for example by budding, division or fragmentation, seem to be very useful for such studies. In these organisms as a result of asexual reproduction a clone is formed, which is considered a modular individual, the so-called genet. The division into unitary and modular organisms has been known since the 1980s and 1990s (Marfenin 1993; Gattsuk 2008). Modular structure is identified mainly with plants, but among animals modular species can be also observed. There are primarily able to reproduce asexual, often sessile and colonist invertebrates such as Porifera, Cnidaria and Tunicata. Some modular species do not form colonies and have the ability to move. In this case, individual modules can live apart from each other and under different conditions. From the genetic point of view, they still form one individual. This is the case with hydras (Cnidaria: Hydridae), sea anemones (Cnidaria: Anthozoa), scyphozoans (Cnidaria: Scyphozoa), some species of flatworms (Platyhelminthes: Turbellaria), ribbon worms (Nemertea), polychaetes (Annelida: Polychaeta), oligochaetes (Annelida: Oligochaeta), starfish (Echinodermata: Asteroidea) and brittle stars (Echinodermata: Ophiuroidea). In the above-mentioned groups of animals, the plasticity of reproduction strategies of individual modules can be observed, which additionally allows the study of factors and mechanisms that may affect the variability of breeding strategies. In modular species that are hermaphrodites, the situation becomes even more complicated because, unlike the hermaphroditic unitary species, the individual modules that make up an individual can differently allocate energy to male and female functions. If modular species are closely related and additionally differ in the strategies of sexual reproduction, e.g. hermaphroditic versus gonochoric, then one can try to identify factors that are responsible for the application of specific reproductive strategies by the individual.

It should be emphasized that the impact of factors affecting the selection of reproductive strategies of modular individuals has not been sufficiently known. Animals with high variability in reproductive strategies that match the above description are cnidarians, among them hydras, sea anemones, e.g. *Aiptasia diaphana* (Armoza-Zvuloni et al. 2014), hydrozoan jellyfish, scyphozoans (Carré and Carré 2000, Helm 2018). In addition to cnidarians, animals with a modular structure and high variability of reproduction strategies are some flatworms (Dugesidae; Kobayashi et al. 2012), ribbon worms (Lineidae; Ament-Valasquez et al. 2016) and polychaetes (Spionidae: e.g. *Pygospio elegans*; Bolam 2004).

Among the above-mentioned groups, hydras are animals with a very simple body structure, cosmopolitan, often occur in high densities in freshwaters (Kanaev 1952, Slobodkin and Bossert 2010), and due to the fact that they do not form colonies, they can move over longer distances (Łomnicki and Slobodkin 1966). Their individual modules are created as a result of budding and exhibit great phenotypic plasticity (they can be functionally males, females, or hermaphrodites). Moreover, some species are sequential hermaphrodites (*Hydra vulgaris*), simultaneous hermaphrodites (*Hydra circumcincta*,

*Hydra viridissima*) or gonochoric (*Hydra oligactis*) (Kanaev 1952, Burnett 1973). Various ecological factors induce particular reproductive modes in hydras. The most important are changes in temperature and day length, density of individuals and availability of food (Whitney 1907, Burnett 1973, Giese and Pearse 1974, Campbell 1999). Hydras, as most invertebrates with modular structure, reproduce mainly asexually under favorable environmental conditions. Changing conditions induce sexual reproduction, which results in zygotes that can survive difficult conditions (Schierwater and Hauenschild 1990, Manconi and Pronzato 1991). The main factor informing about the deterioration of the conditions are temperature changes, to which the hydras and other organisms, such as hydrozoans, flatworms and oligochaetes, respond by induction of sexual reproduction (Vowinckel 1970, Burnett 1973, Giese and Pearse 1974, Carré and Carré 2000). It has been observed that the induction of sexual reproduction depends on the direction of temperature changes. Therefore, the following groups were distinguished:

- „cold-crisis” – species that switch to sexual reproduction after temperature drop (e.g. *Hydra oligactis*, *H. robusta*)
- „warm-crisis” – species that switch to sexual reproduction after temperature rise (*Hydra littoralis*, *H. magnipapillata*, *H. viridissima*)
- „unspecified species”, whose induction occurs regardless of the direction of temperature changes, np. *Hydra vulgaris*, (Burnett 1973).

For some species, such as *Hydra circumcincta*, there is no information on conditions that induce sexual reproduction.

In many organisms, sexual reproduction is associated with the cessation of asexual reproduction. Such a situation is observed in oligochaetes (e.g. from the Naididae family) and many species of cnidarians. However, this is not the rule, since the green hydra (*H. viridissima*), who lives in symbiosis with green algae of the genus *Chlorella*, produces buds also during sexual reproduction. In the previous literature has been reported that the “warm-crisis” hydras, unlike the cold-crisis species, does not interrupt nutrition and asexual reproduction at the time of gonadal production (Brien and Reniers-Decoen 1950, Burnet and Diehl 1964). The asexual reproduction of hydra and factors inducing sexual reproduction was widely described (Stiven 1965, Tökölyi et al. 2016). On the other hand, the data on sexual reproduction, i.e. the type of reproduction (gonochorism, sequential vs simultaneous hermaphroditism) and, in particular, the sex ratio in the population of the hydras, are incomplete and often contradictory.

The reproductive strategies of the hydras are characterized by unusual variability and complexity. Closely related species, reproduce asexually in a similar way producing buds, but the strategies of sexual reproduction can be completely different. There are gonochoric species (*H. oligactis* and *H. pseudoligactis*), sequential hermaphrodites (*H. vulgaris*), simultaneous hermaphrodites (*H. circumcincta*, *H. viridissima*), among them able to self-fertilization e.g. *H. circumcincta*. Diversity of the reproductive strategy of the hydras is the cause of many inaccuracies in the description of environmental factors inducing sexual reproduction, the type of hermaphroditism (sequential or simultaneous), unequal sex ratio, male-biased in populations of gonochoric species and especially the sex ratio in populations of hermaphroditic species. Moreover, when describing the hydras, errors occurred resulting from incorrect taxonomic identification (e.g., often mistaken *Hydra attenuata* Schulze, 1917

and *Hydra vulgaris* Pallas, 1766). Such mistakes also concerned other groups of cnidarians e.g. sea anemones of the genus *Urticina* and *Aulactinia* (Sanamyan and Sanamyan, 2006). The most inaccurately described and full of inaccuracies aspect of the reproduction of the hydras appeared to be the sex ratio. In hermaphroditic species in which functional males and females may be present, studies on sex ratio have been omitted. In gonochoric populations e.g. *Hydra oligactis* and *H. pseudoligactis*, male-biased sex ratio has been described. In some populations, males accounted for up to 100% of the sexually matures hydras (Pennak 1978, Bell and Wolfe 1984). The reasons for this disproportion, diverging from the equal sex ratio according to Fisher's theory (1930), have not been described before and are one of the aims of my research presented here.

## THE AIM OF THE RESEARCH

The main aim of my research was to understand the ecological and evolutionary mechanisms that are important in maintaining the diversity of the reproductive strategies of hydras. In the series of publications, I tried to explain the questions that make up the main aim and concerning:

- the most successful reproductive strategies of a modular individual considered as a genet,
- the sex ratio in populations of the hydra species that differ in the strategies of sexual reproduction
- factors inducing sexual reproduction of selected species of hydra
- trade-offs between asexual and sexual reproduction of the selected gonochoric and hermaphroditic species
- the range of variability of traits of asexual reproduction

## RESULTS

***(1) Many reproductive strategies lead to similar success of a clone considered as a modular individual (genet). Comparison of two aspects of modular reproductive effect in non-colonial hermaphroditic species on the example of hydra***

Results presented in the paper:

Kaliszewicz A. 2019. Variations of hydra reproductive strategies arising from its modular structure. Two aspects of the modular reproductive effect. Ecological Modelling 393: 52–60

*Hydra circumcincta* is a simultaneous, self-fertilizing hermaphrodites, whose type of gonads produced depends on the size of the body. Based on my field studies, I determined that very small polyps (<1.5 mm<sup>2</sup> of the body surface) do not induce sexually, small polyps (1.5-2.5

mm<sup>2</sup>) are functionally males, medium females, larger (> 3.0 mm<sup>2</sup>) are usually simultaneous hermaphrodites. The energetic costs associated with the maturation of females and the production of female gonads exceed the cost of producing male gonads. In natural populations and in the laboratory I observed the presence of various ratios of hermaphroditic polyps, polyps functioning as males and polyps functioning as females. In order to compare the different reproductive strategies of the hydras and to select the strategy that leads to the greatest reproductive success of a single clone, *H. circumcincta*, I built an individual-based model (IBM). The model was prepared on the basis of real data regarding life traits of *H. circumcincta*: age, size of the body, the rate of asexual reproduction, life span, moment of switching from asexual to sexual reproduction, the level of competition for fertilization of oocytes and duration of the sexual season. The model defines body size classes of the polyps and their ability to mature based on the observation of natural and laboratory populations. Large polyps (> 3.0 mm<sup>2</sup> of body surface area) that produce two types of gonads produce five times as many oocytes in last-class size compared to polyps that are one and a half times smaller.

The hydra strategies have been analyzed in terms of the modular structure. Many modules created as a result of asexual reproduction, and therefore genetically identical, make up one individual called a gene or clone. In case of hermaphroditic species, such as *H. circumcincta*, there are hermaphroditic polyps, that can be free living. This approach to the concept of the subject made it possible to introduce the term *modular reproductive effect*, which consists of two possible aspects of strategy changes: (1) different energy allocation to male and female functions in modules, (2) variable sex ratio, e.g. hermaphroditic modules compared to those that are functionally males and those functioning as females (Fig. 1). The modular reproductive effect can also be useful for other, than hydras, modular species of hermaphroditic animals that are non-colonial, e.g. sea anemones (*Aiptasia diaphana*; Armoza-Zvuloni et al. 2014), flatworms (*Dugesia ryukyuensis*; Kobayashi et al. 2012) and polychaetes (family Serpulidae; Huxley 1855, Rouse and Pleijel 2001). On the other hand, in the case of a species with a unitary structure, an individual is a single organism, which may, in the case of hermaphrodite mode of reproduction, only allocate energy differently in male and female functions, so only the first aspect of changes in reproductive strategies can be applied (Fig. 1). The sex ratio in unitary species refers to the level of the population and not to a single, genetic individual.

The results of the individual model on the example of *H. circumcincta* showed that under weak competition for egg fertilization the most favorable strategy for the reproductive success of a clone, as measured by the number of zygotes, is the unequal sex ratio with the predominance of polyps functioning as males. However, this situation is unstable and leads to increased competition. With increased competition in a hypothetical scenario where hydra polyps are capable of storing large amounts of energy and investing in oocyte production, beneficial strategies are: (1) equal ratio of polyps functioning as males and those functioning as females with the ability of the latter to invest large amounts of energy in the production of oocytes; and (2) hermaphroditic polyps with an increased allocation in oocytes (Fig. 2). In a scenario where, according to real data, the ability of polyps to store large amounts of energy and invest in oocyte production is limited, many strategies are beneficial: the presence in different proportions of simultaneous hermaphrodites and polyps functioning as males, the coexistence of simultaneous hermaphrodites and polyps functioning as females,

co-existence of simultaneous hermaphrodites, polyps functioning as females and those functioning as males (Fig. 2).

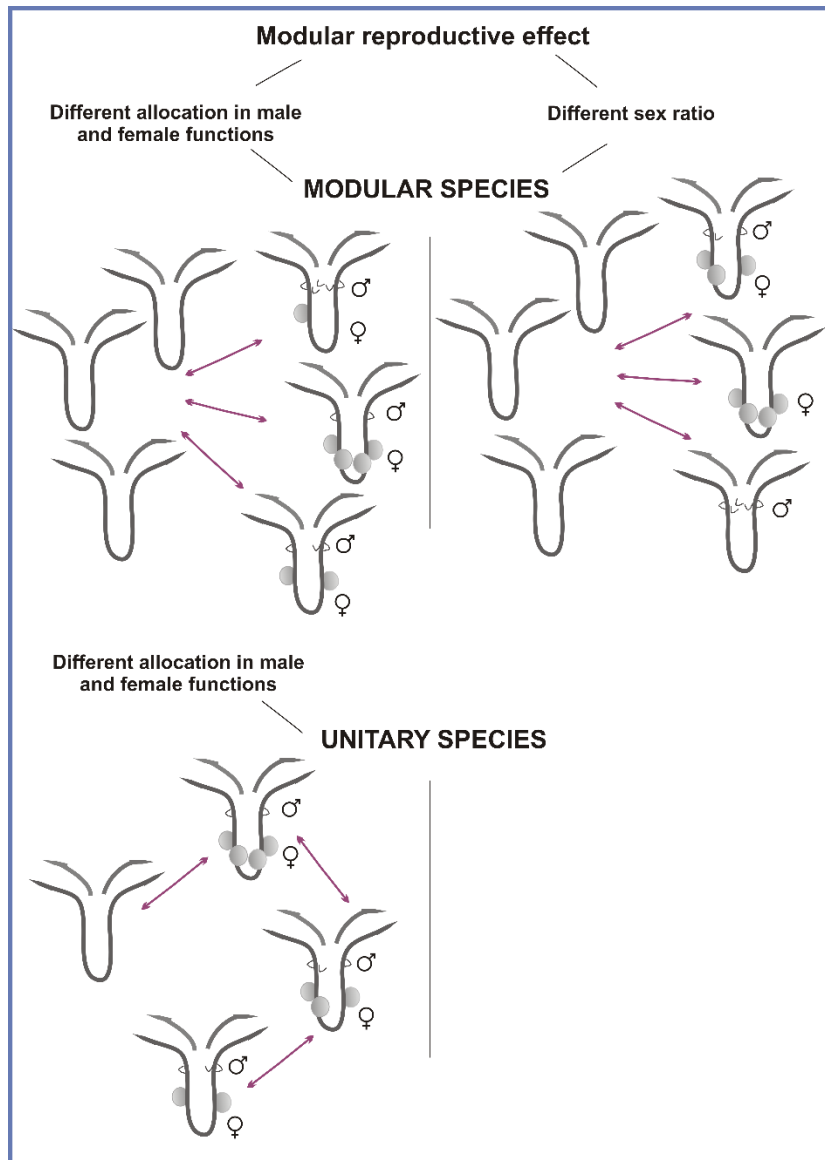


Fig. 1. Diagram showing possible reproductive strategies of a hermaphroditic individual with a modular and unitary structure. The arrows indicate the directions of possible changes in reproductive strategies. In the case of a modular organism, e.g. a hydra, whose modules together constitute a genetic individual, two aspects of change are possible, called by me a *modular reproductive effect* (Kaliszewicz 2019): unequal investment in male and female functions and unequal sex ratio. This last aspect is not possible for a single unitary individual.



The results of the model indicate that the greater importance for the adaptation of the clone, understood as a modular individual, has a variable sex ratio of polyps than the variable allocation into male and female functions of hermaphroditic polyps. Numerous reproductive strategies leading to similar success of the clone cause that there is no strong selection pressure towards one specific strategy. This leads to the persistence of many reproductive strategies in the population of the hydras. The reasons for this state were explained by the model based on analyzing the strategy of the individual in a modular way and the assumptions of the *modular reproductive effect*.

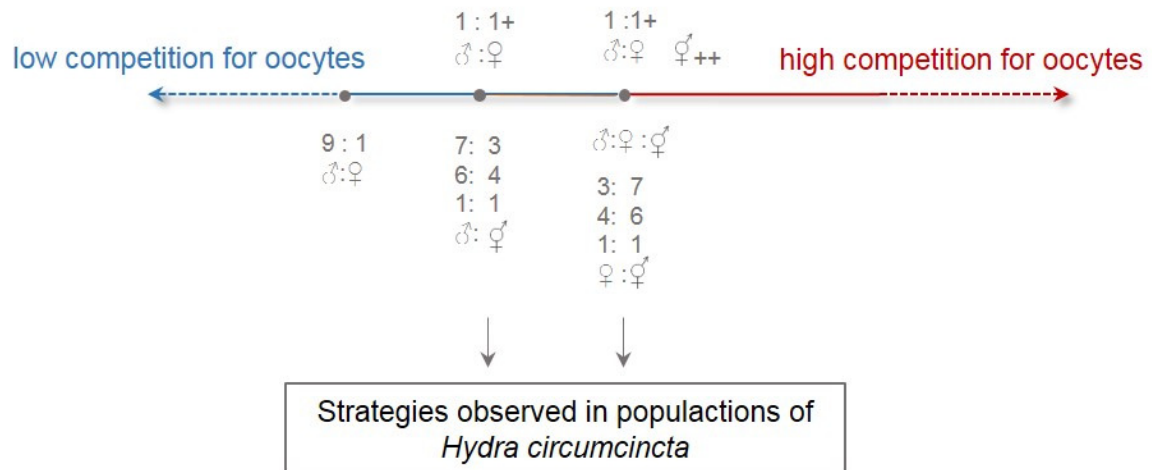


Fig. 2. Diagram summarizing the results of the model of reproductive strategies increasing the reproductive success of the *H. circumcincta* clone as a modular individual. Plus means increased investment in female functions. The numbers indicate the proportions of polyps functioning as males, females or simultaneous hermaphrodites.

#### The most important achievements:

- Demonstrating that a wide variety of sexual reproduction strategies are beneficial for the reproductive success of modular hydras. Because many strategies lead to similar success of the clone, there is no selection pressure towards one specific strategy. Lack of selective pressure is a mechanism that maintains the observed diversity of the reproductive strategies of the hydras
- Introduction of the term *modular reproductive effect*, which consists of two possible aspects of reproductive strategies: unequal investment in male and female functions and unequal sex ratio of modules. This last aspect is not possible for a single unitary individual. The modular reproductive effect is applicable not only to the hydras but also to other hermaphroditic non-colonial species, such as some sea anemones, flatworms and polychaetes.

**(2) *The sex ratio in populations of hermaphroditic species of the hydras is affected by a combination of environmental factors inducing sexual reproduction - the variable sex ratio is consistent with the results of the model***

Results presented in the paper:

Kaliszewicz, A., Lipińska A. 2013. Environmental condition related reproductive strategies and sex ratio in hydras. *Acta Zoologica* 94: 177–183.

and partly in the paper:

Kaliszewicz A. 2011. Interference of asexual and sexual reproduction in the green hydra. *Ecological Research* 26:147–152.

Laboratory research were carried out on clones of three species of *Hydra*. Three selected clones from laboratory culture were used: two simultaneous hermaphrodites (*H. circumcincta* and *H. viridissima*) and one sequential hermaphrodite (*H. vulgaris*). In addition, research was also carried out on *H. viridissima*, derived from the natural population (52°05'N 21°08'E). Studies carried out on clones from laboratory cultures and on field polyps taken from the *H. viridissima* population gave similar results. For the hydra clones reared in the laboratory, the presence of simultaneous hermaphrodites and polyps functioning as males was observed in various proportions: 3:7 for *H. circumcincta* in the treatment with plenty food, 7:3 and 1:9 for *H. viridissima* in the treatments with plenty and limited food, respectively. In contrast, in the natural population of *H. viridissima* in the middle of the season of sexual reproduction, this proportion was 1:1. In the case of *H. vulgaris* clones, the presence of sequential hermaphrodites and polyps functioning as males also occurred in different proportions: 7:3 and 3:7 in the treatments with plenty and limited food, respectively. For the *H. circumcincta* clones, the co-occurrence of simultaneous hermaphrodites and polyps functioning as females in different proportions of 3: 7, 6: 4, 1: 9 were also recorded depending on the temperature changes (increase or decrease). In the case of the natural population of *H. viridissima*, at the end of the sexual reproductive season, the studies revealed the co-occurrence of simultaneous hermaphrodites, polyps functioning as males and those functioning as females. The obtained results show a large variation in the sex ratio of the hermaphrodites to functional males and functional females which is consistent with the results obtained in the model. In comparison to field studies conducted on natural populations, the research in laboratory conditions allow to analyze different variants of factors inducing sexual reproduction. The combination of temperature changes (decrease or increase) and nutrient resources (a 10-fold difference between the MinF and MaxF food treatments) allowed to determine that temperature changes have a greater impact on the sexual induction of hermaphroditic species of the hydras than food resources.

In addition, it appeared that poorly known for sexual reproduction, *H. circumcincta*, similarly to *H. vulgaris*, reacts with sexual induction on both rise and drop in temperature. Therefore, these species cannot be classified as "cold-crisis" or "warm-crisis" (Burnett 1973), so they remain as "unspecified" species. The green hydra *H. viridissima*, has been recognized as a "warm-crisis" species in both field and laboratory research. The sex ratio in the three hermaphroditic species studied depended on environmental factors: the direction of temperature changes and food resources. In the case of the sequential hermaphroditic *H. vulgaris*, both hermaphroditic and male polyps were observed under an increase in

temperature, and only functional females when the temperature dropped. The co-occurrence of simultaneous hermaphrodites and functional females were noted for *H. circumcincta* in all treatments, with one exception of the treatment with dropping temperature with plenty of food. Under these conditions, both simultaneous hermaphrodites and functional males were observed. In *H. viridissima*, both simultaneous hermaphrodites and males were present in all treatments of the experiment. In the conditions of temperature increase for all tested species of hydras, the ratio of hermaphrodites in the variant with the abundance of food was higher than in the variant with limited food resources. This may indirectly indicate higher costs of hermaphroditism (production of two types of gonads) in comparison to functional females or males.

The most important achievements:

- Demonstrating that sex ratio variability in populations and clones of hermaphroditic hydras in dependence on environmental conditions
- Indicating that previously not described for sexual reproduction *H. circumcincta* is a "unspecified species" (sexually matured in both drop and rise of temperature)
- Demonstrating that sex-dependent reproductive costs seem to be a general rule in hydras. In the species *H. circumcincta* and *H. viridissima*, the costs of sexual reproduction in the hermaphrodites are higher compared to males.

***(3) In the populations of brown hydra (Hydra oligactis) the sex ratio changes according to the characteristic, recurrent pattern - the cause is the female delayed maturation compared to males***

Results presented in the paper:

Kaliszewicz A. 2018. Sex ratio patterns and trade-off between sexual and asexual reproduction in the brown hydra. *Freshwater Science* 37: 551–561.

Under conditions of temperature drop occurring in autumn (October-November) in temperate climate, polyps induced for sexual reproduction appear in natural populations of *H. oligactis*. I observed that regardless of the population, the sex ratio in the populations of *H. oligactis* varies during the sexual season according to a repetitive pattern. The research was carried out on populations coming from three sites in Poland (Dziekanowskie Lake 52°22'N 20°50'E, Habdzińskie Lake 52°05'N 21°09'E and Jeziora River 52°05'N 21°08'E). In all cases, first the induced males appeared. Then induced females appeared in the population about 7-14 days after the appearance of mature males. The time of appearance of females in the population depended on the year. Over time, the sex ratio in this species was equal, and at the end of the sexual season (November-December) females dominated. Males that had previously induced themselves to sexual reproduction died or resorbed gonads at the end of the season and switched back to asexual reproduction. Thus, mainly sexually mature females with attached zygotes remained in the population. After some time the zygotes separated. Females mostly degenerated and died. Studies have shown that the sex ratio in two of the three study sites was consistent with Fisher's theory and was 1: 1. In the third site (Habdzińskie Lake), no induced females were observed, only sexually mature males were present. Sex in the brown hydra is genetically determined. Females as a result of budding produce female clones, while male clones produce males. The reason for the lack

of sexually induced females may be a small number of female clones or their lack in the third site (a small lake with an area of 5.5 ha). The laboratory experiment showed that female polyps under conditions of high food resources reproduced asexually at a comparable rate as male polyps. The situation changes under conditions of limited food. With a small amount of food, the female clones reproduced asexually significantly slower than male – the budding rate of a female polyp is lower than male polyp. The hypothesis that may explain the lack of females in the third site concerns the consequences of food shortages, which over time may have had more negative impact on the number of female than male clones. This can be deduced from the data on the density of the hydras. In the season of asexual reproduction, the density of hydras per 100g of plant dry matter was 13 times and 2281 times lower respectively in Habdzińskie Lake (1942 hydras/100g of dry matter of macrophytes) compared to Dziekanowskie Lake (25533 hydras/100g of dry matter of macrophytes) and the Jeziorka River (4430000 hydras/100g of dry matter of macrophytes).

The pattern of changes in the sex ratio of the brown hydra in two sites (Dziekanowskie Lake and Jeziorka River) was observed over several years of research. Therefore, the presented results can be referred to as a repetitive and not an accidental phenomenon. It seems important to ask why the *H. oligactis* females induce themselves later than males - this strategy is repeated every year. On the basis of literature data it is possible to exclude later maturation of females, caused by physiological constrains. In order for the spermatogenesis and oogenesis of *H. oligactis* to proceed properly, the same upper threshold temperature 12°C is required (Littlefield 1985, Littlefield et al. 1991). Females therefore do not require a lower temperature than males in order to reach sexual maturity. In my laboratory experiments on induction of sexual reproduction of hydras, males and females producing gonads appeared at a similar temperature (11°C and 10°C, respectively). Oogenesis does not last longer than spermatogenesis. In the population from Dziekanowskie Lake, sexually matured females appeared at the same time (2006, when a sharp drop in temperature by 8°C/10 days was observed) or even up to 20 days later than sexually matured males in the years 2007-2008, when the temperature drop was milder, by 3°C/10 days. The literature data also do not confirm longer oogenesis than spermatogenesis, but rather delayed sexual induction of female-determined polyps (Littlefield 1986). The cause of delayed maturation of females in relation to males does not result from physiological constrains.

The most important achievements:

- Describing the recurrent pattern of sex ratio changes in the gonochoric species *Hydra oligactis*, resulting from delayed maturation of females in relation to males.
- Indication that clones of brown hydra determined as females under conditions of food deficiency increase significantly slower in numbers as a result of budding than clones determined as males. This may affect the sexually mature male dominance observed in some populations of the brown hydra.

***(4) The sexual induction of the *H. oligactis* females, delayed in relation to males, is the result of evolutionary adaptation based on different reproductive costs for each sex and a trade-off between asexual and sexual reproduction.***

Results presented in the paper:

Kaliszewicz A., Lipińska A. 2012. Maturation costs affect maturation timing: sexual reproduction in a heterogonic hydra. *Hydrobiologia* 679: 19-25.

Polyps determined as males or females at the time of switching to sexual reproduction stop budding and statistically significantly increase their body size, compared to polyps that remain asexual. It should be added that not all polyps switch to sexual reproduction during the sexual season. Asexual polyps are constantly present in the population. Under natural conditions when sexual reproduction occur, 21 to 57% of polyps are induced in the brown hydra. Under experimental conditions, the percentage of induced hydras ranges from 17 to 83% of polyps. Sexually-induced males lose 41% of their body size as a result of the production of gonads and females 45%, which indicates the cost of sexual reproduction. Moreover, males produce on average twice (8) as many gonads as females, which suggests higher investment costs for female gonads than male gonads. The number of gonads is also positively correlated with the body size of both females and males. The gonads are clearly visible and easily distinguishable. The laboratory experiment simulating the conditions of the sexual season in the brown hydra (temperature drop from 18°C to 7°C within 28 days and constant temperature until the 78th day of the experiment) was carried out in two food regimes (MinF and MaxF, which differed 3 times in the frequency of feeding). The results showed that females started to produce gonads 2 weeks later than males, which confirms observations from natural populations. Moreover, in the low feeding treatment the percentage of sexually mature females was significantly lower than in the high feeding treatment. No such differences were observed for males. Additionally, in the MaxF treatment, sexually mature females were still present on the 78th day of the experiment, which was not observed in the MinF treatment. Sexually mature males at the same time were present regardless of food treatment. The results indirectly indicated higher costs of sexual reproduction in females than in males of the brown hydra.

Females of the brown hydra have the higher costs of switching from asexual to sexual reproduction compared to males. A laboratory experiment on males and females that have already started maturation, transferred from the natural environment to the laboratory and acclimatized to a higher temperature appropriated for asexual reproduction has shown that the costs of switching back to asexual reproduction in females are significantly higher than in males. When females are already induced for sexual reproduction, the mortality associated with the switch to asexual reproduction is very high (90%) compared to males (51%) and asexual individuals, which constituted the control group (19%). Both males and females can switch from sexual to asexual reproduction, but in the case of females the switching costs are many times higher. If females have high costs of switching back to asexual reproduction, natural selection should tend to persist individuals who are induced to a clear environmental signal indicating the autumn-winter period, when the temperature remains low for a long period of time, and not as a result of accidental, short-term temperature drops. Since females incur higher switching costs between sexual and asexual reproduction than males, selection will have a stronger impact on one sex. It will be resulted in later induction of females than

males because females respond to more intense or longer lasting temperature changes. This behavior is possible if the hydras are able to distinguish between the direction and strength of the environmental factor that induces sexual reproduction.

The most important achievements:

- Demonstrating that the delayed sexual induction of the *H. oligactis* females compared to males is a result of the higher costs of reproduction and switching between sexual and asexual reproduction. Females are induced by the more intense and longer lasting environmental factor (temperature drop). This is the adaptation to prevent very costly and risky and almost irreversible for females switching to asexual reproduction as a result of an accidental signal from the environment.
- Demonstrating that the production of female gonads in gonochoric *H. oligactis*, similarly to hermaphroditic species, is more expensive than the production of male gonads. It indicates higher costs of sexual reproduction in females and hermaphrodites compared to males.

***(5) Both males and females of H. oligactis can distinguish not only the direction but also the intensity of temperature changes***

Results presented in the paper:

Kaliszewicz A. 2015. Intensity-dependent response to temperature in *Hydra* clones. *Zoological Science* 32: 72-76.

and partly in the paper:

Kaliszewicz A. 2018. Sex ratio patterns and trade-off between sexual and asexual reproduction in the brown hydra. *Freshwater Science* 37: 551–561.

Female and male clones of the brown hydra from Dziekanowskie Lake and Lake Habdzińskie were placed in three different temperature regimes: (1) constant 12°C – threshold temperature for sexual reproduction, (2) gradual - decrease in temperature 1°C /96 hrs. and (3) rapid - decrease in temperature 1°C /24 hrs. The percentage of sexually induced females and males belonging to the similar clones differed significantly depending on the treatment. The highest was in the treatment with a rapid drop in temperature (45% of females from Dziekanowskie Lake and 39% of males from Dziekanowskie and 83% of males from Habdzińskie Lake) and the lowest in the variant in which the temperature was constant (9% of females from Dziekanowskie and 11% and 29% of males, from Dziekanowskie and Habdzińskie Lake, respectively).

The results indicate the ability of the brown hydra polyps, both those determined as females and those determined as males, to distinguish the degree of intensity of temperature changes and to respond appropriately to these changes. In temperate climates, the arrival of the winter period means a lack of food for the hydras, which may result in the death of the animals. (Littlefield et al. 1991). The ability of such simple animals as brown hydras to estimate the direction and intensity of temperature changes indicates the importance of induction of sexual reproduction before the winter season. This ability is also important to avoid costly sexual induction. Too rapid reaction to accidental and short-term temperature

drops, which may then increase, can lead to the death of induced polyps - especially females. Due to the higher costs of sexual reproduction and the higher costs of switching between sexual reproduction and asexual reproduction, females require a clearer environmental signal than males in order to start sexual maturation. This was confirmed by a laboratory experiment lasting 15 weeks and simulating different rates of temperature changes in the range observed in the natural environment. The brown hydras, collected and transferred from the natural population of Dziekanowskie Lake, which during the first 3 weeks were exposed to sharp temperature changes (from 15°C to 4°C), were sexually induced in a larger number than polyps placed in the moderate treatment (from 15°C to 7°C) and with a mild drop in temperature (from 15°C to 8°C). In the treatment with a sharp drop in temperature, sexually induced males and females appeared 7 to 14 days earlier than in the treatment with a mild drop in temperature. The difference between the percentage of sexually induced males in treatments with sharp and mild temperature drop was smaller than in the case of females. Females required an intense and longer cue from the environment and responded in greater numbers if the temperature drop was more intense. In all three treatments sexually matured females appeared 5-9 days later than males but in the treatment with a sharp temperature drop in a higher number. The response that depends on the intensity of the factor, has been previously only sporadically documented in animals with a more complex structure than in hydras, such as insects, fish and birds. (Shirakashi i Goater 2002, Lehane 2005, Wiltschko et al., 2007). It should be assumed that the effect of intensity of environmental factors on the behavior of animals is stronger than it seemed so far.

The most important achievement:

- Demonstrating that an organism with such a simple structure of the nervous system as the brown hydra (*H. oligactis*) is able to assess the intensity of changes in the environmental factor and adapt the time to induce sexual reproduction

***(6) The trade-off between sexual and asexual reproduction in hermaphroditic species, such as H. viridissima, is not as strong as in the gonochoric H. oligactis***

Results presented in the paper:

Kaliszewicz A. 2011. Interference of asexual and sexual reproduction in the green hydra. Ecological Research 26:147–152.

Polyps of the brown hydra at the moment of sexual induction stop producing buds and start production of gonads only. Such separation of the two types of reproduction in time is not the rule in hydras. Hermaphroditic species, especially those classified as "warm-crisis" do not interrupt the production of asexual offspring when maturing (Brien i Reniers-Decoen 1950, Burnet i Diehl 1964). The scale of the overlap between the two types of reproduction was examined on the example of the green hydra *H. viridissima*. This species is characterized by having endosymbionts, green algae of the genus *Chlorella*, that provide polyps with carbohydrates produced as a result of photosynthesis, an additional source of energy. (Kanaev 1952). Polyps of the green hydra, collected from a natural habitat (Jeziorka River 52°05'N 21°08'E) during the breeding season of this species (May-June), were grouped depending on the induction and type of gonads produced on: (1) asexual, (2) simultaneous

hermaphrodites, (3) functional males and (4) functional females. The latter were the least (about 10%) and appeared at the end of the sexual season. Polyps functioning as males did not interrupt the production of buds and produced as many of them (up to 5 buds at the same time) as polyps, which remained asexual. The analysis of body size of polyps and the number of offspring buds created by them revealed a positive correlation between body size and the number of produced buds in functional males and asexual individuals. Due to the natural shrinkage of living hydras I did not measure the length of polyps but I introduced the body surface measurement according to the proposed equation  $A_H = \pi \cdot w \cdot l$ , where  $w$  is the width (mm) at its widest point and  $l$  is the length of the polyp (mm) measured without tentacles. Such a method of body size measurements allowed for higher accuracy and repeatability in comparison to body length measurements, which, depending on the degree of extension of the polyp, may change several times.

Simultaneous hermaphrodites, unlike functional males, produced only one bud and were less numerous (16%) than polyps, which remained asexual (31%). Functional females did not produce any buds. The production of buds involves the need to invest energy. The fact that hermaphrodites and functional females limit or cease the production of buds indirectly indicates the high costs of female gonad production. This is also confirmed by the fact that both functional females and hermaphrodites are able to produce only one oocyte per sexually propagation season. On the other hand, the production of buds by functional males takes place at the same rate as in asexually polyps. There is also a similar, positive correlation between the number of buds and body size, which indicates the low cost of producing male gonads. It should be noted that reproduction costs depend on gender - this applies to both hermaphroditic and gonochoric species. This conclusion is confirmed by the results obtained by me for *H. circumcincta*, *H. oligactis* and *H. viridissima*. Higher reproductive costs in females compared to males were also described for other animal species, e.g. polychaetes, fish, reptiles (Berglund 1986, Berglund et al. 1986, Hendry i Berg 1999, Madsen i Shine 2000, Okuda 2001, Hayward i Gillooly 2011)

#### The most important achievements:

- Indicating that the trade-off between sexual and asexual reproduction in hermaphroditic species is not as strong as in the gonochoric *H. oligactis*. In the symbiotic green hydra *H. viridissima* both sexual and asexual types of reproduction interference, especially in males in whom sexual maturity and gonad production do not limit the rate of budding
- Introducing the measurement of the size of the hydra's polyps based on the surface, not on the length of the body



**(7) Asexual reproductive traits depend on the *Hydra* species and clone**

Results partly presented in the papers:

Kaliszewicz, A., Lipińska A. 2013. Environmental condition related reproductive strategies and sex ratio in hydras. *Acta Zoologica* 94: 177–183.

Kaliszewicz A. 2011. Interference of asexual and sexual reproduction in the green hydra. *Ecological Research* 26:147–152.

Kaliszewicz A. 2018. Sex ratio patterns and trade-off between sexual and asexual reproduction in the brown hydra. *Freshwater Science* 37: 551–561.

The high variability of the sexual reproduction modes of the hydras seems to contrast with one type of asexual reproduction strategy common to all species - budding. The research conducted by me and presented in the articles above also included traits related to asexual reproduction. The results showed that the individual species of the hydras are distinguished by many traits associated with this type of reproduction. Significant differences concern on the one hand the rate of budding and on the other hand the size of offspring buds. These traits clearly depend on the size of the body. Larger species, e.g. *H. vulgaris*, reproduce asexually slower but produce larger buds, while smaller hydras, e.g. *H. circumcincta* have a higher rate of budding and smaller buds. The highest rate of asexual reproduction has been reported for the symbiotic green hydra *H. viridissima*, which is also indicated by previous literature describing the green hydra as a species with a high rate of growth and a rapid rate of production of asexual buds. (Loomis 1953; Stiven 1965).

The species of hydras studied by me produce at the same time a different number of buds. Most of them, five, can be observed on the polyps of the green hydra. In other hydra species one to three visible buds are observed. The distance from the settlement of the young polyps to the mother polyp also depends on the species. The least mobile are polyps of *H. circumcincta*, compared to *H. vulgaris* and *H. viridissima*. In the latter species, the temperature had a positive effect on the distance of settlement of the offspring buds.

In the case of the gonochoric *H. oligactis*, the rate of budding depended on the sex of the clone (whether male or female), the food resources and the habitats from which the individual polyps originated. High variability between clones, e.g. in body size, has been described in the literature for different species of hydras (Bossert 1987). According to the available data, my studies seems to be the first that documents the differences in the rate of asexual reproduction depending on the sex of the clone of gonochoric *H. oligactis*.

The most important achievement:

- Demonstrating that, despite one common strategy of asexual reproduction for all species of the hydras – budding, the individual species and their clones, depending on the determined sex, differ in many of the traits associated with this type of reproduction.

## THE POSSIBILITY OF A WIDER USE OF THE RESULTS

The presented achievements in relation to the favorable reproductive strategies of the hydras and the trade-off between the two types of reproduction can be extended to other species of animals capable of asexual and sexual reproduction. They constitute a significant group of invertebrate animals, including parthenogenetic species, representatives of as many as 8 taxonomic types have the ability to reproduce in two ways. The modular approach of the individual used in my research and the results of the model, confirmed in field and experimental studies, show how important are the correct initial assumptions in evolutionary research. Examination of optimal strategies and traits of life history is based mostly on the concept of the individual. Its proper definition is therefore extremely important. The modular approach has so far been used primarily in plant and colonial invertebrates, e.g. sponges and corals. My application of the modular approach to clonal animals, whose modules are not colonial, allowed me to explain the persistence of the high plasticity of the reproductive strategies of the hydras. This modular consideration of an individual may be extended to other species capable of asexual reproduction, the modules of which are separated. These include individual species of anemones, flatworms, ribbon worms, polychaetes, oligochaetes, starfish and brittle stars. If we extend the list by species with apomictic parthenogenesis, we can add rotifers, cladocerans and aphids. Analysis of the strategy of these animals in a modular approach could lead to new, interesting results, especially with the use of mathematical modelling.

The *modular reproductive effect* introduced on the example of the hydras can be useful for the analysis of optimal reproductive strategies of hermaphroditic modular species, which is characterized by high plasticity of reproductive strategies. Two aspects of possible changes in reproductive strategies, consisting of *modular reproductive effect*, can be used to understand the diversity of strategies of animals such as selected species of cnidarians, flatworms and polychaetes. If there are different sexual reproduction strategies of individual modules (functional hermaphrodites, females or males) within a clone then the *modular reproductive effect* will allow the correct analysis of strategies beneficial for the reproductive success of the individual and increase the knowledge about the mechanisms of sex allocation.

### 5. Discussion of other scientific achievements

#### ***Different predator contra prey strategies - ability to receive chemical signals and react to them in hydras and in oligochaetes from the family Naididae***

Original papers concerning the presented results:

Kaliszewicz A 2003. Sublethal predation on *Stylaria lacustris*: a study of regenerative capabilities. *Hydrobiologia* 501:83–92

Kaliszewicz A, Johst K, Grimm V, Uchmański J 2005. Predation effects on the evolution of life-history traits in a clonal oligochaete. *Am Nat* 166:409–417

Kaliszewicz A, Uchmański J 2009. A cross-phyla response to *Daphnia* chemical alarm substances by an aquatic oligochaete. *Ecol Res* 24:461–466

Kaliszewicz A, Uchmański J 2009. Damage released prey alarm substances or predator odours? Risk assessment by an aquatic oligochaete. *Hydrobiologia* 618:57–64

- Kaliszewicz A. 2013. Is larger better in sit-and-wait predators? Competitive superiority in Hydra. *Hydrobiologia* 714:105–114
- Kaliszewicz A. 2015. Conspecific alarm cues induce an alternative reproductive strategy in aquatic oligochaetes. *Limnology* 16: 85-90.
- Kaliszewicz A. Gołębiewska A. 2017. Detection ability and response of *Hydra* to the presence of conspecifics. *Fundamental and Applied Limnology* 190:309-317.

The presented papers refer to the effect of predation on life strategies of prey (I started this research before my doctorate) and intra-species competition in predators "sit-and-wait" tactics, such as hydras or freshwater larvae of some insects. I have shown that predation has a sublethal effect on aquatic oligochaetes of the family Naididae - 45% of individuals survive an attack. After the predator's attack, the oligochaetes effectively regenerated damage and missing parts of the body. Sublethal predation turned out to have a long-term effect on the traits of life strategies of oligochaetes, first of all on the proportion of paratomic fission in those animals able to reproduce asexually. The individual-based model constructed on the basis of real data of *Stylaria lacustris* has shown that optimal strategy is production of the longest possible offspring, which leads to an almost equal proportion of the fission observed in these oligochaetes in nature. This increases the chance of survival of an attack of invertebrate predator, e.g. Zygoptera dragonflies larvae and effective regeneration of damage - the lethal effect of predation decreases in these animals as the body length increases. Oligochaetes of the family Naididae are also able to detect chemical signals released as a result of injury of conspecifics and heterospecifics. These substances, often defined as chemical alarm signals, indicate the presence of a predator close to potential prey. Two species of oligochaetes *Stylaria lacustris* and *Nais christinae* responded with alternative reproductive strategies to the presence of chemical alarm signals released by individuals of their species. The studied oligochaetes increased the rate of fission and produced as a result of larger descendants, which correlated with the results of the individual-based model. The presented results are described in the article: Kaliszewicz A. 2015. Conspecific alarm cues induce an alternative reproductive strategy in aquatic oligochaetes. *Limnology* 16: 85-90, for which I received the Best Paper Award from the Japanese Society of Limnology in 2016.

*Stylaria lacustris* also responded by increasing the fission rate to chemical alarm signals from other species belonging to a different taxonomic group, such as the *Daphnia magna* cladoceran, which may be prey to the same predators, i.e. hydras and dragonfly larvae.

I have also shown that predatory invertebrates such as hydras react to the chemical presence of conspecifics - this could be a signal of increased competition. The green hydra (*H. viridissima*) reacted with twice increased induction of sexual reproduction in the presence of conspecifics, although this did not affect the living conditions (level of available oxygen in the water, accumulation of carbon dioxide and metabolites). Induction of sexual reproduction is considered to be a strategy for survival of difficult conditions, e.g. drought or lack of food. In their natural environment, hydras can occur at high densities, often located close to each other, forcing them to compete for food. Studies of direct competition for food between polyps of different clones and species of hydras revealed that more competitive are not those polyps that are larger but those that have more penetrants - the largest type of cnidom. Penetrants are directly involved in capturing prey and their number depends on the

*Hydra* species and clone. Polyps with a higher number of penetrants, located mainly in tentacles, are able to capture a prey organism more effectively and attract it to their mouth even if they compete with larger polyps able to catch the same prey organism. In the case of *sit-and-wait* predators, structures that are directly involved in catching prey have a significant impact on the success in intraspecific and interspecific competition for food.

***The movement of selected freshwater and marine cnidarians depends on their reproductive strategies***

Original papers concerning the presented results:

Kaliszewicz A., Panteleeva N., Olejniczak I., Boniecki P., Sawicki M. 2012. Internal brooding affects the spatial structure of intertidal sea anemones in the Arctic-boreal region. *Polar Biology* 35: 1911-1919.

Kaliszewicz A., Dobczyńska O. 2017. A comparative study of mobility in three *Hydra* species with different reproductive strategies. *Israel Journal of Ecology and Evolution* doi: 10.1080/15659801.2016.1276426

Both hydras and sea anemones are little mobile organisms. Sea anemones living in the tidal zone of the littoral often apply the strategy of internal brooding and the release of fully formed young anemones. Studies carried out on two species, *Aulactinia stella* and *Urticina crassicornis*, which follow this strategy and settle in the littoral of the Barents Sea, revealed that young anemones settle close to the mother specimens, thus forming aggregations. In aggregation, larger anemones of the offspring are located at a greater distance from the parent than small ones. Aggregations of both species usually consist of sea anemones of similar coloring which would suggest that *U. crassicornis*, like *A. stella*, reproduces asexually, but so far this has not been clearly documented. The strategy of internal brooding limits dispersion, but in the case of a harsh environment such as the tidal zone, it allows for the settlement of the offspring next to the mother animals, which survived in sites providing shelter from wave action.

Hydras are considered to be little mobile animals and there has been no mention so far that their ability to move is significantly different and depends on the species and reproductive strategy. In case of hydras, the movement of polyps may be caused by unfavorable conditions, e.g. lack of food (Łomnicki i Slobodkin 1966). My research indicated that the mobility of the hydras is natural and depends on the species and reproductive strategy and not on the size of the polyp body. Polyps of *Hydra circumcineta*, which is a simultaneous hermaphrodite with the ability to self-fertilize, showed less mobility than polyps of gonochoric *Hydra oligactis* and sequential hermaphrodites *Hydra vulgaris*. The most mobile polyps of *H. vulgaris* were able to move to an average distance of 20 mm over a 24-hour period at 22°C.

***Adverse effect of unsaturated omega-3 fatty acids on survival and life strategies of the hydra***

Original papers concerning the presented results:

Kaliszewicz A., Jarzabek K., Szymańska J., Karaban K., Sierakowski M. 2018. Alpha-linolenic acid, but not palmitic acid, negatively impacts survival, asexual reproductive rate, and clonal offspring size in *Hydra oligactis*. *Lipids* doi: 10.1002/lipd.12026.

In recent years I have undertaken research on the importance of saturated and unsaturated fatty acids in the diet of aquatic and terrestrial invertebrates. The research was conducted on invertebrates with different nutritional strategies. Preliminary results show that omega-3 fatty acids, mainly  $\alpha$ -linolenic acid (ALA), which is essential to most animals, despite the widespread positive opinion, do not always have a positive effect on the growth and survival of invertebrates. Studies on hydras, which are predators, have shown that omega-3 fatty acids can even have a negative impact on survival, the rate of asexual reproduction and the size of the body of offspring' polyps, as I have proved on the example of *Hydra oligactis*. The negative effect of omega-3 fatty acids on the life history of simple invertebrates has not yet been documented. My findings suggest that hydras are not capable of converting  $\alpha$ -linolenic acid to EPA and DHA, which are essential for the proper functioning of cell membranes, metabolism of fatty acids, cellular signaling and gene expression (Adkins i Kelley 2010). Research on the effects of unsaturated (omega-3, omega-6, omega-9) and saturated fatty acids on the life-history traits of freshwater, marine and soil invertebrates is currently being continued by me to determine the real role of these acids and their importance for various trophic groups.

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