

Review

# Knowing the Enemy: Inducible Defences in Freshwater Zooplankton

Patricia Diel <sup>1,†</sup>, Marvin Kiene <sup>1,†</sup>, Dominik Martin-Creuzburg <sup>2</sup>  and Christian Laforsch <sup>1,\*</sup>

<sup>1</sup> Department of Animal Ecology, University of Bayreuth, Universitätsstrasse 30, D-95447 Bayreuth, Germany; patricia.diel@uni-bayreuth.de (P.D.); marvin.kiene@uni-bayreuth.de (M.K.)

<sup>2</sup> Limnological Institute, University of Konstanz, Mainaustrasse 252, D-78464 Konstanz, Germany; dominik.martin-creuzburg@uni-konstanz.de

\* Correspondence: Christian.Laforsch@uni-bayreuth.de

† These authors contributed equally to this work.

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**Abstract:** Phenotypic plasticity in defensive traits is an appropriate mechanism to cope with the variable hazard of a frequently changing predator spectrum. In the animal kingdom these so-called inducible defences cover the entire taxonomic range from protozoans to vertebrates. The inducible defensive traits range from behaviour, morphology, and life-history adaptations to the activation of specific immune systems in vertebrates. Inducible defences in prey species play important roles in the dynamics and functioning of food webs. Freshwater zooplankton show the most prominent examples of inducible defences triggered by chemical cues, so-called kairomones, released by predatory invertebrates and fish. The objective of this review is to highlight recent progress in research on inducible defences in freshwater zooplankton concerning behaviour, morphology, and life-history, as well as difficulties of studies conducted in a multipredator set up. Furthermore, we outline costs associated with the defences and discuss difficulties as well as the progress made in characterizing defence-inducing cues. Finally, we aim to indicate further possible routes in this field of research and provide a comprehensive table of inducible defences with respect to both prey and predator species.

**Keywords:** aquatic ecology; behavioural defences; diel vertical migration; freshwater zooplankton; inducible defences; kairomones; life–history defences; morphological defences; predator–prey interactions

## 1. Introduction

Community diversity is greatly influenced by a variety of selection pressures, one of which is predation (e.g., [1–4]). To increase their fitness, prey species have evolved a variety of defensive mechanisms [5–9]. In general, defences are established as either constitutive or inducible. Constitutive defences are the result of a constant predation pressure, whereas inducible defences are expressed in response to a variable, but at times strong predation risk. The cue signalling the presence of a predator should be reliable and the induction of the defence linked to costs that exceed the benefit in the absence of the respective predator [7,9]. The ability of organisms to form inducible defences in response to environmental changes is based on phenotypic plasticity, i.e., the ability of a genotype to express different phenotypes [10,11]. While immobile plants tend to profit from inducible physiological and morphological defences [8], mobile animals additionally express inducible defences concerning behaviour and life-histories [12]. In freshwater communities, inducible defences have been extensively studied and numerous examples have been documented, highlighting their potential to modulate interactions between organisms and to shape food web processes [13]. Zooplankton are key to transferring carbon and energy from primary producers to higher trophic levels and inducible defences

in zooplankton may thus crucially influence trophic cascades and the diversity of species [4,14]. Throughout the past 50 years, inducible defences were studied in various taxa of zooplankton across the globe (e.g., [15–19]).

Particularly relevant for the induction of defences are chemical cues, so-called kairomones. These are semiochemicals, which predators release unintentionally, signalling the presence of a respective predator to its prey. Generally speaking, they are advantageous for the receiver and disadvantageous for the emitter [20–23]. The phenomenon of thusly induced defences is expressed in fascinating and often striking changes in morphology, life history, and behaviour of various zooplankton species (e.g., [24–31]).

In 2003, Lass and Spaak reviewed inducible antipredator defences in plankton, which is the basis for this review. The studies then, as well as today, predominantly featured species of the genus *Daphnia* (Branchiopoda: Cladocera), important model organisms in ecology, evolutionary biology, and ecotoxicology. *Daphnia* are characterized by relatively short generation times and cyclical parthenogenesis, i.e., they shift between asexual and sexual reproduction. Under favorable conditions, *Daphnia* typically reproduce asexually, rendering all offspring as clones of their mother, which is a great advantage for ecological and evolutionary experiments. Furthermore, some of its species have fully sequenced genomes [32,33]. Results obtained in laboratory studies on these organisms are crucial for reconstructing and understanding ecological processes in nature [34–36].

In this review, we aim to draw attention to the recent progress that has been made in the basic research on inducible defences in freshwater zooplankton. We summarize newly discovered defences as well as aspects that may influence defence induction or expression. We highlight the complications that accompany attempts to design and compare experiments, with special attention to multipredator setups. Additionally, we will discuss recent findings about costs of inducible defences and highlight recent progress in identifying and characterizing defence-inducing cues. However, we do not focus on the evolution, evo-devo, nor genetic and molecular mechanisms underlying inducible defences in zooplankton as they have been reviewed already by Stollewerk [37] and more recently by Weiss et al. [38]. Finally, we point out possible future directions of research and provide a comprehensive table of recent studies (since 2003) on inducible defences in zooplankton (Table A1).

## 2. Inducible Defences

Induced changes in behaviour allow the prey to respond almost instantly to an appearing predation threat. Additionally, behavioural changes are easily reversible if the predator vanishes. Thus, changing the behaviour in response to increased predation risk may be the most beneficial defence strategy in terms of cost–benefit trade-offs. However, behavioural defences of freshwater zooplankton are often complemented with other defences. Firstly, prey can reduce the predation impact by life-history adaptations that counteract the predator’s hunting or feeding strategy or compensate for population losses. Secondly, the expression of morphological defences may reduce predation losses as these morphological changes may interfere with the catching and/or feeding process of the predator or may prevent an attack. However, despite a sometimes high genetic variation of traits (e.g., [39–41]), freshwater zooplankton prey show a variety of inducible defences in different traits, between species and between clones. The reasons for this variance may be manifold. Besides natural conditions that might influence the expression of defences (see further below), induced defensive responses might differ according to the species- or clone-specific vulnerability at a certain life stage, with respect to a specific, present predator regime (e.g., [42–45]). A high variance in the temporal and structural alternation of defences within a population with mixed reaction norms, might secure the population’s endurance in nature. It may reduce individual costs of defence expression, and additionally provide an array of defences against various predators or other threats (e.g., low food or changing temperatures). Thus, a high variance makes the extinction of the entire population less likely (e.g., [42,46,47]). In the following sections, we will highlight new findings and newly discovered aspects of inducible defences in freshwater zooplankton, as well as point out some examples of variation between species and clones.

### 2.1. Behavioural Defences

The phenomenon of diel vertical migration (DVM) is a well-known defensive behaviour found in a variety of aquatic invertebrates (e.g., [48–51]). It has been studied in cladocerans for more than one century [52,53]. During DVM, the prey migrates periodically up and down in the water column to avoid well-lit water layers and thus also visually orientated predators (e.g., fish), or in an opposite direction to the predator, i.e., reversed DVM, avoiding night-hunting phantom midge larvae (*Chaoborus*). A reversed DVM may also provide protection against hunting strategies of both predators (fish and *Chaoborus*) when fish show a similar migration pattern to that of *Chaoborus* [54]. Even without prior exposure to a predator, *Daphnia* are capable of responding to the appearance of a new predator with DVM, as has been shown for the invasive predator *Bythotrephes* [55]. This may indicate a general capacity to respond to introduced predators or a similarity of predator cues within a predator guild (e.g., invertebrates). Nevertheless, studies show ambiguous results for zooplankton species exhibiting DVM only under certain predator regimes. Some respond to *Chaoborus*, some to fish, and others to both, while some do not exhibit DVM at all (e.g., [44,56–58]). Within the past 17 years, diverse factors have been found to impact DVM, rendering this behaviour a good example of the extraordinarily high complexity of inducible defences in zooplankton.

There are three factors that have been found to specifically affect DVM and that are highly linked with seasonal variation throughout the year: light, food, and temperature. The rate of change in light intensity (i.e., at dusk or dawn) is an important proximate factor controlling DVM [59] to avoid predator encounters. Thereby, a high rate of change in light intensity increases the migration velocity (downwards when light intensity increases, upwards when light intensity decreases). The slower the change in light intensity is, the slower is the vertical movement of the daphnids, until they stay at a certain depth [59]. This pattern of accelerated movement under increased rate of change in light intensity was also found with increased UV-radiation, which led to a prolonged sojourn of *Daphnia* in deeper water, because they reach the deep water earlier and start migrating upwards later [60,61]. Additionally, young daphnids have been shown to respond more strongly than adults to UV-radiation [62–64], which has been reported for predator avoidance by DVM as well [44,61]. Despite this, zooplankton is able to increase pigmentation to protect itself against UV-radiation (see further below) [33,65,66]. Thus, the ultimate factor for DVM in response to both UV-radiation and light intensity is the increase in predation risk due to increased visibility to visually hunting predators.

At low food concentrations, while under fish exposure, *Daphnia* show a tendency to stay in upper water layers, where food is more abundant and the temperature is higher [49,59]. This risky behaviour is not found at high food densities, suggesting that food availability is an important factor with respect to DVM [49]. The low temperature in deeper water layers, resulting in a slowdown of development, has been proposed to be an important cost factor of DVM [67]. It seems, however, that *Daphnia* are more likely to move to deeper, low-temperature water layers at high food densities [67]. Therefore, *Daphnia* trade a short development time for safety in the deep only under sufficient food supply. Besides food quantity, food quality, mediated by primary producers [68–71], has been shown to affect the strength of DVM and maybe also the capability to perform DVM [72,73]. Laboratory experiments with *Daphnia* and vertebrate predators suggest that the amplitude of DVM and the capacity to cope with DVM-related temperature fluctuations is affected by the availability of long-chain polyunsaturated fatty acids (PUFAs) in phytoplankton [74–76]. *Daphnia*, similar to most other animals, lack the capacity to synthesize PUFAs de novo and thus rely on an adequate dietary PUFA supply. PUFAs play an important role in membrane temperature adaptation [77] and seem to be crucial for the performance at low temperatures [78]. Thus, the capability to cope with the low temperatures found in deeper water strata may depend on an adequate dietary PUFA supply in the upper water layers [72,73], i.e., the presence of PUFA-rich phytoplankton species. The potential of PUFAs to constrain DVM under field conditions remains to be studied.

On the one hand, food and temperature are crucial for the growth and development of zooplankton. On the other hand, a response to light and UV-radiation may comprise a trade-off between protection

against UV-radiation (e.g., by pigmentation) and the increase in vulnerability (due to increased visibility) to visually hunting predators [33,65,66]. Winder et al. [60] proposed that temperature and food abundance modulate the depth selection in *Daphnia*, while predator kairomones and UV-radiation modulate the timing of the DVM (i.e., synchronizing with dusk and dawn), emphasizing the importance of considering these factors in experiments.

Besides light, food, and temperature, other factors have been found to impact DVM, one of which is competition. Gliwicz et al. [79] showed that distribution patterns of *Daphnia* are also influenced by cues released by prey during crowding (high density of organisms per unit of water). The authors hypothesized that daphnids seek refuge in deeper water layers with lower population densities to profit from higher per capita food concentrations. Adamczuk [80], as well as Dawidowicz and Wielanier [81], also proposed a change in depth-selection due to competition for food, where large species that exhibit DVM lose competitive superiority over small, nonmigrating species [81]. However, those might be more susceptible to fish predation, as indicated by the results of a field study investigating the gut content of young perch, which revealed that only smaller prey individuals (<1.75 mm) had been eaten [82]. Nevertheless, depending on the size of predatory fish, it might be beneficial for the prey to suspend DVM, to benefit from access to higher food levels throughout night and day. Thus, the depth distribution of the prey may be additionally based on individual prey size [83], and it is either beneficial to grow small to be visually inconspicuous or to grow large to escape the preferred size range of the predator. Therefore, competition for food and individual prey size might modulate the vertical distribution pattern of zooplankton under size-selective predation pressure.

As demonstrated by Gélinas et al. [82] with young perch, not only the prey size but also the predator size seems to matter for the expression of DVM. Evidence for this has been shown by Young and Riessen [84] in mesocosms and by Lagergren et al. [26] in a field study, both suggesting that *Bosmina* and *Daphnia* species are flexible in their depth-selection, depending on the size and larval instar of two *Chaoborus* species. During times when third instar larvae of larger *Chaoborus* species or fourth-instar larvae of smaller *Chaoborus* avoided the surface layer up to 1 m depth, the cladocerans used this water layer as a refuge. At times when fourth instar larvae of smaller *Chaoborus* species or third instar larvae of larger *Chaoborus* were hunting at this depth, prey organisms avoided this water layer to evade their predators. Depth selection of *Chaoborus* larvae in nature is commonly related to fish predation. However, in the mesocosm experiment of Young and Riessen [84], where daphnids responded to differently sized *Chaoborus* species, no fish were present. Hence, cladocerans seem to be capable of responding even to larvae of different *Chaoborus* species, and/or to larvae at different developmental stages [26,84]. The potential recognition of predator size by the prey is in concordance with a study on crayfish, showing that crayfish are able to respond differently to specific predator sizes [85], pointing towards a high complexity of defence-inducing cues (see below). Thus, it is reasonable to assume that such a mechanism for predator-size-specific responses also evolved in other species such as freshwater dwelling zooplankters. Therefore, future studies should include predator size and developmental stage to get a more detailed insight into predator-induced DVM.

Instead of DVM, some zooplankton species exhibit horizontal migration (e.g., [86,87]), which may be the same response as the so-called habitat selection [88,89]. Daphnids as well as mysids select habitats with less vegetation, meaning open water, when exposed to kairomones of damselfly larvae (i.e., *Ischnura*), since these are ambush predators hiding in the vegetation [88,89]. In contrast, they avoid open water in the presence of *Chaoborus* larvae [88], which are ambush predators that occur mainly in the epilimnion, and seek refuge in littoral waters with macrophytes, even though *Daphnia* seem to prefer sediment instead of macrophytes [90]. These findings further indicate that the prey is capable of sensing or estimating where predators are present or hunt, and where predation risk is low. In this context, Gutierrez et al. [91] showed that *Ceriodaphnia dubia* avoids places of predatory cue origin. Likewise, species of the rotifer *Brachionus* increase the propensity of surface attachment, among others on the carapace of *Daphnia*, when exposed to the predatory rotifer *Asplanchna*, the first record of inducible behavioural defences in rotifers [92].

Alertness [93] is regarded as another inducible defensive behaviour. Individuals with increased alertness show faster evasion responses [93] and increased swimming speed [94]. The latter seems to be an effective precapture defence [58,94–96], for which copepods seem to be more optimized in comparison to cladocerans due to their elongated and streamlined body shape [91]. Nevertheless, predation trials, using a hydraulic apparatus, showed the effectiveness of evading or escaping the predator of fish-induced individuals of both cladocerans and copepods in comparison to their respective noninduced control [58]. Chang and Hanazato [95] hypothesized that the size of the prey positively correlates with the escape efficiency. They observed an increase in powerful strokes under predator exposure in *C. reticulata* and two *Daphnia* species (*D. ambigua* and *D. pulex*). These strokes allowed the prey to escape the predator by swimming faster and to tear themselves away from the predator even after being caught. The larger the preys' size, the higher was the escape efficiency. However, whether this is due to stronger strokes, or some other functional differences (e.g., gape-limitation of the predator), some of which are mentioned below, remains unclear.

Szulkin et al. [97] reported uniformity in swimming speed, hop and sink rate, and swimming angle induced by kairomones of fish and *Chaoborus*. The authors state that this might be an adaptation to reduce the detectability of individuals by the predator. As this similarity in movement was also exhibited in isolated individuals, the authors conclude that this response is based on individually perceived cues rather than a consequence of swarming behaviour. This uniformity in movements among individuals within a prey group may hamper the fixation on one particular prey item, thus confusing visually hunting predators.

Instead of increasing swimming speed, the exposure to kairomones can also trigger a decrease in activity, which may act as a pre- or a postcapture defence. Studies have shown a decrease in feeding and an increase in respiration rate in cladocerans exposed to predator cues [23,98,99]. While the latter might be a general physiological response to stress, the former may reduce the detectability and probability to encounter a predator (precapture), due to decreased activity in the upper water stratum. The dead-man-response has been reported as a postcapture defence [100]. This sudden motionlessness has been shown to be an effective survival technique applied by *Bosmina* against copepod predators [95].

In addition to behavioural defences that are directly linked to predator avoidance or evasion, mating behaviour is also influenced by predator presence. Male daphnids usually fight against other males, which occurs more often when sexually reproducing females are present [101]. Sexually reproducing females carry resting eggs instead of parthenogenetically produced eggs. When exposed to fish kairomones the males fight less amongst each other, and the mating rate increases. Furthermore, the males tend to attach more often to sexually reproducing females under predator exposure [101]. This increase in potentially successful mating may enhance sexual reproduction and thereby the adaptation to a changing environment.

A more offensive, inducible defensive behaviour has been observed by Sarma et al. [102]. When preyed upon by the worm *Aeolosoma*, cladocerans, especially *Simocephalus serrulatus*, exert defensive use of their postabdominal claw to prevent the worms from invading their brood chambers to feed on their eggs. This even led to fatal injuries of some worms. As the worms feed on algae as well, the authors hypothesized that this is not only a behavioural defence, since the putative prey may even feed on the disrupted tissue of the worms [102].

## 2.2. Morphological Defences

Many species of freshwater zooplankton have evolved inducible morphological defences, which act during various stages of the predation cycle, mainly postcontact [9,103]. These defensive structures generally evolved in response to specific predation regimes. They are bound to specific predator density schedules during the year in nature and have therefore also been described using the term cyclomorphosis (e.g., [12,18,104–106]). Inducible morphological defences show great variance among prey species and clones, according to the predatory regime of the prey-organism to which the prey adapted through previous encounters [107–109]. In the decades prior to the review by Lass and

Spaak [17], many inducible morphological defences in response to fish were discovered in freshwater zooplankton. Some larger zooplankton species were found to reduce their body size but elongate their tail spine in response to visually hunting fish of a relatively small size [21,104,110]. In contrast, smaller zooplankton prey species do not show a general pattern of reduction in body size, but they enlarge or reshape body parts, like their antennulae, head and tail spines, or helmets, develop specific defensive structures such as *neckteeth*, and even change the appearance of their entire body to increase the survival rate in the presence of a specific invertebrate predator [15–19,104,110]. According to Dodson [104], these inducible morphological defences against invertebrate predators, might act via an “antilock and key mechanism”. His theory suggests that induced morphological defences of zooplankton prey lead to a mismatch of the prey’s morphology with the catching- or feeding-apparatus of invertebrate predators, and therefore to a higher escape and survival rate [12,104,111]. In general, inducible morphological defences should not be understood as one single trait that changes, but rather as a suit of armour that acts concertedly as a full body defence against predators. The defensive morphological alterations that act together as a protection are thought to have their individual justification at specific points during the predation cycle [9]. Various traits have already been taken into consideration, but many may still be undiscovered. Throughout the past 17 years, some previously unreported morphological defences were found and some already known defences were linked to specific predator traits, as pointed out below.

### 2.2.1. Defences against Vertebrate Predators

The hunting strategy of vertebrate predators of zooplankton, meaning mostly planktivorous fish, is visual foraging [24,112]. In contrast to invertebrate predators, fish do not depend on fine morphological chitinous catching structures, like parts of limbs, antennulae, and mandibles [31,100,113,114]. The general defensive response to fish is a decrease in body length, to reduce detectability, which we mainly refer to in the paragraph on life-history defences (e.g., [108,115–121]). This pattern was previously found for several *Daphnia* species [21,122,123] and only recently for *Bosmina longirostris* and *Eubosmina longispina* [117]. A theoretical and more thorough explanation for this morphological developmental pattern in contact with fish is given by Stoks et al. [124]. The authors reconstructed the contribution of ancestral plasticity, constitutive evolution, and evolution of plasticity to the defensive shifts in body length of *D. magna* in response to changing fish predation. While the introduction of fish into a previously fish-free pond lead to the expression of a reduced body length in neonates and adults, a subsequent reduction in fish abundance caused the daphnids to still express this induced decrease of body length, albeit to a lower extent. Whereas mostly ancestral plasticity and the evolution of plasticity contributed to the defensive shift in body length at the first stock transition in the pond, all three components contributed to the defensive shift in body length at the second stock transition in the pond, indicating that morphological changes in response to fish predation can result from different combinations of nonevolutionary (phenotypic plasticity) and evolutionary (evolution of plasticity, constitutive evolution) processes. It is important to point out that these concepts of evolutionary and nonevolutionary processes underlying inducible defences are not restricted to the predator–prey combination of *D. magna* and fish or to morphological defences, but are applicable to inducible defences in general (e.g., [124–127]).

Only a few exceptions to the general pattern of a fish-induced reduction in prey body size to limit the visibility for the predator are documented. In these, the induced morphological enlargement of specific appendages was found to impair feeding by fish (e.g., [128–130]). One example of this is *D. lumholtzi*, which has been shown to develop large fornices and head and tail spines, protecting it against small (20–25 mm) fish [116,128,129]. *D. lumholtzi*’s spines were found to get entangled in the mouth roof of these small fish, leading to the release of the prey [129]. On this basis, it was postulated that the protection through these spines can be connected with the potential gape-limitation of the predator’s mouth and thus leads to a preference of smaller, less spined prey [129]. Engel et al. [131] demonstrated the advantage of longer head and tail spines through the comparison of two *D. lumholtzi*

clones, one with longer, the other with shorter spines, against predatory fish. These clones were not exposed to the predator prior to the experiment, to rule out other, possibly hidden structural, morphological defences and a singularly test for the advantage of longer spines. The tested fish were large enough to feed on either morph, but still chose the less-spined clone significantly more often. Moreover, the previously suspected defensive advantage of induced spines across several life stages of *D. lumholtzi*, when encountering fish [132], could recently only be confirmed for adult *D. lumholtzi* [131]. These findings suggest that the advantage of the induced spine elongation takes effect at different points during the predation sequence for different life stages or sizes of prey. Therefore, it may not be purely effective at the point of ingestion (postcapture) but might operate as a precapture defence as well, making the predator less decisive on whether or not to attack a prey organism. The induced spine elongation in *D. lumholtzi* was found to vary among clones regarding the time until defence expression (compared with Tollrian [128]) [116]. This further suggests that clones may differ in reaction time or susceptibility to kairomones, the latter possibly depending on the origin of the clone and the predator regime the prey organism encountered there (compare with Boeing et al. [42]).

In addition to the defensive head and tail spines, defences on a larger scale or with a larger effect on the overall prey morphology can occur as a result of the exposure to a vertebrate predator. As mentioned in the paragraph on behavioural defences, Tollrian and Heibl [66] detected phenotypically plastic pigmentation in premature *D. pulex* in the presence of the fish *Phoxinus phoxinus*. They suggested that, because of their visual foraging strategy, fish might induce changes in pigmentation towards higher transparency. However, the response differed between species, according to the UV exposure to which they had to protectively adapt. A similar transparency in the presence of planktivorous fish was previously found in *D. middendorffiana*, which were more deeply pigmented in fish-free than in fish-containing ponds [110]. These discoveries might emphasize respective, specific habitat adaptations of *Daphnia*, as shown by Tollrian and Heibl [66], as trade-offs between UV-protection and visibility. For example, the increased transparency of a *D. pulex* clone indicates that it is either generally exposed to less direct UV-radiation or carries other protective mechanisms against it. In addition to that, the reduction in visibility as a defensive strategy was discussed regarding the eyespot size of zooplankton, which was found to be smaller in the presence of fish [110,133].

### 2.2.2. Defences against Invertebrate Predators

While in the past, studies primarily focused on larger and more conspicuous defence structures against invertebrate predators, recent studies additionally addressed smaller and more unobtrusive morphological defences. For the investigation of inducible morphological defences of freshwater zooplankton in response to their invertebrate predators, some predators have been chosen repeatedly. Within this section, we arrange the reviewed studies according to the taxonomic order of the studied predator species and provide brief insights into the predator's feeding mechanisms.

*Chaoborus* larvae are the most studied invertebrate predators that induce defences in freshwater zooplankton. *Chaoborus* are ubiquitous and their larvae can be very abundant both in fish-free and fish-containing lakes and ponds, thereby representing an important trophic link between small zooplankton and higher trophic levels. The *catching basket* of the ambush predator *Chaoborus* limits the size range of its prey [9,10,27,31,134]. Chemical cues released by *Chaoborus* have been shown to enhance changes in body size in daphnids [15,135,136] and to induce helmets, head spines and elongated tail spines. The most unique defence, that only *Chaoborus* has been shown to induce in several *Daphnia* species, is *neckteeth* in the dorsal region of the head with an enlarged neck-pedestal underneath (see Figure 1) [10,15,112,135,137–141]. All defensive traits differ in their reaction norm and effectiveness between different instars of *Daphnia* [140,142], predator instar, and predator species within the genus of *Chaoborus* [136,140].

In particular, several studies investigating *neckteeth* were able to show large variation within this defensive trait between different *Daphnia* species and clones [27,41,107,143–145]. The induced *neckteeth* have been shown to differ in number, in their arrangement (line or rosette), and in the size of the

neck-pedestal underneath them [107,109,144–148]. The defensive effect of the *neckteeth* is suspected to be a mechanical interference with the predator's fine mouthparts [31].

In addition, some experiments investigated the variation of this inducible defence throughout development. Laforsch and Tollrian [143] found that the developmental changes concerning the *Chaoborus*-induced neck-pedestal take place during the last embryonic stage in *D. pulex*. Adding to this, Imai et al. [148] showed the need for continuous induction of *D. pulex* through *Chaoborus* cues during embryonic development and even at an early postembryonic stage, for the maintenance of the *neckteeth* during the first three juvenile instars. The *neckteeth* reach their developmental maximum at the second or third juvenile instar, when they are at the preferred prey-size of *Chaoborus* [149]. After the third juvenile instar, the *neckteeth* decline and disappear. Another example for variance in this trait is *D. longispina*, which exhibits clonal differences in *neckteeth* development in response to *Chaoborus* across juvenile instars [145]. However, in the second juvenile instar, the *neckteeth* were most expressed in all tested *D. longispina* clones, and the neck-pedestal was also enlarged compared to the control. This emphasizes that an induced prey may show a defensive response according to its vulnerability at a certain life stage, with respect to the specific *Chaoborus* presence at that time. An example for the temporal alteration in defensive *neckteeth* production and the related competitive advantage under predation by *C. crystallinus* has been demonstrated for *D. hrbackei*, which show a stronger tendency to form *neckteeth* compared to *D. curvirostris* [107].

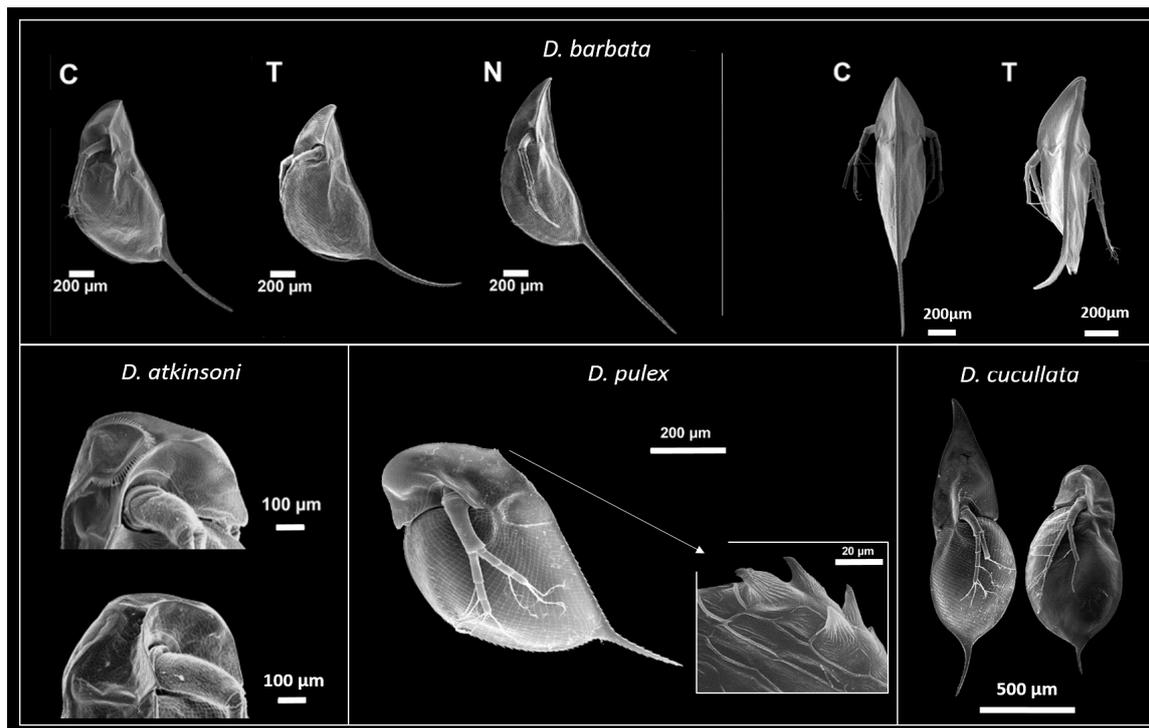
In addition to the development of *neckteeth*, research revealed the induction of less predator-specific morphological defences in response to the predator *Chaoborus*, i.e., helmets and head and tail spines, which offer protection for various prey size classes in different *Daphnia* species against this invertebrate predator [150]. In *C. flavicans*-induced *D. longispina* the relative tail spine length was found to be longer than in induced *D. pulex*, which was attributed to the higher responsiveness of the smaller *D. longispina* to this invertebrate predator in comparison to the larger *D. pulex* [144]. The reason for this may be that an elongated tail spine could render *D. longispina* too large to fit into *Chaoborus'* *catching basket*. The same may be the case for *Chaoborus*-induced juvenile *D. lumholtzi*, which develop longer head and tail spines when encountering this predator [131]. Here, the defence may lead to a similar outcome (i.e., survival or escape) as under predation by fish, but the mode of operation of these defences differs. The longer spines could impede handling by *Chaoborus* since they might interfere with the *catching basket*, whereas in fish, the entire prey may get stuck at once.

The *Chaoborus*-related inducible morphological defences on a large scale have been shown to be accompanied by ultrastructural defences. Induced, inconspicuous changes to the carapace were found in *Chaoborus*-induced *D. pulex* and *D. cucullata* by using ultrasound microscopy [151]. In induced *D. pulex*, an increase in carapace hardness by 350% compared to the noninduced morph was observed, and in induced *D. cucullata* the carapace was twice as hard as in noninduced individuals. This study was also the first to reveal structural changes in the so-called pillars, which connect the inner and outer epidermal layers of the carapace in *Daphnia*. The study found an increase of pillar diameters in induced *D. cucullata* to about twice their original size. These structural alterations supposedly save costs for the defending prey organism through the production of a relatively small amount of material, in comparison to the investment necessary for larger defences. For *D. pulex*, this was further explored in a study by Kruppert et al. [30], where species-specific structural alterations in *Chaoborus*-induced *D. pulex* and *Notonecta*-induced *D. longicephala* were detected. While *D. pulex* developed a thicker procuticle with additional layers, induction of *D. longicephala* also lead to an increase in the number of layers, but without a change in total procuticle thickness. This study additionally tested for the contribution of the known defences to the carapace stiffness and found the induced ultrastructural carapace adjustments to be of more importance than the more prominent shape alterations. According to this study, with an increased number of layers in *Daphnia's* carapace, the possible orientations of chitin fibres, which make up a large part of each of these layers, increased. This resulted in an increased modulus of rupture, while the structural alterations may lead to an increased resistance to puncturing, either by *Chaoborus* mandibles or the *Notonecta* proboscis, during the predation process. The thicker

procuticle with added layers in *Chaoborus*-induced *D. pulex* led to additional crush resistance and made up for the loss in carapace stiffness that is connected to the shape alterations, i.e., *Chaoborus*-induced *neckteeth* and neck-pedestal formation, in this species.

The loss in carapace stiffness, in connection with an induced morphological defence, i.e., *crest* formation, does not appear in *Notonecta*-induced *D. longicephala*. *D. longicephala* had previously been found to develop a unique, large *crest*, meaning a large extension of the dorsal side of the head region in a crescent-like form, and some even an elongated tail spine in reaction to backswimmers (*Notonecta/Anisops/Buenoa*) [111,152,153]. These predators are common in small ponds and lakes, where visual and mechanical cues originating from the prey organism trigger the predator's orientation and dash towards the prey [112,113]. The prey is grasped with its first two leg pairs, positioned, stung, liquefied, and the extraintestinally digested prey sucked out of its carapace [113]. The *crest* is thought to enhance the escape efficiency of the induced morph when under attack and there are various theories on its mode of action [111,152].

Inducible morphological defences in freshwater zooplankton have been further discovered in response to the tadpole shrimp *Triops cancriformis*. Several clones of the *D. atkinsoni* species complex were found to adapt to coexisting tadpole shrimp by forming a so called *crown of thorns*, an enormously wide, spined carapace extension in the form of a lobe on each side of their head proven to be effective against *Triops* predation (Figure 1) [154,155]. *D. magna* also coexisting with *Triops* in temporary waters induce a bulky morph, meaning an increased body width and body length, with an elongated tail spine [156]. Different *Triops*-induced *D. magna* clones were discovered to develop the "bulky" morph and an elongated tail spine together with an increase in the width of the shoulder shield [108]. However, the magnitude of the defensive traits varied among the three tested clones. Further, a gradual alternation of these defensive traits over the course of several instars of the prey was shown. This alteration secures the most effective protection of the organism for every developmental stage. *D. magna*'s earlier instars seem to profit from an elongated tail spine, that is folded out after hatching as a start-up defence [143], while for adult daphnids the "bulkiness" seems to be the most effective combination of defensive traits. The benefit of the "bulkiness", enlarged tail spine, and wider shoulder shield throughout all of *D. magna*'s life stages was proven via predation trials across size classes of predator and prey. Another extraordinary example for *T. cancriformis*-induced morphological defences was found in *D. barbata* by Herzog et al. [157]. This *Daphnia* species abandons its entire bilateral symmetry, forming a thoroughly twisted morph as a defence against the tadpole shrimp (Figure 1). In addition to these prominent defences, small-scale defences were also detected in *Triops*- and *Notonecta*-exposed *D. barbata* [28]. Spinules along the carapace margins were shown to increase in density, grow longer, and orientate sideways, compared to the control. While *Triops* induces small-scale defences, like spinules, this invertebrate predator also induces the expression of ultrastructural defences. *D. magna* exhibit an approximately five-times harder and two-times thicker cuticle with an increased diameter of the pillars in response to *T. cancriformis* [158]. Similar to the ultrastructural changes previously found in *Chaoborus*-exposed *D. cucullata* and *D. pulex*, these structural changes in *D. magna* lead to an increased resistance against the predator's, i.e., *Triops*'s, feeding mechanism [29,158]. The benefit of all the mentioned defences in contact with *Triops* might be explainable through the feeding mechanism of the tadpole shrimp, where the gnathobases of the anterior trunk limbs form a food groove in which prey is trapped, cage-like by the limbs, and moved towards the mandibles, where it is crushed [108,114,158,159]. Here, the interaction of induced defensive traits with fine chitinous predator structures may lead to either an increase in handling time, a tilt of structures, or an injury of the predator, in any case followed by a higher escape or release rate of the prey. This predator-prey interaction may confirm the proposed "antilock and key mechanism" of morphological defences [104].



**Figure 1.** Inducible morphological defences in *Daphnia*. Top row: *D. barbata* expressing morphological defences in tail spine, helmet, and bilateral symmetry under exposure to *Triops cancriformis* (T) and *Notonecta glauca* (N) compared to the control (C) [28,158]. Bottom row: *D. atkinsoni* expressing a crown of thorns against *T. cancriformis* (top) compared to the control (bottom) [156]. *D. pulex* with neckteeth as defence against *Chaoborus* ([160], [www.schweizerbart.de/journals/fal](http://www.schweizerbart.de/journals/fal)). *D. cucullata* with *Chaoborus*-induced helmet and tail spine (left) compared to the control (right).

*Bythotrephes longimanus* (Cladocera: Cercopagididae) is an invertebrate predator that has been shown to induce morphological changes in its prey's head morphology [161]. These changes include longer helmets in three clones of *D. mendotae*, comparable in degree to previously found helmets in response to *Chaoborus* [161]. The tactile predatory water flea *Bythotrephes* is known to prefer small sized *Daphnia*, which are caught and ripped apart during the predation sequence [162]. Therefore, an elongation of the head, in the form of a helmet, might potentially exclude *D. mendotae* from the preferred size spectrum and lead to handling difficulties for the predator.

Another prominent invertebrate predator of zooplankton is *Leptodora kindtii*, which can severely affect the populations dynamics of small zooplankton species, such as *Bosmina* and *Eubosmina* (Cladocera: Bosminidae), during its high abundances [163–165]. For *Leptodora* feeding on *Eubosmina*, the prey handling time was found to be correlated with its own body size and the species-specific antennule length of *Eubosmina*, emphasizing the importance of these elongated appendages for the prey's survival rate [163]. Also, certain *Bosmina* species were found to react specifically to *Leptodora*. This predator triggered *B. fatalis* to become dominant earlier in the year, compared to *B. longirostris* [106,164,166]. The induced longer mucro, which is comparable to a tail spine in *Daphnia*, in combination with a changed antennule shape and increased antennule length seem to provide *B. fatalis* with a defensive advantage, compared to *B. longirostris*, in the presence of *Leptodora* [164]. The induced changes in prey morphology may be related to *Leptodora*'s trapping basket, which is formed by its pairs of legs [162,167]. An interference of the mucro or antennule with the legs, or an overall mismatch of the enlarged body with the size-limited handling ability of these legs may cause an increase in handling time and thus may increase the escape probability [163,168].

A further invertebrate predator inducing elongated and shape-wise changed antennule in *Eubosmina* and *Bosmina*, similar to those expressed in response to *Leptodora*, is *Mesocyclops* (Cyclopoida:

*Cyclopidae*) [169,170]. In fact, *Bosmina* and *Eubosmina* presumably build on a mixture of pre- and postcontact defences against invertebrate predators, including the protection of the ventral opening between the carapace-sides and the lateral antennae, the elongated antennule and mucro, as well as the consequential dead-man-response. Through this defence combination the mechanic stimulation of an invertebrate predator is behaviourally avoided while, in case of a contact, the next lines of defence, i.e., the induced morphological traits, ensure an increased handling time, similar to *neckteeth* in *Chaoborus* (e.g., [104,171,172]).

Further inducible morphological defences of freshwater zooplankton can be found in response to the freshwater jellyfish *Craspedacusta sowerbii*. *B. longirostris* was found to elongate its mucro and antennule in response to this predator [168]. The hunting strategy of *Craspedacusta* is dependent on the water flow that carries prey towards its floating tentacles [168]. The author discusses the need for further experiments to show the exact mode of action in this freshwater jellyfish and its prey.

The rotifer *Asplanchna* (Ploima: Asplanchnidae) was one of the first predators shown to induce morphological defences in its zooplankton prey [173,174]. *Asplanchna* was found to induce spine elongation in the smaller rotifer *Brachionus calyciflorus* (Ploima: Brachionidae). The work with this predator genus was continued in several experiments, which tested marine, brackish, and freshwater zooplankton for inducible morphological defences. An elongation of multiple spines along the prey's body was found for several *Asplanchna*–prey (*Keratella*, *Brachionus*, *Plationus*) combinations (e.g., [40,92,175–179]). Further, the strength of this induction seems to be related to *Asplanchna* density [180]. Nandini et al. [177] were able to show the important contribution of the spine length in differently spined, yet noninduced *Brachionus* species, as well as the prey density for limiting the catching and consumption by *Asplanchna sieboldi*. This might be similar for induced *Brachionus* but is still to be tested. *Asplanchna* were shown to selectively prey on less spined morphs, if these are available, making the changed spine morphology in prey organisms beneficial by means of gape-limitation, since *Asplanchna* feeds on its prey by sucking it up entirely [19,177]. While morphological defences in other groups of zooplankton can vary over developmental stages, the morphology of rotifers is determined at birth, and could therefore be understood as a maternal-induced defence [19].

### 2.3. Life-History Defences

Changes in life-history, comprising, e.g., size at first reproduction (SFR), age of maturation, number and size of offspring, production of resting eggs, and longevity, are well-known inducible defences in many zooplankton species (e.g., [99,120,181–184]). Thus, functionally oriented response patterns, such as a change in SFR, are often combined with other (e.g., morphological) predator-induced defences. Given that most invertebrate predators are gape-limited, freshwater zooplankton prey organisms of a matching size range will increase their SFR by increased growth and/or formation of morphological structures (e.g., helmets or elongated spines) potentially at the cost of reduced reproduction (e.g., delayed maturity or less offspring). In contrast, most freshwater zooplankton will reduce their SFR and visibility but increase their resource allocation into reproduction in response to predation by visually hunting vertebrate predators. These patterns are often passed on to the next generation, producing bigger or smaller offspring, respectively [185,186].

Some studies report no or varying predator-induced life-history changes in different *Daphnia* species, or even clones of single species. Some literature reports are contradictory. For example, some species have been found to increase their SFR in one study, but to reduce it in another one in response to the same predators [4,148,187–190]. Such contradictory results may derive from factors influencing the response that were not considered in the respective studies, such as the origin and the developmental stage of the prey, or the light intensity.

There is evidence that a multitude of predator-induced response patterns depend on the prey's origin (e.g., temporary pond vs. lake), and on the type of predators the prey has encountered previously [42,191]. *D. pulex* for example, responded stronger to fish or *Chaoborus* when the clone that was used derived from a location that was inhabited by the respective predator. In other cases,

the prey responded in a pattern they usually exhibit against another predator, even though it was maladaptive or they showed indefinite, mixed responses [42]. On the other hand, invasive predators are also able to induce life-history defences that follow the predicted patterns previously mentioned. In a 12 year long-term study, life-history changes in zooplankton were related to the invasion of a new fish species [117] that had been introduced in addition to other native fish species. During this study, the zooplankton community (mainly *Daphnia* spp. and *Bosmina* spp.) generally reduced their SFR and increased their clutch sizes, while the largest species (*D. longispina*) was eliminated. This again may hint to a potential similarity of predator cues (e.g., one fish cue). However, it is still unclear to what extent the predatory history or prey's origin affect the induction of defences in general.

Furthermore, the type of defence or the defence strength can differ, depending on the developmental stage or instar at which the organism was exposed to the predator cues [192,193]. The most pronounced life-history change (i.e., earlier maturation) was achieved by exposing fourth instar daphnids to fish cues. Additionally, when the mothers were already exposed to fish, the reaction norm of their offspring was found to be much broader, which has been discussed as an adaptation to an unpredictable environment for the offspring [193].

As reported for behavioural defences, life-history changes in *Daphnia* are also affected by light [119,120,189,194]. Life-history changes were inversely coupled to light intensity (the SFR was reduced when exposed to intense light), but there was no induction in the dark [119,120]. Resting egg production in *Daphnia* was found to increase in response to fish exposure and to be suppressed in the dark as well, and thus has been discussed as a strategy to escape fish predation [189]. Both reactions (reduced SFR and suppression of resting egg production) may provide an advantage by decreasing the visibility to fish, which would be obsolete in the dark.

Slusarczyk and Rybicka [188] also found reduced resting egg production in *Daphnia* that were simultaneously exposed to fish kairomones and high temperatures, but not in *Daphnia* that were solely exposed to high temperatures in the absence of kairomones. The authors discuss that *Daphnia* used the shorter developmental times at increased temperatures, and thus increased the number of offspring to counteract population losses by predation. Under exposure to fish kairomones at low temperatures they increased the production of resting eggs to escape times with high predation pressure and slower developmental rates. In *D. galeata* and *D. similis*, La et al. [121] additionally found the egg type (asexually or sexually produced) determined the inducibility of defensive morphological changes in hatchlings. While they found defences to be regularly inducible in hatchlings of asexually produced eggs, defences in sexually produced eggs (i.e., resting eggs) were constitutively expressed and an amplification of the defence was not inducible. This might be an adaptation to a hatching phase of the resting eggs, during which predation pressure may be predictable [121]. On the other hand, this might also be an adaptation to an unpredictable future into which the offspring is released, where it may need high protection directly after hatching.

Not only external factors can influence the expression of inducible defences. Wolinska et al. [195] revealed that the strength of the induced defence is a function of the intrinsic values of defence traits in *Daphnia*. That means a small individual is supposed to respond more strongly (with an even stronger increase in growth) to an invertebrate predator than a large individual.

However, especially with regard to life-history changes, two contrasting hypotheses are discussed: on the one hand adaptations (i.e., reduced SFR and changes in reproduction) may be responses to size selection as a defence against specific predators. In contrast to this, it has been discussed whether adaptations are trade-offs due to changed activity and subsequently reduced food intake [196]. Following the latter hypothesis, size-selective predation by fish should lead to reduced SFR, which then would lead to delayed maturity, because maturation would be coupled to growth. In that case, a reduction in size at maturity under predation would merely be the consequence of an increased resource allocation, from somatic investment into reproduction, rather than a purposive defence that aims to reduce visibility and increase the offspring number to overcome predation losses. On the other hand (still following the latter hypothesis), negative-size-selective predation (i.e., by invertebrates)

would lead to an increased SFR and therefore to an earlier maturation. This issue has been summarized by Beckerman et al. [196]. The authors tested both theories and found that *Daphnia* matured earlier, even though their growth rate slowed down, when exposed to fish, while SFR was increased, but maturity was delayed under invertebrate predation [99,196]. This shows that somatic growth and individual development (i.e., maturing) can be decoupled by predator exposure [99,196] and therefore can be seen as a purposive defence mechanism. Nevertheless, this mechanism is still affected by food intake. Riessen [197] concluded from his experiments with *D. pulex* and *Chaoborus* that a delay in reproduction is not a real trade-off with increased growth, but that there is a strong linkage between those traits, even though the mechanism is still unclear. Additionally, Klintworth and Von Elert [198] showed that food intake and resource allocation have an impact on the expression of multiple defences, including SFR. However, changes in life history, such as SFR, cannot be fully explained by food availability [196,199]. Therefore, the ultimate factor for life-history changes is the individual predation risk, rendering this inducible defence a purposive response to size selective predation.

#### 2.4. Conceptual Approaches for Multipredator Studies

In a natural context, defences rarely evolve in response to a single predator. In freshwater habitats, multiple predators co-occur and therefore exert their selective pressure simultaneously [12,134]. The induced defences are inferred to be the optimum defensive trade-off for a prey species encountering a respective predation regime at a specific time. Previous studies found the development of defences to be oriented towards the dominant predator at a particular time, with respect to, e.g., abundance or prey-preference, or towards an intermediate compromise [28,200]. This dominant predator may vary seasonally, according to its respective life cycle [12].

When studies try to address inducible defences of freshwater zooplankton in a natural multipredator situation, there are two basic approaches. In some cases, a sampling of predators and prey in nature is the starting point, which is followed by comparing the data obtained in this way with that from follow-up laboratory studies with the obtained organisms (e.g., [201]). Other studies start with a number of laboratory experiments with various potentially co-occurring predators as well as their prey and compare these results to data they find in the field, in later studies (e.g., [131,176,202]). On one hand, in concepts that start off with sampling in the field, it is difficult to distinguish individual influences of predators on different characteristics of inducible defences. This approach is limited at its basis by the sampling, meaning the method, spot (biodiversity, characteristics of the specific habitat), and seasonality (including weather). On the other hand, in the concept where laboratory studies are executed first, the design of these laboratory studies is crucial. A multitude of aspects has to be considered to clearly separate influences of predators on different induced defence characteristics in experiments. Therefore, a basic framework is needed to distinguish the predator-influence on certain aspects of the induced defence. In 2003, Relyea reviewed multipredator-prey studies on the induction of defences, most of which were conducted in aquatic systems. He noted that in order to disentangle influences of various predators in multipredator studies, (a) the prey consumption should be managed in a controlled manner, (b) the number of observed traits should generally be high, (c) there should be a variation in the predator combination, and (d) there should be some distinction between changes in total predator abundance and changes in predator regime. The studies conducted so far generally do not meet these requirements, making a clear interpretation of the individual predator contribution to an induced morph very difficult.

In a different approach, to better understand the quality of the selection pressure for the induction of defences in response to multiple predators, Herzog and Laforsch [28] introduced the “concept of modality”. The three categories, functionally equivalent, functionally inverse, and functionally diverse, which can be further distinguished, were introduced to differentiate the pattern in which two different predators can impact the expression of a defence in a prey organism. The induction through two invertebrate predators (*T. cancriformis* and *N. glauca*) that exert very different qualities of selection pressure led to the development of two very different appearances of the same induced

traits in *D. barbata* (Figure 1). These served as distinct defences when encountering the two predators separately. The thorough use of either of the introduced concepts would open new paths for the explanation of inducible defences of freshwater zooplankton in a multipredator context.

### 3. Costs for Inducible Defence

Although a wide spectrum of inducible defensive traits and a huge variety of factors modulating these defences have been discovered, our knowledge about the costs that accompany an inducible defence is still scarce and inconclusive. Costs of inducible defences can be assigned to five categories: plasticity costs, self-damaging costs, allocation costs, opportunity costs, and environmental costs [7]. However, as we do not cover genetics and molecular contexts in this review, we will not go into plasticity costs that include costs for maintaining the ability to be plastic, as well as maintaining sensory structures to detect predators. Further, to our knowledge, there are no reports about self-damaging costs in freshwater zooplankton.

Food availability plays a role in the expression of induced defences in freshwater zooplankton, indicating the existence of allocation costs. They are represented by direct metabolic demands, e.g., due to increased respiration rate [23,203], or direct energy and material costs for forming and maintaining defences, such as morphological structures or increased reproduction (e.g., [99,194–196]). Several studies already reported increasing demands of nutrients with increasing predation risk, or reduced defence expression under nutritional constraints [99,204–208]. However, it is difficult to estimate allocation costs with definite numbers, as it is not easy to determine whether the resources are allocated into a defence, like PUFAs that are needed for increased reproduction [75], or whether constraints are caused by other factors as well, such as the previously mentioned increase in PUFA demand due to low temperatures. Furthermore, prey species might compensate for nutritional losses by changing their activity or feeding modes [209].

Opportunity costs comprise the loss of benefits that the prey would have experienced if it had not developed defences, such as reduced growth and fecundity, or loss of competitive ability. They can also be seen as long-term allocation costs [7]. These costs might even be passed on to future generations that might consequentially suffer from the predation pressure to which their parents were exposed. The abandonment of DVM under low food conditions may indicate such opportunity costs [49,59,210]. Under generally limiting food concentrations, staying in upper water layers that provide higher food concentrations than deep strata seems to outweigh the benefits of DVM. A loss of the competitive ability in response to fish-induced DVM was shown by Dawidowicz and Wielanier [81]. In their study, *Daphnia* performed DVM, whereas *Ceriodaphnia* stayed in upper water layers. As a consequence, *Daphnia* suffered from reduced population growth because of the costs associated with DVM, while *Ceriodaphnia* increased their population growth, which the authors attributed to the increased resource availability for *Ceriodaphnia* after *Daphnia* vanished from surface waters. Food intake is also decreased due to lower feeding rates, or lower activity to reduce the encounter probability [23,98,99]. Therefore, this might also be counted as an opportunity cost as well. The same might be true for decreased reproduction and increased developmental time due to lower temperatures [60,67,79]. However, the classification of food availability as well as temperature into certain categories of costs may be context dependent, as they are generally considered as environmental costs [7]. Nevertheless, a decrease in reproduction is not necessarily detrimental. In combination with increased somatic growth, it can indirectly increase the overall population growth under predation due to decreased mortality by predation [182], indicating clear trade-offs. Reduced longevity might be another cost linked to defence induction that indirectly influences population growth. However, an acceleration of senescence, which might act as a long-term cost, could not be detected in a study with *D. pulex* and *D. magna* [211] and even an increase in longevity was detected in *D. similis* and *Moina macrocopa* [184].

The best studied and most reported costs are environmental costs. They are occasional costs that are caused by the surrounding environment. An increased visibility due to pigmentation against UV-radiation is one example for environmental costs [60,65,66,79]. Another example is that the defence

against one predator may render the prey more vulnerable to another predator (e.g., [42,88]), such as the optimal size against invertebrate predators (large) and vertebrate predators (small) [185]. However, there are defences that act against several predators at the same time [28,42,54,202], like the inducible defences in *D. barbata* against *N. glauca*, which also provides protection against *T. cancriformis* [28]. Also, the life stage of the predator might provoke environmental costs, depending on the preferred prey size of the predator's instar, age, or size [26,82,84,199]. With fish as the predominant predator, a reduction in prey size may be beneficial against large fish, but in turn might be maladaptive against smaller, young fish of the same species, as those may prefer smaller prey. Even though a reduction in size in the presence of young fish can be considered a maladaptation, Hülsmann et al. [199] found a reduction in prey size under high food availability. The authors discuss that this is an unrealistic event in nature, as young perch occur in late spring, where food levels are relatively low, due to the clear water phase.

Additionally, not only the vulnerability of the prey to predators can be increased, but also the vulnerability to parasites might be affected under predation [212,213], which would be counted as an environmental cost as well. Vice versa, the parasites may also affect the ability of the prey to defend themselves against predators [214].

For a thorough understanding of the costs that are associated with inducible defences in freshwater zooplankton, it is insufficient to investigate only one stressor at a time. Hammill et al. [215] stated that knowledge about long-term costs is necessary to understand the evolution of inducible defences. Especially, multipredator- and multistressor-systems should be investigated more in future research, as prey is rarely exposed to only one predator and stressor at a time under natural conditions. Moreover, many costs might be diffused or hidden in experiments by sufficient food supply, or other environmental conditions that cover potential costs. Further to this, costs are difficult to quantify (see also Riessen [197] and Tollrian and Dodson [112]). They may be measured as a relative reduction in growth rate, or reproduction, or might be estimated as an increased resource demand. Depending on the considered defence, this might not be possible, especially when more elusive costs need to be considered (that might not have been found so far), such as evolutionary costs.

While inducible defences have thus far been thought to be connected with costs, they might instead provide an evolutionary benefit. In contrast, a constitutive defence may have an evolutionary cost. A constitutive defence is more predictable for the predator, allowing it to adapt more easily to a prey's defence. Thus, the expression of an inducible defence by the prey, with high variability and an occurrence only under certain circumstances (e.g., after passing a threshold of predation pressure), would prevent or slow down the adaptation process of the predator. Therefore, the direct costs associated with expressing an inducible defence might actually be less relevant than the costs associated with having a constitutive defence, rendering an inducible defence beneficial rather than costly in an evolutionary context.

#### 4. Defence-Inducing Cues

The characterization of defence-inducing chemical cues has been a major challenge in the last few decades. The following reasons for this have been discussed previously [216,217]: Defences might be induced by more than just one chemical compound, which complicates the identification and testing of putative kairomones. Furthermore, chemical cues might be potent already at picomolar concentrations, making their proof and quantification in nature challenging. Developing and conducting suitable bioassays, to test the substances in question, is another prerequisite for characterizing chemical cues. Since the review by Lass and Spaak [17], tremendous effort has been invested, especially for cladocerans, in identifying and describing chemical and physical cues that trigger inducible defences [14,194,218–224]. Nevertheless, the chemical structures of kairomones as well as their mode of action are still unknown in most cases.

In general, there are some suspected substances for kairomones that are commonly used for intra- as well as interspecific information transfer. Invertebrates often release peptides or peptide-based substances [14,225,226], while vertebrates seem to release bile salts that induce a defence in prey

species [227,228]. Aliphatic sulphates released from *Daphnia* have been found to induce defences in algae [229]. The chemical structure of these substances can be manifold [225,228]. Moreover, they can be modified (e.g., [14]), producing even further complexity in information transfer. In general, there seems to be a wide array of substances that are perceived as predator cues by prey. Furthermore, their putative combination to cocktails adds to their complexity and putative specificity as kairomones, as pointed out, for example, in the reviews of Parejko and Dodson [230] and Pohnert et al. [216]. Therefore, it is likely that those (combined) substances can be largely species-specific and prey should have evolved the ability to distinguish between predator species, or at least between several predator types (such as invertebrates vs. vertebrates), allowing the prey to display defences that are specifically effective against the most relevant predator at a given time and space.

However, the controversy, pointed out by Lass and Spaak [17], about whether there is one *fish factor*, or whether prey are able to distinguish between different fish species, still continues. Even though there is evidence that prey organisms are able to react differently to some fish species [222], there are contradictory studies that still find no difference in defence induction when *Daphnia* were exposed to different fish species (e.g., [220,231]). As pointed out in the former sections, the response to fish predators is usually expressed in accordance with a general pattern, i.e., reduced size and increased reproduction (e.g., [203,210,232]). Thus, the reaction norm may depend on kairomone concentration [220,221], which would not only explain the differences in the reaction norm between fish species (bigger fish might produce more kairomone) but also the response differences between small juvenile and fully-grown adult fish [199]. A potential kairomone concentration dependency of the induction of defences could be shown in invertebrates with *Triops* in one study [108] and also over various other taxa by demonstrating that the predator as well as the prey density can modulate the strength of defence induction [233].

Recently, Hahn et al. [227,234] identified and described a fish factor that induces diel vertical migration in *Daphnia* as 5'- $\alpha$ -cyprinolsulfate, a bile salt excreted by carp (*Cyprinus carpio*) and roach (*Rutilus rutilus*) during digestion. They also stressed that this bile salt may be a general kairomone in cyprinid fish, although it also seems to exist in smaller concentrations in rainbow trout (*Oncorhynchus mykiss*). This implies that there are different bile salts or substances with a similar structure that may act as kairomones and derive from other fish orders [227,234]. Bile salts are a common by-product of the digestion process in all vertebrates, thus explaining why predators are not able to control production and excretion of these substances [228]. Nevertheless, there probably is more than one chemical cue exuded by fish. In 2006, Beklioglu et al. [219] found mucus-dwelling bacteria to contribute to the production of kairomones, which had previously already been suggested by Ringelberg and Van Gool [235]. Fish incubation water usually induces distinct migratory behaviour in *Daphnia*. Water containing only fish mucus resulted only in intermediate response strength in *D. pulex* as compared to incubation water containing fish. Incubation water produced with antibiotics-treated fish also resulted in intermediate response strength. Such findings support the idea of a cocktail of chemical compounds that interact to induce different, more or less predator-specific, defences. However, bacteria may also be responsible for a relatively short half-life of kairomones, due to degradation [205].

Recently, a combination of different substances released by an invertebrate predator was found to induce defences in *Daphnia*. The kairomone of the phantom midge larvae (*Chaoborus*) induces *neckteeth* in *D. pulex*. Weiss et al. [14] reported that the *Chaoborus* kairomone consists of fatty acids conjugated with the amino group of glutamine via the N-terminus. These compounds are thought to be a by-product of the digestion process of *Chaoborus*, similar to bile salts in fish. Several combinations of fatty acids conjugated with glutamine were found in the extract, each by itself inducing a response in *D. pulex*. They showed that fatty acids with a chain length of 14 carbon atoms or more have a higher potential of inducing *neckteeth* in *D. pulex*. The naturally-found fatty acids  $\alpha$ -linolenic acid and linoleic acid seem to be the most potent conjugates for the induction of defences. Likewise, glutamine can be exchanged by glycine or alanine; the latter lowering the actual defence expression. These findings suggest that kairomones released by predatory invertebrates consist of a mixture of compounds,

rather than single substances. In addition, the concentration of each compound may be important for the modulation of the defence against specific predators. However, this remains unclear until more detailed studies on the single compounds of putative chemical-cue cocktails have been carried out.

Beside kairomones, other cues are used by prey to assess the acute predation risk. Several studies have investigated chemical cues released by harmed or killed prey: so-called alarm cues. Extracts gained from injured or macerated daphnids can also induce defences in *Daphnia*, similar to predator kairomones, though less pronounced [22,23,194,236]. Cues generated through feeding on conspecifics seem to exert stronger responses than cues derived from feeding on other prey species, or from a *Daphnia*-free diet [22]. Thus, Mitchell et al. [237] proposed a distinction between predator cues that are directly originating from the predator itself, dietary cues that are a result or a by-product of the digestion process of the predator, and alarm cues originating from injured prey. These different classes of cues are often difficult to separate experimentally. Therefore, distinct prey responses to either one or the other kind of cue are, for now, not detectable as long as we are not able to synthesize pure kairomones and/or alarm cues, respectively. From an ecological point of view, this might not be relevant, as those cues are unlikely to occur singularly under natural conditions.

More than just chemical cues can induce defences. There is evidence that zooplankton also use physical stimuli for predation risk assessment. It has been demonstrated that small scale turbulence can induce defences in *D. cucullata* and in *B. longirostris* as well as in (marine) copepods [150,223,238,239]. The induction through turbulence is presumably not triggered by wind or storm events, but is thought to result from the predator's movement while swimming or hunting [223]. Visual cues can also be important for the recognition of predators. A behavioural response in mysids has been triggered by a combination of chemical and visual stimuli, but not by one stimulus alone [89]. It is thought that these cues act synergistically for the prey's assessment of whether there is an actual predation risk, and to save costs if predators are present in the system, indicated by chemical cues, but are not in physical proximity [223].

Lass and Spaak [17] have pointed out that the induction scenario becomes even more convoluted in the context of a complex chemical environment with multiple stressors. In addition to the abiotic and biotic factors pointed out before, many recent studies have investigated interactions between predator cues and anthropogenic substances, such as drugs, heavy metals, and chemical additives (e.g., flame retardants, plasticisers, or stabilisers). Indeed, many substances have been found that are able to interfere with, counteract, or inhibit the induction of a defence (e.g., [236,240–247]). Reasons for this influence on inducible defences in zooplankton are poorly understood and presumably manifold. They may also involve the inhibition of receptors or molecular pathways, or may provoke reversed responses that counteract defence development. The transfer of information may also be diminished through the adsorbance of kairomones to surfaces, e.g., to plastic waste, as was shown using high-density polyethylene (HDPE) and polyethylene terephthalate (PET). When the respective plastic particles were present in the water, they significantly reduced the defence strength in *D. longicephala* against *N. glauca* [248]. This might be important, as plastic vessels should be avoided when kairomones are stored and/or applied. However, we will not go into detail of those eco-toxicological aspects here, as they are not the focus of this review.

## 5. Conclusions and Future Perspectives

Although huge efforts have been invested into research on inducible defences within the last century, hitherto unknown inducible defences are still being discovered, especially regarding morphological defences. Here, striking discoveries of previously unknown defences include the *crown of thorns*, the thickening of the carapace, and the loss of the bilateral symmetry [157]. The exact mode of action for each of the above explained morphological defences is still not known, and it seems that we have only scratched the surface of the effects that combinations of multiple factors may evoke on inducible defences [28,202]. Those factors comprise abiotic (i.e., light, UV-radiation, oxygen, temperature, pCO<sub>2</sub>, or water chemistry), biotic (i.e., bacterial degradation and/or facilitation,

predator species, predator age or instar, predator and prey density, food availability, and the predatory history), and anthropogenic factors (i.e., drugs, heavy metals, and xenobiotics), which may even interact in their effects on defence induction. All the research (see Table A1) conducted in the past few decades highlights the complexity of inducible defences in freshwater zooplankton, and also reveals significant gaps in knowledge, especially regarding the specific mechanism modulating defence induction and their significance for ecosystem processes. Thus, we need to keep up the recent trend for more multifaceted experiments, such as the investigation of stressor interactions. Furthermore, multipredator studies are required, considering the above mentioned recommendations of Relyea [249]. Following these recommendations may facilitate the interpretation of experimental data and may allow for the creation of a more holistic understanding of inducible defences against multiple predators.

With the growing knowledge in this research field, we are forced to increase the complexity of our experiments to understand interaction effects and how they affect the dynamics of predator–prey interactions. For this, it will be necessary to combine laboratory experiments with field observations and to test whether findings and conclusions drawn from laboratory experiments can be found in the field. Additionally, new findings on kairomones will help to work with and to standardize the application of kairomones and may allow for the quantification of the kairomones in the field in future studies. We have just opened an exciting new chapter in the field of predator–prey interactions, in which the recent work on freshwater zooplankton has revealed new avenues that now need to be explored in future research.

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## Appendix A

**Table A1.** Collection of studies completed since 2003 on inducible defences in zooplankton, each listed with their specific characteristics. Prey and predator species are specified to the level mentioned in the respective study. In cases of uncertainty, whether a single or a set of clones were used or where no clonal lineages were applicable, n.a. is quoted.

Zooplankton Species	Predator	Behaviour	Morphology	Life-History	Single Clone	Multiple Clones	Field Study	Laboratory Study	Source
<i>Argyrodiaptomus falcifer</i>	<i>Cnesterodon decemmaculatus</i>	x			n.a.	n.a.		x	[58]
<i>Bestiolina similis</i>	<i>Amphiprion ocellaris</i>	x			n.a.	n.a.		x	[239]
<i>Bosmina coregoni</i>	Fish	x			n.a.	n.a.	x		[80]
<i>Bosmina longirostris</i>	<i>Acanthocyclops vernalis</i>		x			x		x	[238]
	Copepoda		x	x	n.a.	n.a.	x		[106]
	<i>Coregonus alba</i>		x	x	n.a.	n.a.	x		[117]
	<i>Craspedacusta sowerbii</i>		x	x	n.a.	n.a.	x		[168]
	Fish	x			n.a.	n.a.	x		[80]
	<i>Leptodora kindtii</i>		x	x	n.a.	n.a.		x	[164]
	<i>Mesocyclops leuckarti</i>		x	x	n.a.	n.a.	x		[13,106]
	<i>Mesocyclops sp.</i>		x	x	n.a.	n.a.		x	[95]
<i>Bosmina fatalis</i>	Copepoda		x	x	n.a.	n.a.	x		[170]
	<i>Leptodora kindtii</i>		x	x	n.a.	n.a.		x	[106]
	<i>Mesocyclops leuckarti</i>	x	x	x	n.a.	n.a.	x		[164]
	<i>Mesocyclops sp.</i>		x	x	n.a.	n.a.		x	[13,106]
	<i>Mesocyclops leuckarti</i>	x	x	x	n.a.	n.a.		x	[95]
<i>Bosmina sp.</i>	Fish	x			n.a.	n.a.	x		[170]
	<i>Mochlonyx fuliginosus</i>	x			n.a.	n.a.	x		[54]
<i>Brachionus calyciflorus</i>	<i>Asplanchna brightwelli</i>		x		x			x	[54]
	<i>Asplanchna sieboldi</i>		x	x	n.a.	n.a.		x	[179]
	<i>Asplanchna sp.</i>		x		x			x	[178]
	<i>Asplanchna sp.</i>		x		x			x	[177]
	<i>Daphnia pulex</i>		x		x			x	[233]
			x		x			x	[179]

Table A1. Cont.

Zooplankton Species	Predator	Behaviour	Morphology	Life-History	Single Clone	Multiple Clones	Field Study	Laboratory Study	Source
<i>Brachionus havaensis</i>	<i>Asplanchna sieboldi</i>		x		x			x	[177]
<i>Brachionus macracanthus</i>	<i>Asplanchna sieboldi</i>		x		x			x	[177]
<i>Brachionus patulus</i>	<i>Asplanchna sieboldi</i>		x		x			x	[177]
<i>Brachionus rubens</i>	<i>Asplanchna sieboldi</i>		x		x			x	[177]
<i>Brachionus variabilis</i>	<i>Asplanchna girodi</i>	x	x		x			x	[92]
	<i>Daphnia pulex</i>	x	x		x			x	[92]
<i>Chydorus Sphaericus</i>	Various	x			x		x		[80]
<i>Ceriodaphnia cornuta</i>	<i>Aeolosoma sp.</i>		x	x	x			x	[102]
	<i>Skiffia lermiae</i>		x	x	x			x	[102]
<i>Ceriodaphnia dubia</i>	<i>Aeolosoma sp.</i>		x	x	x			x	[102]
	<i>Chaoborus sp.</i>	x			n.a.	n.a.		x	[91]
	<i>Cnesterodon decemmaculatus</i>	x			n.a.	n.a.		x	[58]
	<i>Macrobrachium borellii</i>	x			n.a.	n.a.		x	[91]
	<i>Melanotaenia duboulayi</i>	x			n.a.	n.a.		x	[98]
	<i>Skiffia lermiae</i>			x	x	x		x	[102]
	<i>Trichodactylus borellianus</i>	x				n.a.	n.a.	x	[91]
<i>Ceriodaphnia reticulata</i>	<i>Mesocyclops leuckarti</i>	x	x		x			x	[95]
	<i>Rutilus rutilus</i>	x		x	x			x	[81]
<b>Copepoda</b>	<i>Gambusia hubbsi</i>		x		n.a.	n.a.		x	[33]
	<i>Rutilus rutilus</i>	x	x		n.a.	n.a.	x		[65]
<i>Cyclops abyssorum</i>	Fish	x			n.a.	n.a.	x		[48]
<i>Daphnia ambigua</i>	<i>Chaoborus sp.</i>		x		x			x	[143]
<i>Daphnia atkinsoni</i>	<i>Triops cancriformis</i>		x			x		x	[154,155]
<i>Daphnia barbata</i>	<i>Notonecta glauca</i>		x		x			x	[28]
	<i>Triops cancriformis</i>		x		x			x	[28,157]

Table A1. Cont.

Zooplankton Species	Predator	Behaviour	Morphology	Life-History	Single Clone	Multiple Clones	Field Study	Laboratory Study	Source
<i>Daphnia cucullata</i>	<i>Chaoborus flavicans</i>		x		x			x	[22,223,233]
	<i>Chaoborus</i> sp.		x		x			x	[143]
	<i>Cyclops</i> sp.		x		x			x	[202,223]
	<i>Leptodora kindtii</i>		x		x			x	[202]
	Fish	x			n.a.	n.a.	x		[80]
	<i>Phoxinus phoxinus</i>			x		x		x	[66]
	<i>Rutilus rutilus</i>				x	x		x	[205]
<i>Daphnia curvirostris</i>	<i>Chaoborus crystallinus</i>		x			x		x	[107]
<i>Daphnia dentifera</i>	<i>Chaoborus punctipennis</i>			x		x		x	[212]
	<i>Lepomis macrochirus</i>			x		x		x	[212]
<i>Daphnia galeata</i>	<i>Chaoborus</i> sp.			x		x	x	x	[195]
	<i>Gasterosteus aculeatus</i>			x		x		x	[222]
	Fish	x			n.a.	n.a.	x		[54,60]
	<i>Lepomis macrochirus</i>		x			x		x	[101]
	<i>Leucaspis delineatus</i>	x				x		x	[60]
	<i>Leuciscus idus</i>			x	x	x		x	[4]
					x	x	x	x	[195]
	<i>Mochlonyx fuliginosus</i>	x				n.a.	n.a.	x	[54]
	<i>Perca fluviatilis</i>	x				x		x	[72]
					x	x		x	[222]
	<i>Rhodeus sericeus amarus</i>				x	x		x	[213]
	<i>Scardinius erythrophthalmus</i>			x		x		x	[203]
<i>Daphnia hrbaceki</i>	<i>Chaoborus crystallinus</i>		x			x		x	[107]

Table A1. Cont.

Zooplankton Species	Predator	Behaviour	Morphology	Life-History	Single Clone	Multiple Clones	Field Study	Laboratory Study	Source
<i>Daphnia hyalina</i>	<i>Chaoborus sp.</i>			x		x	x	x	[195]
	<i>Leuciscus idus</i>			x		x	x	x	[195]
	<i>Perca fluviatilis</i>	x			x			x	[72]
	<i>Poxinus phoxinus</i>		x		x			x	[66]
	<i>Rutilus rutilus</i>			x	x			x	[205]
<i>Daphnia hyalina x galeata</i>	<i>Chaoborus sp.</i>			x		x	x	x	[195]
	Fish	x			x			x	[79]
	<i>Leuciscus idus</i>			x		x	x	x	[195]
	<i>Perca fluviatilis</i>	x			x			x	[59,72]
	<i>Rutilus rutilus</i>	x		x	x			x	[81]
	<i>Rutilus rutilus</i>			x	x			x	[210]
<i>Rhodeus sericeus amarus</i>				x		x	x	[213]	
<i>Daphnia laevis</i>	<i>Oreochromis spp.</i>		x	x		x		x	[45]
<i>Daphnia longicephala</i>	<i>Notonecta glauca</i>		x		x			x	[22,233]
	<i>Notonecta sp.</i>		x	x	x			x	[248]
	<i>Notonecta sp.</i>		x		x			x	[143,245]
<i>Daphnia longispina</i>	Various	x			x		x		[80]
	<i>Coregonus alba</i>		x	x	n.a.	n.a.	x		[117]
	<i>Chaoborus flavicans</i>		x		n.a.	n.a.	x		[144]
	<i>Chaoborus sp.</i>		x			x	x	x	[145]
	Fish	x			n.a.	n.a.	x		[80]
	<i>Gambusia holbrooki</i>			x	x			x	[220]
	<i>Lepomis gibbosus</i>			x	x			x	[220]
	<i>Notonecta glauca</i>			x		x		x	[30]
	<i>Scardinius erythrophthalmus</i>	x			x		x	x	[240]

Table A1. Cont.

Zooplankton Species	Predator	Behaviour	Morphology	Life-History	Single Clone	Multiple Clones	Field Study	Laboratory Study	Source	
<i>Daphnia lumholtzi</i>	<i>Chaoborus flavicans</i>		x			x		x	[131]	
	<i>Chaoborus punctipennis</i>		x	x	x			x	[116]	
	<i>Gasterosteus aculeatus</i>		x			x		x	[131]	
	<i>Lepomis macrochirus</i>		x	x	x			x	[116]	
	<i>Leucaspis delineatus</i>		x	x		x		x	[132]	
	<i>Phoxinus phoxinus</i>			x		x		x	[22,143]	
<i>Daphnia magna</i>	<i>Abramis brama</i>	x				x		x	[96]	
	<i>Carassius carassius</i>			x	x			x	[192,193]	
		x				x		x	[232]	
	<i>Chaoborus crystallinus</i>			x	x			x	[241]	
		x					x	x	[96]	
	<i>Chaoborus obscuripes</i>			x	x			x	[241]	
	<i>Danio rerio</i>	x					x	x	[96]	
	Fish	x	x	x			x	x	[124]	
					x	x			x	[188]
	<i>Gambusia holbrooki</i>				x	x			x	[183]
	<i>Gasterosteus aculeatus</i>	x			x	x			x	[99]
	<i>Ischmura elegans</i>	x				n.a.	n.a.		x	[88]
	<i>Lepomis gibbosus</i>				x		x		x	[208]
	<i>Leucaspis delineatus</i>		x				x		x	[96]
					x	x			x	[189,194]
<i>Leuciscus idus</i>				x	x			x	[221]	
				x		x		x	[190,206]	
<i>Notonecta glauca</i>				x	x			x	[183]	
<i>Notonecta sp.</i>	x					x		x	[96]	

Table A1. Cont.

Zooplankton Species	Predator	Behaviour	Morphology	Life-History	Single Clone	Multiple Clones	Field Study	Laboratory Study	Source
	<i>Perca fluviatilis</i>			x	x			x	[119,120]
		x			x			x	[72]
	<i>Pseudorasbora parva</i>	x			n.a.	n.a.		x	[90]
	<i>Rhodeus amarus</i>			x	x	x		x	[190]
				x	x				[214]
	<i>Rutilus rutilus</i>	x			x			x	[227]
		x		x	x			x	[23]
	<i>Salmo trutta</i>			x	x			x	[236]
			x		x			x	[156,158]
			x			x		x	[108]
	<i>Triops cancriformis</i>			x		x		x	[191]
				x	x			x	[211,214]
	<i>Bythotrephes longimanus</i>		x			x		x	[161]
		x		x	n.a.	n.a.		x	[55]
<i>Daphnia mendotae</i>	<i>Chaoborus punctipennis</i>		x		n.a.	n.a.		x	[201]
	<i>Lepomis macrochirus</i>			x	x			x	[181]
	<i>Leptodora kindtii</i>		x		n.a.	n.a.		x	[201]
	<i>Perca flavescens</i>	x		x	n.a.	n.a.	x		[82]
<i>Daphnia middendorffiana</i>	<i>Phoxinus phoxinus</i>		x		x			x	[66]
<i>Daphnia minnehaha</i>	<i>Chaoborus americanus</i>		x			x	x		[27]
	<i>Chaoborus trivittatus</i>		x			x	x		[27]
<i>Daphnia obtusa</i>	<i>Micropterus salmoides</i>	x			x			x	[101]

Table A1. Cont.

Zooplankton Species	Predator	Behaviour	Morphology	Life-History	Single Clone	Multiple Clones	Field Study	Laboratory Study	Source	
<i>Daphnia pulex</i>	<i>Alburnus alburnus</i>	x			x			x	[49,218,219]	
		x			n.a.	n.a.		x	[49]	
	<i>Alburnus escherichi</i>				x	n.a.	n.a.		x	[246]
		x					x		x	[56]
	<i>Chaoborus americanus</i>				x		x		x	[197,204]
				x		x			x	[243,247]
				x			x	x		[27]
		x			x	x		x		[84]
	<i>Chaoborus crystallinus</i>			x			x		x	[244]
				x					x	[107]
	<i>Chaoborus flavicans</i>				x	x			x	[196]
							x		x	[44]
		x		x	x		x		x	[42]
				x			x		x	[14,148,233]
				x			n.a.	n.a.	x	[144]
		x					x		x	[44]
				x				x		[109]
				x		x	x			[198]
						x		x		[211,215]
		<i>Chaoborus obscuripes</i>			x		x			x
<i>Chaoborus sp.</i>			x		x			x	[143,245]	
<i>Chaoborus trivittatus</i>		x				x		x	[44]	
		x	x	x		x		x	[42]	
		x	x			x	x		[182]	
			x			x	x		[27]	
		x				x		x	[44]	
		x			x	x			[84]	

Table A1. Cont.

Zooplankton Species	Predator	Behaviour	Morphology	Life-History	Single Clone	Multiple Clones	Field Study	Laboratory Study	Source	
	<i>Gasterosteus aculeatus</i>			x	x			x	[196]	
	<i>Mesocyclops leuckarti</i>	x	x		x			x	[95]	
	<i>Notemigonus crysoleucas</i>	x				x		x	[44]	
		x	x	x		x		x	[42]	
		x					x	x	[44]	
	<i>Phoxinus phoxinus</i>		x		x			x	[66]	
	<i>Scardinius erythrophthalmus</i>			x		x		x	[203]	
	<i>Chaoborus flavicans</i>	x	x	x		x		x	[42]	
	<i>Chaoborus sp.</i>			x		x		x	[242]	
		x				x		x	[97]	
	<i>Chaoborus trivittatus</i>	x	x	x		x		x	[42]	
	<i>Daphnia pulicaria</i>			x	x			x	[207]	
		<i>Lepomis macrochirus</i>			x	x		x	[181]	
		x				n.a.	n.a.		x	[57]
		x				x			x	[97]
		<i>Leucaspius delineatus</i>		x	x		x		x	[132]
	<i>Notemigonus crysoleucas</i>	x	x	x		x		x	[42]	
	<i>Perca flavescens</i>	x		x	n.a.	n.a.	x		[82]	
	<i>Rutilus rutilus</i>			x	x			x	[210]	
	<i>Chaoborus obscuripes</i>			x	x			x	[184]	
	<i>Gasterosteus aculeatus</i>			x	x			x	[184]	
	<i>Lepomis macrochirus</i>		x			x		x	[101]	
	<i>Oreochromis spp.</i>		x	x	x			x	[45]	
	<i>Cyclops vicinus</i>		x		n.a.	n.a.	x		[123]	
<i>Daphnia similoides sinensis</i>	<i>Leptodora richardi</i>		x		n.a.	n.a.	x		[123]	
	<i>Neosalanx taihuensis</i>		x		n.a.	n.a.	x		[123]	

Table A1. Cont.

Zooplankton Species	Predator	Behaviour	Morphology	Life-History	Single Clone	Multiple Clones	Field Study	Laboratory Study	Source
<i>Daphnia spinulata</i>	<i>Oreochromis spp.</i>		x	x	x			x	[45]
<i>Daphnia sp.</i>	<i>Coregonus alba</i>		x	x	n.a.	n.a.	x		[117]
	<i>Lepomis macrochirus</i>	x			n.a.	n.a.	x		[61]
	<i>Rutilus rutilus</i>	x			n.a.	n.a.	x		[83]
<i>Diaphanosoma brachyurum</i>	Fish	x			n.a.	n.a.	x		[54,80]
	<i>Mesocyclops leuckarti</i>	x	x		x			x	[95]
	<i>Mochlonyx fuliginosus</i>	x			n.a.	n.a.	x		[54]
	Various	x			x		x		[80]
<i>Diaphanosoma birgei</i>	<i>Hyphessobrycon bifasciatus</i>			x		x		x	[187]
<i>Eubosmina coregoni</i>	Various	x			x		x		[80]
<i>Eubosmina coregoni coregoni</i>	<i>Mesocyclops leuckarti</i>		x			x		x	[169]
<i>Eubosmina coregoni gibbera</i>	<i>Mesocyclops leuckarti</i>		x			x		x	[169]
<i>Eubosmina coregoni kessleri</i>	<i>Mesocyclops leuckarti</i>		x			x		x	[169]
<i>Eubosmina coregoni thersites</i>	<i>Mesocyclops leuckarti</i>		x			x		x	[169]
<i>Eubosmina longispina</i>	<i>Coregonus alba</i>		x	x	n.a.	n.a.	x		[117]
<i>Eudiaptomus gracilis</i>	Fish	x			n.a.	n.a.	x		[48]
<i>Keratella tropica</i>	<i>Asplanchna brightwelli</i>		x	x	n.a.	n.a.		x	[176]
			x		n.a.	n.a.		x	[179]
	<i>Daphnia pulex</i>		x	x	n.a.	n.a.		x	[176]
			x		n.a.	n.a.		x	[179]
<i>Moina macrocopa</i>	<i>Chaoborus obscuripes</i>			x	x			x	[184]
	<i>Gasterosteus aculeatus</i>			x	x			x	[184]
<i>Moina micrura</i>	<i>Gasterosteus aculeatus</i>			x	x			x	[187]
	<i>Hyphessobrycon bifasciatus</i>			x		x		x	[187]
<i>Neomysis integer</i>	<i>Perca fluviatilis</i>	x			n.a.	n.a.		x	[89]

Table A1. Cont.

Zooplankton Species	Predator	Behaviour	Morphology	Life-History	Single Clone	Multiple Clones	Field Study	Laboratory Study	Source
<i>Notodiaptomus conifer</i>	<i>Chaoborus sp.</i>	x			n.a.	n.a.		x	[91]
	<i>Cnesterodon decemmaculatus</i>	x			n.a.	n.a.		x	[58]
	<i>Macrobrachium borellii</i>	x			n.a.	n.a.		x	[91]
	<i>Trichodactylus borellianus</i>	x			n.a.	n.a.		x	[91]
<i>Plationus macracanthus</i>	<i>Asplanchna brightwellii</i>		x	x	n.a.	n.a.		x	[178]
<i>Praunus flexuosus</i>	<i>Perca fluviatilis</i>	x			n.a.	n.a.		x	[89]
<i>Pseudosida variabilis</i>	<i>Cnesterodon decemmaculatus</i>	x			n.a.	n.a.		x	[58]
<i>Simocephalus serrulatus</i>	<i>Aeolosoma sp.</i>		x	x	x			x	[102]
	<i>Skiffia lermæ</i>		x	x	x			x	[102]
<i>Simocephalus vetulus</i>	<i>Aeolosoma sp.</i>		x	x	x			x	[102]
	<i>Skiffia lermæ</i>		x	x	x			x	[102]
Various zooplankton	<i>Chaoborus flavicans</i>	x			n.a.	n.a.	x		[26]

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