

Review

# Parental Effects and Reproductive Potential of Fish and Marine Invertebrates: Cross-Generational Impact of Environmental Experiences

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**Abstract:** The reproductive success of aquatic animals depends on a complex web of relationships between the environment, the attributes of the reproductive individuals and human-induced selection. All of them are manifested directly or indirectly through parental effects, which can also compensate for certain external impacts. Parental effects refer to the influence that the phenotype and environmental conditions in which individuals develop exert on the phenotype of their offspring, and they can even have transgenerational impact. This paper describes the different types of parental effects and reviews the published literature to analyze the causes of their variation and their impact on reproductive resilience and population dynamics.



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## 1. Introduction

During the 20th century, studies of fish population dynamics were based on the erroneous assumption that all individuals in a population have the same productivity [1]. In 1999, the term *reproductive potential* was coined to define the ability of a population to produce viable offspring that become recruited to the fishery [2]. This capacity depends on the parental characteristics (length, age, condition, etc.); therefore, the reproductive potential of a stock (SRP) is not proportional to the spawning stock biomass. The parameters mostly used to measure the SRP are fecundity, number of spawning, size and quality of eggs and larvae, and the time and duration of the spawning season, among others [3]. Parental effects refer to the influence that the phenotype and environmental conditions in which individuals develop exert on the phenotype of their offspring. The phenotype of an individual would not only be determined by its own genotype (inherited from its parents) and the environment in which it develops, but also by the phenotype and environmental experience of its parents [4]. An example of a parental effect would be the influence of the condition of reproductive females on larval size, which would reflect how the environment experienced by the mother (food availability) affects offspring characteristics (larval length) [5].

To date, the study of parental effects in aquatic animals has been dominated by research on maternal effects (i.e., derived from females), considering that the role of males was limited to gene transmission; and therefore, any paternal influence on offspring would derive exclusively to genotypic aspects [6,7] or fertilization success [8]. However, an increasing number of studies demonstrate the existence of paternal effects in aquatic

organisms, ranging from the direct influence of paternal attributes on offspring quality [9,10] or from the influence of parental behavior [11] on offspring survival, to the impact of the environment on male reproductive success [12–14]. Recent evidence shows that epigenetic factors transferred in the sperm to offspring, such as non-coding RNAs, DNA methylation or chromatin structure, also affect gene expression in developing embryos [15].

However, parental effects can have much more complex dynamics, with interactions between maternal and paternal effects. In this sense, Siddique et al. [16] demonstrated that different family combinations have an important impact on fish embryonic development. Lymbery and colleagues [17] reported how egg chemical fluids interact with sperm to define fertilization rate and offspring variability in blue mussel (*Mytilus galloprovincialis*). Even more, life strategy can be an additional source of complexity (see Section 3). For example, in some syngnathid species, such as *Syngnathus fucus*, nutrient transfer from the father to the offspring during the period of offspring care has been demonstrated, and such transfer could compensate for nutritional deficiencies of the eggs derived from a reduced maternal energetic investment [18]. Furthermore, in aquatic animals, the weight of maternal over paternal effects on offspring phenotype may be related to environmental stability [19]. In summary, the phenotype of the offspring is the result, not only of the interaction of its own genotype with the surrounding environment, but also of a complex web of relationships between the environment, genotype and phenotype of both parents.

Parental effects are not necessarily positive or adaptive; examples of negative effects would be pollutant transmission during embryonic development [20] or inappropriate site [21] or timing [22] of spawning.

Parental effects can result from: (i) the genetic or phenotypic characteristics of the parents, for example when larger females produce larger offspring [23], which is known as *parental inheritance* or *indirect genetic effects*, (ii) the parental behavior, for example the impact of parental care on offspring survival [24], which is known as *parental selection*, or (iii) the environment experienced by the parents, as in the case of ingested pollutants that are transmitted to the embryos, affecting their development used as an example above, which is known as *indirect environmental effects* [1,2].

Depending on the offspring life stage at which the parental effect occurs, they can be classified as: (i) *prezygotic* (the effect is on the characteristics of gametes and, therefore, is prior to fertilization), (ii) *prenatal postzygotic* (the effect is on embryonic development, both in fetuses and eggs) or (iii) *postnatal postzygotic* (the effect is on larvae and juveniles).

The existence of parental effects has a great influence on population dynamics. There are studies reporting that parental effects propagate through several generations [19,25,26]. Furthermore, they can play an important role in the evolutionary dynamics of a population, since selection for certain traits would no longer be determined exclusively by the genotype and phenotype of individuals, but also by the phenotype of preceding generations, i.e., parental effects can have a substantial impact on the rate and direction of genetic change in response to selection [27]. This issue is of particular relevance in the context of global change, as intergenerational parental effects can enhance rapid transgenerational responses to changing environments [28]. Parental exposure to a particular environment or stress has been shown to modify the phenotype of offspring to adapt to that environment; if the conditions in which the parents lived and reproduced are different from those experienced by their offspring, the offspring would be unable to adapt to the new conditions [11,29].

There are several papers that review in depth the mechanisms and implications of parental effects in general [4,30]. Regarding paternal effects, Curley et al. [31] and Rando [32] provide a review of some of the molecular mechanisms underlying such effects in animals, while Crean and Bonduriansky [33] describe the different types of paternal effects and their interactions with maternal effects.

## 2. Parental Effects and Population Dynamics

Parental effects and reproductive potential are key elements in the stock recruitment process and, therefore, for its dynamics. In the early larval stages, there is a high

mortality caused by environmental effects, including predation intensity and food availability [34]. However, survival in this period is selective and is mainly influenced by maternal effects [35,36], such that the number of survivors is largely determined by the quality of eggs and larvae [37]. Thus, the size of a population's cohort (year class) and its variability are mainly determined in the larval stage [38]. Therefore, it is a life stage with high potential for population regulation [39], as small differences in larval mortality can lead to large differences in cohort success.

Among the maternal effects, one of the most universal is the existence of an allometric relationship between female size and fecundity, i.e., larger females produce much more offspring than smaller ones [40,41]. Likewise, in some species, parental effects also affect offspring distribution and dispersal [35,42]. This is what has been termed *the bigger-is-better* hypothesis, which suggests that large females produce more and better eggs that result in larger larvae that are more likely to survive [36]. This is because, beyond the number, many of the factors that influence larval behavior and physiology are associated with their size. For example, large larvae develop larger and more energy-rich yolk sacs [39,43]; when these larvae hatch, they begin feeding earlier, exhibiting greater predation success and greater resistance to starvation than small ones [43]. Large size and high feeding ability are associated with higher rates of swimming activity and growth [44,45]; thus, they avoid predators better than small larvae [43]. Consequently, larvae that grow fast have higher survival, not only in the larval, but also in the juvenile [46] stages, which would enhance recruitment to the population. However, there are exceptions to this theory, as there is evidence that large larvae may also be more vulnerable to size-selective predation [47].

Beyond size, age and condition of females also affect offspring performance. Inter-annual variation in condition of spawning females leads to changes in fecundity in numerous species [48,49], in extreme cases even leading to the omission of spawning when females are in low condition [50]. Regarding age, in some species, females spawning for the first time (primiparous) have lower reproductive success than those that have already spawned in previous reproductive seasons (multiparous), affecting final recruitment [51]. Furthermore, it has been found that the age structure of the parental stock determines the timing and duration of the spawning season [52,53]. A protracted spawning period, especially in highly variable environments, reduces the impact of punctual events of high egg and larval mortality [54] by increasing the probability that some of the clutches coincide with optimal environmental windows. In that sense, species that are multiple spawners (females produce several batches within the spawning period or have several spawning periods within the year) would have greater reproductive and recruitment success in stochastic environments than species that spawn in a single event [35], as they increase the chances of finding favorable conditions for offspring survival and decrease intraspecific competition in early life stages [38]. In summary, a prolonged spawning season or multiple spawning increases reproductive success in changing environments [55].

In relation to paternal effects, there are few studies relating male attributes directly to recruitment, although their influence on reproductive success has been demonstrated. For example, in Atlantic cod (*Gadus morhua*), the length of spawning males affects fertilization success [56] and embryo and larval survival [57]. In species where the male takes care of the offspring, a clear relationship between paternal attributes and larval growth and survival has been reported [58,59]. In the case of invertebrates, density-dependence can modulate paternal effects as well; for example, in ascidians, sperm phenotype is density dependent and influences offspring fitness [60], and similar male and female gamete plasticity with consequences in offspring adaptive capacity has been observed in other invertebrates [29,61]. Paternal effect on offspring resistance to parasitism has been also reported in three-spined sticklebacks, in which both genetic and non-genetic paternal inheritance modulates parasite tolerance of descendants and hence survival [62]. These cases demonstrate that population dynamics and parental effects are linked. In some cases, paternal effects are only manifested in male offspring [63] or only in female offspring [28], or sometimes even skip a generation, affecting grandchildren rather than the offspring

themselves [64]. Moreover, in some freshwater species, paternal effects on embryonic stages can outweigh maternal effects [16]. Although studies focusing on paternal effects on recruitment are scarce, research on male reproductive potential and its influence on offspring fitness indicates that the impact of paternal effects on population dynamics is greater than previously considered.

Another important aspect that impacts on larval survival and recruitment and is influenced by the demographic structure of the stock is the location of spawning areas [65,66]. The spawning area is also the larval habitat; thus, choosing spawning areas with optimal environmental conditions will favor larval survival and recruitment [67]. Spawning spatial patterns vary depending on the size and age of the spawners as well, with larger females being located in optimal zones [68,69]. The effect of age on breeding site location is clearly established in the *entrainment hypothesis* developed by Petitgas et al. [70] based on observations of migratory fish. According to this hypothesis, repeat (older) females are responsible for maintaining migratory routes to spawning grounds. In these species, individuals spawn in the area where they first spawned, and after, adult individuals mix with juveniles in the feeding grounds. In the following reproductive season, the multiparous adults “entrain” the primiparous individuals to the areas where they have already spawned successfully. Once these primiparous individuals have spawned in a particular location, they will always return to the same site. This behavior means that changes in age structure of the population or environmental conditions of the spawning area impact the reproductive success of the stock. In the case of North Sea flounder, overexploitation depleted the larger and more experienced individuals to such an extent that the reproductive migration routes changed because there were no individuals able to guide the rest to the traditional spawning grounds [70].

Quantifying the direct impact of parental effects on annual recruitment is difficult, as great uncertainty is associated with the larval stage, where mortality due to environmental causes is high. However, recruitment has been shown to be positively correlated with the proportion of old females in several species, both in marine and freshwater vertebrates [71,72], as well as invertebrates [73]. However, beyond recruitment, it is necessary to take into account that parental effects can propagate over several generations [74–76]. The issue is that in the case of a sparse offspring in poor conditions producing a second generation with reduced reproductive potential, parental effects would have a deeper and more prolonged impact on stock dynamics than expected a priori, based on the traditional stock-recruitment relationship.

### 3. Influence of Life Strategies on Parental Effects

The degree of impact that parental effects have on population dynamics is defined by how individuals experience and respond to different environmental factors. This response is mediated in part by specific physiological mechanisms, which in turn are intimately linked to their life (range of strategies between K and r), energetic (growth vs. reproduction, capital and income breeders, sexual dimorphism, etc.) and reproductive strategies (oviparity vs. viviparity, polyandry, etc.), as well as their behavior (reproductive migrations, mating system, courtship, offspring care, etc.). Therefore, the type of parental effects (*parental inheritance*, *parental selection* or *indirect environmental effects*) and the time at which they exert their influence (*prezygotic*, *prenatal-* or *postnatal-postzygotic*) are intimately related to the life strategy and tactic of each population.

According to the *Life History Theory* (LHT), K-strategists are defined as species that invest more in the care of offspring than in numbers, as opposed to r-strategists, with a continuum of intermediate strategies between the two extremes [77]. In general, it is assumed that species in fluctuating and unpredictable environments tend to an r-type strategy, and to the K-type when living in stable environments [78]. In this sense, it is expected that parental selection (resulting from the behavior of the parents) and *postnatal postzygotic effects* (influencing larvae and juveniles) be more common in K-type species, due to the special investment they make in the care of the offspring. Benefits of parental care on

offspring fitness and survival have been documented in several studies [79,80], although no significant effects are relatively common at least in fish [24].

Conversely, in capital breeder species, i.e., those that accumulate reserves for reproduction in advance of the spawning season onset, the *indirect environmental effects* will be delayed with respect to the time of spawning. By contrast, in income breeder species, the influence of these effects will be simultaneous, since the energy acquired through feeding is used in reproduction almost immediately [81].

In the case of species with internal fertilization, courtship systems or offspring care, mate selection undoubtedly has a profound impact on the characteristics of the offspring, and this selection can be influenced by the environment. A clear example of this type of interaction is the common goby (*Pomatoschistus microps*), a species in which the male uses the noises emitted by the swim bladder to attract the female (Ref. [13] and references therein). When males of this species form nests in areas of high noise pollution, their probability of successful mating decreases, as females evaluate the suitability of males based on the sounds they emit [13]. Thus, males with the same characteristics (size, vocal ability, etc.) will have lower reproductive success in noisy areas.

In aquatic ecosystems, polygynandry (males and females have multiple mating partners along the breeding season) is the most extended reproductive strategy in species, especially in those with external fertilization, but not the only one. However, having multiple mating partners during a breeding season influences their descendants' fitness, as it increases the chances of mating with a compatible partner, promotes sperm competition, and enhances genetic diversity [82]. For example, high sire diversity increases larval growth rate of the gastropod *Crepidula fornicata* [83], and the fertilization and hatching rates in the polychaete *Galeolaria caespitosa* [84]. In that sense, it is expected that greater genetic diversity will lead not only to an increase in the survival of the offspring, but also to a greater adaptive capacity of the offspring to environmental changes (see Section 5). Interspecific regulation of parental effects have been documented as well in parasite–host systems. Parental effects of parasites are largely determined by the choice of host, and at the same time, the parasite itself modulates the host's parental effects on its offspring. [30]. This could have profound implications for parasite–host co-evolution and sympatric speciation processes. Although no such studies have been found in aquatic animals, similar interactions should be expected. Similarly, predator stress can also modulate parental effects, altering the mating behavior of descendants [28].

With respect to reproductive strategy at the population level, those species that have a synchronized spawning season over a relatively short period of time (the entire population reproduces in one or two months), will be less resilient to external changes than those that have a prolonged reproductive season or several annual spawning peaks, as the offspring are usually adapted to the environmental conditions to which their parents are exposed [11,29]. Therefore, their progeny will have a lower adaptive capacity, reducing the survival rate if the environment changes.

In conclusion, not only does the specific life strategy modulates parental effects, but the interspecific interactions do as well, adding complexity to the mechanisms that regulate the reproductive success of aquatic organisms.

#### 4. Temporal and Geographic Variability of Parental Effects and Reproductive Potential

As mentioned above, environmental factors and parental effects coexist and modulate the early life stages of aquatic organisms and are key in terms of recruitment variability [85,86]. Since environmental and parental attributes vary spatially and geographically, parental effects and their degree of impact on population dynamics will also vary. Such spatio-temporal variability is evident in *indirect environmental effects*. For example, marked seasonal fluctuations in temperature and productivity, characteristic of high latitudes, influence food availability and quality for both adult and juvenile fish [87,88]. Consequently, the accumulation of energy reserves and the physiological condition of spawning individuals may show temporal variations in relation to natural production cycles [89]; thus,

years with good conditions during the feeding season will allow adult fish to enter the spawning season with high energy reserves. Conversely, the amount of energy devoted to reproduction—for example, linked to reproductive migrations or physiological changes related to courtship—varies according to individual metabolic expenditure [90], which responds to temperature and oxygen availability [91]. This energy balance between basal metabolism, energetic reserves, growth and reproduction will determine fecundity, egg quality [92,93], fertilization rate [94] and larval survival [95], even leading to no annual spawning when the condition of breeding females is low [50]. Therefore, temporal or spatial variations in temperature and oxygen will affect the quantity and quality of available food and the metabolic tradeoffs of spawners, causing spatio-temporal changes in conditions and, therefore, in reproductive success.

An example of the intra-annual or seasonal variability of parental effects can be found in European hake (*Merluccius merluccius*) in the Atlantic waters of the Iberian Peninsula. This species in this area presents three annual spawning peaks (winter–spring, summer and autumn) [96]. When analyzing the variability of maternal effects on the development of eggs and larvae in the three spawning peaks, it was observed that more and better quality eggs (larger diameter and dry weight) were produced in winter–spring than in the other spawning peaks [97]. For larvae, growth rates were similar regardless of hatching date, although those hatched in summer had more developed anterior body parts than those in winter–spring at the same age, which could also be associated with greater predatory capacity and, consequently, higher survival rate [97]. These authors propose that temporal differences in larval fitness and, hence, annual recruitment, are influenced by a combination of maternal attributes and environmental conditions. This suggests that the intensity of the impact of any stressor on the population dynamics of European hake in this area depends on the time of year it occurs. Another example of seasonal variability of maternal effects has been documented for some clupeiformes in which egg size decreases as the reproductive season progresses, which is related not only to variations in maternal energy reserves, but also to changes in the age structure of the spawning stock and changes in temperature that affect oogenesis [98].

Inter-annual differences in parental effects have their origin in both dense-dependent and dense-independent factors. Among the most studied dense-dependent factors in fish are those related to growth and condition, the greater the abundance of individuals, the greater the intraspecific competition (less resources available), which causes a lower growth rate and poorer condition of individuals, with consequent effects on length and age at maturity, growth and reproductive potential [99,100]. However, there are other dense-dependent mechanisms that regulate parental effects, although they have been less studied. In some species that form reproductive aggregations, such as sea urchins of the genus *Strongylocentotus*, the rate of egg fertilization decreases with increasing distance between individuals or when the abundance of breeders (especially males) falls, mainly due to sperm dilution in the aquatic environment [101,102]. In the case of species with social mechanisms of reproductive control, such as the damselfish (*Pomacentrus amboinensis*) which forms reproductive pairs, an increase in the number of females in the breeding area, even when they do not have access to the reproductive partner, induces aggressive behavior of the spawning females, which increases cortisol levels (the stress hormone), causing a reduction in the size of the larvae produced by these females [37]. In other words, in years when the abundance of reproductive females decreases, the reproductive potential could increase.

Dense-independent factors driving inter-annual variation of parental effects have been especially studied in short-lived pelagic fishes, where environmental influence is much more pronounced. For example, in the Humboldt upwelling system of Peru, the reproductive success of anchoveta (*Engraulis ringens*) is high in years considered normal or during cold events of La Niña [103]. In the case of *Engraulis anchoita*, reproductive success is related not only to sea surface temperature, but also to the abundance of copepods, which is the main food of adults during the spawning season [104]. These types of environmental

variations can be particularly pronounced in highly changing ecosystems, such as coastal lagoons, such as the Laguna de Rocha (Uruguay). During 2010–2011, as a consequence of La Niña, the lagoon showed a drastic increase in salinity that caused an interruption of *Brevortia aurea* spawning during autumn and late maturation in spring [105], which probably affected egg and larval survival.

The observed geographic differences in reproductive patterns are linked to variable environmental conditions, which is considered strong evidence of intraspecific life history evolution in fishes [106]. In keeping with *Bergmann's rule*, which indicates an increase in body size toward higher latitudes, ectothermic organisms inhabiting relatively lower temperatures (characteristic of high latitudes) typically mature later and at larger sizes compared to conspecifics inhabiting higher temperatures [107]. The magnitude and direction of this variation is predicted by the *temperature–size rule*, whereby lower temperatures result in a lower initial growth rate and delayed maturation with larger body size [107]. Fernandez-Torres et al. [108] concluded that fish clearly follow such a pattern, with the largest species in temperate and cold regions. Furthermore, they observed a differential response of body size to the environment related to temperature, salinity and human impact, which in turn would affect reproductive potential and the ability to adapt to changing environments.

Therefore, it is to be expected that low temperatures and short reproductive seasons at high latitudes would result in low annual production. However, within a theoretical framework of compensation, organisms inhabiting high latitudes may develop compensatory responses to these climatic effects, such as higher egg production rates [109]. The rate of egg production can be increased by consuming and/or assimilating more energy or by varying the way in which assimilated energy is distributed among growth, reproduction and metabolism [110]. In some brachyuran crabs, latitudinal differences in embryo size have been reported, being larger at higher latitudes, probably related to the greater amount of yolk deposited in the egg [111]. In marine invertebrates inhabiting low latitudes, with high temperatures and low dissolved oxygen concentration, females support high energetic cost associated with the active ventilation of eggs to provide sufficient oxygen to the embryos and to maintain them at an optimal temperature [112]. The higher metabolic cost derived from the care of the offspring leads to a decrease in the energy available for reproduction, which is reflected in a low number of eggs [113]. In addition, the high intensity of active ventilation also produces mechanical loss of embryos. Both mechanisms provoke variations in the reproductive potential of these species as a function of latitude [113]. Similarly, latitudinal environmental changes cause differences in the conditions of the parents [114,115], to such an extent that Lloret et al. [93] propose using the condition of individuals as an indicator of habitat quality to identify optimal environments and design marine protected areas.

## 5. Human-Induced Variability of Parental Effects and Reproductive Potential

In addition to natural variability, there are changes in maternal effects that can be human induced, through selection for certain traits or behaviors that can affect the diversity and, ultimately, the resilience of populations. Industrial effluents, agricultural activities, urban waste, increases in urbanization and accidental spills are sources of pollutant-driven physiological stress for aquatic animals. The effect of noise pollution in the mating selection of the common goby (*Pomatoschistus microps*) and how similar males would have lower reproductive success in noisy areas [13] has already been mentioned. However, there is extensive research on how pollution impacts the reproduction of aquatic organisms in both fresh [116] and marine waters [117]. For example, endocrine disruptors affect sexual maturation, gamete production and transport, sexual behavior, fertility, and gestation by altering the integrity of the reproductive system of aquatic animals [118,119]. Microplastics reduce reproductive potential of some aquatic animals [120], while heavy metals such as mercury directly affect the reproductive system but also indirectly influence parental effects by provoking dysfunction of coordination, loss of appetite, osmoregulation, orien-

tation or prey location [121]; some contaminants even alter the reproductive behavior of these animals [122].

Contaminants not only affect the physiological processes of the spawners, but also those of the offspring; that is, the effect may be cross-generational. For example, Yin et al. [123] observed that parental Benzo[a]pyrene (BaP) exposure induced circadian rhythm disorder in offspring. Being that the larvae of exposed parents were more sensitive to BaP, paternal exposure to BaP produced more severe damage on offspring DNA than maternal exposure.

Fishing is also a mechanism for human-induced selection of parental attributes, as in many cases, it tends to target certain fractions of the population (large individuals, juveniles, spawning migrants, males, etc.). For example, the removal of individuals of greater length and age in the population, generated by fishing activity, can lead to a negative effect on the reproductive potential of the stocks, by reducing the number and quality of spawned eggs, which would reduce larval survival rates [124]. In some commercial invertebrates such as spider crab (*Lithodes santolla*), the fishery is based on the selective exploitation of males greater than 110 mm carapace length, a management measure that aims to protect females that carry the fertilized eggs [125]. However, despite prohibiting the commercialization of ovigerous females, during the last few years, there has been a significant decrease in population fecundity [126]. The two hypotheses that explain this phenomenon are that: the elimination of larger males, which produce more and better sperm, has reduced fertilization rates in the population; conversely, the capture and subsequent return to the sea of ovigerous females causes a loss of eggs due to the stress generated during this process [127]. As mentioned above, if selectivity is intense, it may even result in genetic and evolutionary changes in populations [128], which are difficult to reverse, leading to regime shifts that directly affect the resilience of the population and ecosystem [129]. Beyond the selective effect of fishing, the stress generated by the fishing operation itself can have negative effects on offspring development derived from the physiological response of females [130]. The changes generated by overfishing in the different reproductive traits of populations, which affect their renewal potential, are much more marked in species particularly vulnerable to exploitation, such as hermaphrodites [131], elasmobranchs [132] or deep-sea species [133]. In the case of hermaphrodite species, the magnitude of this effect could depend on the type of factor, social or genetic, that prevails in the control of sex change [131]. While in elasmobranchs and deep sea species, it is their complex reproductive strategies, which include late maturation, slow growth and low fecundity, among other aspects, that are the main sources of reproductive vulnerability [133,134].

Aquaculture can also be a source of disturbance to the parental effects of wild populations. Transmission of parasites and diseases from cultured to wild fish can lead to a decline in the health status and condition of wild populations [135]. The escape of captive fish and hybridization with wild individuals can lead to a reduction in the genetic variability of the wild populations, which can cause maladaptations, reducing the fitness and reproductive success of wild individuals [56,136]. An example of these effects was observed in sockeye salmon (*Oncorhynchus nerka*) of the Cedar River (USA). A captive rearing program of sockeye salmon was initiated in the Cedar River for restocking wild populations in the mid-1990s. These salmon were fed an enriched diet and tended to begin spawning earlier than wild populations, before optimum water temperature was reached. Release of these individuals to the wild resulted in a 1–3 week earlier spawning onset than observed in the 1990s. This early reproduction affects embryonic development that is strongly influenced by temperature, as earlier spawning exposes embryos to warmer water, provoking a low survival rate of juveniles and reducing the reproductive success of the population [22]. Finally, climate change, one of the most global anthropogenic disturbances facing aquatic ecosystems, also causes reproductive alterations by affecting environmental conditions that modulate the neuroendocrine axis [137]. In addition, environmental variations are capable of changing the demography and attributes of a population, with important consequences on resilience. However, parental effects can compensate for these impacts, and their role

is especially relevant in situations of environmental stress, such as that caused by climate change. In this sense, different or even contradictory effects can be observed depending on the species or population. For example, the increase in temperature has caused in *Gadus morhua*, an advance of spawning season, with low fertility [138], and in *Thymalusthy mallus*, a low egg survival [139], while in *Salvelinus alpinus*, it has resulted in delayed spawning and inhibition of ovulation [140], [141], and in *Anarhichas lupus* to low embryonic survival [142]. Even more, global warming may favor reproductive potential in some cases, as has been reported for some invasive species [143,144]. Temperature changes can also affect the sex ratio in fish by regulating the expression and activity of certain hormones and enzymes that control sex determination, such that an increase in sea temperature would produce a tendency toward masculinization in gonochoric species [145], a premature transition from female to male in protandric hermaphrodite species, or an inhibition of the transition to female in protandric hermaphrodite species, even in the presence of an appropriate social context [146].

In summary, reproductive success is modulated by environmental factors and parental attributes, as well as by human-induced effects. Under climate change scenarios, small environmental variations can result in major changes in reproductive and biological traits [147], as well as at the physiological level [148]. These effects will be more marked in species that are limited in their ability to shift geographic distribution or are already at their tolerance limits [146]. In the last decades, numerous papers have reported changes in the distribution of marine species associated with rising sea temperatures in both the northern [149,150] and southern hemispheres [151], as well as in freshwater species in both hemispheres [152,153], which will undoubtedly have an impact on their reproductive success, given the characteristics of the new habitats and communities of which they will become part, and which will determine, among other things, the availability of food, the type of interspecific relationships or the degree of stress, modulating parental effects. Furthermore, different mechanisms of resistance to reproductive stress have been documented in many vertebrates, although these mechanisms are also regulated by a complex framework of environmental interactions [154]. All these issues must be taken into account to properly managing aquatic ecosystems if their resilience is to be preserved.

## 6. Studies on Parental Effects and Reproductive Potential: Future Perspectives

As we have mentioned, numerous studies of reproductive potential and parental effects have been carried out on different marine and freshwater species. Many studies focus on maternal effects and species with high commercial or ecological value. However, there are few studies on reproductive potential and parental effects in crustaceans, cephalopods, elasmobranchs and inland water species, which are of great importance in terms of socio-economic impact or ecological relevance.

Most of the work on reproductive potential and parental effects of aquatic organisms has focused on the maternal part, analyzing the influence of the length, age and condition of females on egg production and egg quality, as well as on the selection of the spawning area and the duration and frequency of reproductive events, including the phenomenon of skipping spawning that has been observed in some species [50,70,155]. There are also some papers on maternal effects on larvae [97,156], although they are scarce. In addition, although much has been theorized about the impact that these maternal effects may have on recruitment to the fishery based on the study of temporal and geographic variation in maternal attributes or egg and larval characteristics, there are hardly any papers that directly relate recruitment to these attributes [157]. Conversely, most papers refer to parental heritage and *indirect environmental effects*, both *prezygotic* and *prenatal postzygotic*, as well as a few studies on *postnatal postzygotic effects*, but parental selection effects associated with parental behavior and experience have been poorly studied. Similarly, there are few studies on the transgenerational impact of parental effects, even though such transgenerational effects have already been reported in some fish species [25,26]. Likewise, studies on paternal effects are scarce. In that sense, although it is true that the impact of females on

their offspring may be greater than that of males, it has been shown that males also play a relevant role in the development of offspring [10,158]. More and more studies highlight the importance of paternal effects and their interaction with maternal effects on early life stages survival, which may be particularly relevant in environments with changing conditions [58,80]. Conversely, it is expected that paternal effects are especially determinant in the case of species in which males are responsible for the care of the offspring, the selection of the breeding area and the construction of nest, and in marked social and territorial behavior [11,80].

In relation to the transgenerational concept of reproductive potential, it is essential to further analyze the reproductive resilience of exploited species, especially in the context of climate change. This involves analyzing the factors that ensure long-term reproductive success under different climate scenarios and exploitation regimes, studying several generations of reproductive fitness. Most of the studies analyzing the effects of climate change have focused on shifting species distributions, but less attention has been paid to changing life rates (such as growth and reproduction), which may also determine life history strategies and population resilience in a changing climate. Reproductive success occurs at the individual scale and results in both density- and fitness-dependent feedback loops that act to maintain the reproductive success of the population over time and determine the reproductive resilience of that population [159]. Therefore, any stressor that affects individual fitness will have consequences throughout the population that may also be transmitted generation after generation. However, despite all these studies, some authors conclude that transgenerational parental effects are not as relevant in the adaptation to stress as expected [160].

In summary, although much progress has been achieved in the study of reproductive ecology, reproductive potential and maternal effects in aquatic organisms, there is still a long way to go. First, more studies on reproductive potential of invertebrates (crustaceans and cephalopods), elasmobranchs and inland water species are needed. Second, and for all families (including teleosts), other aspects of parental effects that have not been thoroughly investigated to date, such as *postnatal postzygotic parental effects*, parental selection, paternal effects and the transgenerational impact of reproductive potential, need to be investigated. Finally, it is necessary to analyze the reproductive–recruit system in a broader context, incorporating spatial and temporal perspectives at different scales that are appropriate to the life cycle of the individual, the population and the species, as well as the influence of the environment and evolutionary pressure on the reproductive–recruit system. In this context, it will be necessary to develop new tools for monitoring populations and ecosystems in all their dimensions with a transdisciplinary approach. In parallel, the construction and implementation of integral models is necessary to understand the multiple processes that determine reproductive potential and parental effects and their complex interrelationships at different scales of ecological organization (from the individual to the ecosystem).

The last purpose of research on reproductive potential and parental effects should be to evaluate the reproductive resilience of populations of aquatic organisms through holistic models that predict their variations under different environmental scenarios. Only in this way can populations be adequately managed under the climate threat and ocean pollution we are facing for a sustainable development of the blue growth strategy.

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