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Article *in* Reviews in Fisheries Science & Aquaculture · August 2021

DOI: 10.1080/23308249.2021.1957772

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Reviews in Fisheries Science & Aquaculture

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/brfs21

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To cite this article: Joacim Näslund & Laith A. Jawad (2021): Pugheadedness in Fishes, Reviews in Fisheries Science & Aquaculture, DOI: 10.1080/23308249.2021.1957772

To link to this article: https://doi.org/10.1080/23308249.2021.1957772

REVIEWS IN FISHERIES SCIENCE & AQUACULTURE
https://doi.org/10.1080/23308249.2021.1957772

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REVIEW

Pugheadedness in Fishes

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ABSTRACT
This review summarizes the current state of knowledge of pugheadedness in fish. Records in the scientific literature range from detailed descriptions to brief notes and mere remarks. In total, at least 164 species from 60 families were identified to exhibit pugheadedness, with records published over a span of 465 years (1555 – 2020). The main osteological feature behind pugheadedness appears to be shortening or deformation of the parasphenoid bone, which leads to additional deformations of the ethmovomer- and frontal region. Several other deformations and abnormalities of other cranial bones, eyes, and tongue are occasionally observed, depending on the severity of the pugheadedness. Possible cases in elasmobranchs are also encountered, although the developmental causation may differ from actinopterygians, since their crania have a different organization. Natural cases of pugheadedness are found world-wide, covering a wide range of environments and lifestyles (freshwater-, brackish- and marine environments; benthic, neritic and pelagic species). Cases are found in all life-stages, from embryo to mature adults, suggesting that it does not necessarily lead to early-life mortality. There is some evidence for natural selection acting against pugheaded individuals, likely because of e.g. inappropriately functioning mouth parts, sense organs, and possibly brain deformation. High numbers of pugheads are mainly found in aquaculture, but moderate numbers have been found at some localities also in the wild. Abnormally high occurrence in the wild is commonly attributed to pollution, non-normal water chemistry parameters, or temperature. The causation, however, it typically speculated upon. Based on the reviewed literature, there is support for several causative factors, including genetic mutation and embryonic environmental conditions (toxic and non-toxic) affecting development. Pugheadedness, as the term has been used in the literature, is not a single well-defined pathology, but rather a suite of pathological conditions with similar phenotypic expression.

KEYWORDS
Brachygnathia; parasphenoid; prognathism; pughead; teratology

Introduction

Teratological specimens of fish are relatively uncommon but often receive attention when found, particularly among aquaculturists (Buckland 1863), fishermen and anglers (Gudger 1933a; Barnard 1935; Fjelldal et al. 2015) and among naturalists and scientists who, at least historically, often collected them in both private and official collections, either as curiosities or for scientific investigation (Gudger 1933a; Hickey et al. 1977; Heron et al. 1988). Deformities are important to recognize as they can be indicative of pollution or other unfavorable environmental conditions (Bengtsson et al. 1988; Lindesjöö and Thulin 1992; Klumpp et al. 2002; Simon and Burskey 2016). High frequencies of morphological anomalities in wild fish populations are typically conspicuous to the investigators and raise concern about the environment (Slooff 1982; Ziskowski et al. 1987; Browder et al. 1993; Jawad and Ibrahim 2018). Hence, several authors have suggested that anomalities within fish populations should be monitored as indicators of environmental issues in aquatic ecosystems (Dahlberg 1970; Hickey 1973; Bengtsson 1979; Karr 1981; Lemly 1997; Sfakianakis et al. 2015).

One particularly conspicuous craniofacial skeletal deformity found in fish is pugheadedness (*brachygnathia superior*; also known as e.g. simocephaly, snub-nose, pug-nose, lion-head, bulldog-head, or dolphin-head; Gudger 1936). The fact that it is conspicuous has caused particular scientific interest over several centuries, but no recent comprehensive summary of available information has been made. Many recent publications on fish diseases and deformities

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mention this condition, but often only with a very brief description of the characteristic morphology and short notes on possible causation (e.g. Branson and Turnbull 2008; Hellström et al 2012; Boglione et al. 2013; Bruno et al. 2013). The older literature often goes into more detail (e.g. Hofer et al. 1906; Gemmill 1912; Lundbeck 1928; Marquard 1936; Schäperclaus 1954) but is also, naturally, associated with possibly outdated information. This review aims at synthesizing the currently available information about pugheadedness in fishes.

Historical notes

Teratological cases of human and non-human animals (historically often referred to as "monstrosities") have fascinated people for a long time (e.g. Aldrovandi 1642). Hence, descriptions of such cases, including fishes, are found in the scientific literature through the past centuries (e.g. Barrington 1767; Cuvier & Valenciennes 1828-49; Cobbold 1858; Crawford 1948). Pugheaded fish have been observed and received attention for centuries. The first graphically documented specimen with this deformity in the academic literature is likely a common carp published in 1555 CE (Rondelet 1555; Gudger 1936); sometimes erroneously dated to 1554 (e.g. in Gudger 1928, as noted in Gudger 1930).

The deformity also features in folklore. Norwegian fishermen have paid particular attention to pugheaded cod *Gadus morhua*, or 'kongetorsk' (English: 'king cod'; an equivalent term 'torskekungen' was used in Sweden; Lilljeborg 1891), which are believed to bring good luck to the fishermen (Lilienskiold 1701; Fjelldal et al. 2015). Pugheadedness also raised the interest of Charles Darwin, who communicated with Jeffries Wyman (who described two cases from Atlantic cod *Gadus morhua*; Wyman 1849) on the phenomenon after noting similar skull deformities in the Nãta cattle breed (Darwin 1868; Dupree 1951). Gudger (1929) noted that the pughead deformity is fairly common, with particularly high numbers noted among cyprinid and salmonid fishes.

An interesting historical side-note is the description of pugheads as distinct species, which has occurred at least once. Macleay (1886) described a pugheaded specimen of *Maccullochella macquariensis* as a new species *Oligorus gibbiceps*, with the description reading "*the head descends almost vertically in front of the eyes to the mouth, which is horizontally protruded, the lower jaw being the longest*". Pugheadedness in the same species was described in Whitley (1944), who also commented on the erroneous species description.

Description of the deformity

Pugheadedness is a brachycephalic deformity characterized by antero-posterior compression, or hypoplasia, of the forehead (Figures 1-3). A typical pugheaded fish have abruptly rounded and short foreheads, which arch steeply downward just anteriorly of the eyes (Gemmill 1912; Gudger 1936; Bruno 1990; Branson and Turnbull 2008; Boglione et al. 2013) (Figure 2). The lower jaw typically remains normal-like (but see section on roundheadedness below). Not all cases are extreme; there is a large variation in the severity across documented cases (Figure 3) and some specimens

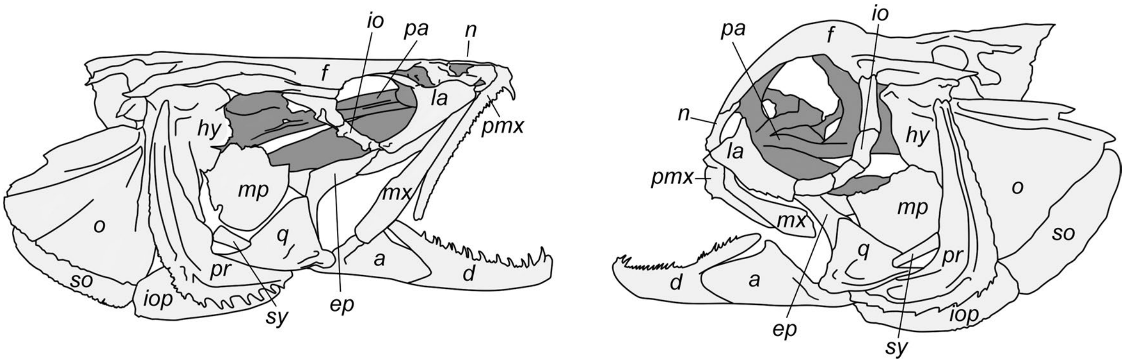

Figure 1. Skulls of normal and pugheaded pikeperch, *Stizostedion* (previously *Sander*) spp.*; normal (left): *S. lucioperca*, pughead (right): *S. volgensis*. Selected visible bones denoted as follows: a – angular, d – dentary, ep – ectopterygoid, f – frontal, hy – hyomandibular, io – infraorbitals, iop – interoperculum, la – lachrymal, mp – metapterygoid, mx – maxilla, n – nasal, o – operculum, pa – parasphenoid, pmx – premaxilla, pr – preoperculum, q – quadrate, so – suboperculum, sy – symplectic. Normal skull drawn based on Zuber (2020); pugheaded skull redrawn after Berinkey (1959); also see Antipa (1909) for a similar case. *No image of a skull from *S. volgensis* could be found; *S. lucioperca* is closely related with highly comparable head morphology.

assigned with pugheadedness have barely noticeable deformities (e.g. Barnard 1935; Bortone 1971; Grinstead 1971; Hickey et al. 1977; Lemly 1993; Bueno et al. 2015).

The main osteological regions typically affected are the ethmovomer block (parethmoids, mesethmoids, vomer, and nasal bone canal), maxillaries, frontals and parasphenoid. Ethmoids and vomer are typically reduced, maxillaries shortened, frontals abnormally curved and the parasphenoid shortened and/or deformed. Fusion of the parasphenoid and vomer has also been observed (Jawad and Ibrahim 2019; Jawad et al. 2020), and ethmoids and prefrontals are sometimes missing (Marlborough and Meadows 1966).

Tornier (1908) studied the neurocranium of a pugheaded common carp *Cyprinus carpio* and attributed the shortened parasphenoid bone (the keel bone of the fish neurocranium) as the primary anomaly (Figure 2). Parasphenoid deformation re-occurs in

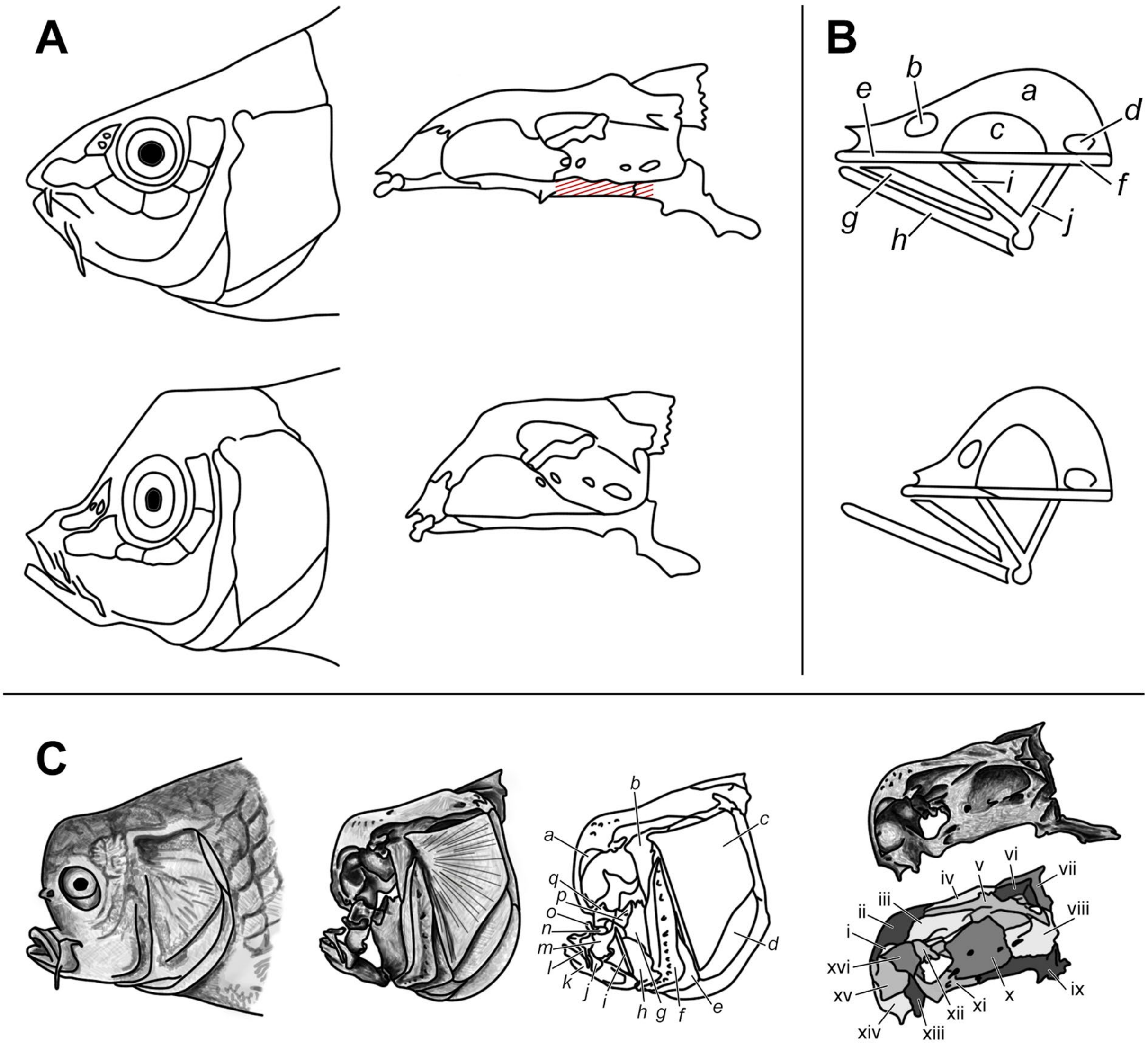

Figure 2. Illustrations of normal and pugheaded common carp (*Cyprinus carpio*). A) Heads (left) and the respective neurocrania (right). The red-hatched lines in the normal neurocranium indicate the particular parasphenoid region, below the brain case, that is shortened. Head illustrations depict additional deformations of the eye-socket and the infraorbitals. Redrawn after Tornier (1908). B) Schematic illustration of normal (upper) and deformed (lower) skulls; a-skull case, b-nasal cavity, c-ocular cavity, d-auditory cavity, e-vomer, f-parashenoid, g- upper jaw, h-lower jaw, i-j-bifurcated support of lower jaw. Redrawn after Tornier (1908). C) Severely pugheaded carp. From left: head, cranial bones, and neurocranium; skull: a-supraorbital, b-hyomandibular, c-operculum, d-suboperculum, e-interoperculum, f-preoperculum, g-metapterygoid, h-quadrate, i-ectopterygoid (transverse), j-lower part of maxillary, k-lower jaw, l-intermaxillary, m-upper part of maxillary, n-intercalary (maxillary), o-intercalary (intermaxillary), p-pterygoid, and q-palatine; neurocranium: i-supraorbital, ii-frontal principal, iii-frontal posterior, iv-temporal, v-pterotic, vi-external occipital, vii-occipital superior, viii-occipital lateral, ix-occipital basilar, x-petrous, xi-sphenoid principal, xii-orbito-sphenoid, xiii-vomer, xiv-ethmoid, xv-frontal anterior, xvi-alisphenoid. Redrawn after Jaquet (1902).

much of the literature as the hypothesized primary anomaly, and the degree of parasphenoid deformation can intuitively determine the severity of the pugheadedness in terms of how strong the curvature of the frontals becomes (Figure 2B). Hence, pugheadedness could possibly be a sequence (i.e. a cascading developmental "snowball-effect"), depending on parasphenoid malformation in bony fishes. For comparison with other cases, a variety of detailed descriptions and figures are found in e.g. Carlet (1879), Nyström (1889), Fasciolo (1904), Gemmill (1912), Sutton (1913), Hankó (1922), Lundbeck (1928), Marquard (1936), Gudger (1937), Whitley (1944), Berinkey (1959), Bortone (1972), Chew (1973).

Deformation or displacement of several additional bones may be associated with pugheadedness (e.g. lachrymal, palatine, ectopterygoid, premaxillary, and/or infraorbitals) (Hopewell-Smith 1908; Sutton 1913; Bortone 1972; Riehl and Schmitt 1985; Jawad et al. 2015; Jawad and Ibrahim 2019). Affected bones are often substantially deformed and can be either thicker (Talent 1975) or thinner (Chew 1973) than normal ones. Pugheadedness can also be associated with additional malformations of the branchial apparatus (Berinkey 1959; Komada 1980). In some specimens, the mouth is also abnormally crumpled, twisted or showing signs of cross-bite to different severity degrees (e.g. Gudger 1937; Hickey et al. 1977; Pickett 1979; Jawad and Hosie 2007; Jawad et al. 2014), or tube-like (Jaquet 1911, Parenzan 1967; Michajlowa 1968).

Exophthalmia (protrusion of the eyeballs from the skull, or 'pop eye') can be associated with the deformity (e.g. Sutton 1913; Gudger 1930; 1937; Mansueti 1960; Isaacson 1965; Chew 1973; Shariff et al. 1986; Palmas et al. 2020), but is not always markedly obvious or present (e.g. Gudger 1930; Goodwin and Vaughn 1968; Bortone 1971, 1972; Franks 1975; Pickett 1979). Based on described cases, exophthalmia seem to depend on the severity of the pughead deformation (e.g. Hickey et al. 1977). One hypothesis, which does not seem to have more than anecdotal evidence, is that it occurs specifically when the parasphenoid has become buckled up, forcing the eyes outwards from the center of the skull (Whitley 1944). The orbit and, consequently, the eyes can also become deformed in shape, so that the horizontal diameter is reduced relative to the vertical diameter, making the eyes oval-shaped (Tornier 1908; Gemmill 1912; Catelani et al. 2017; Figure 2). Furthermore, deformation of the bones in the orbital region can sometimes cause the eyes to become located closer together and facing more forward than in normal conspecifics (Gudger 1930; Adams and Ryan 1982). In extreme cases, the reduction of the frontal cranial bones may be so severe that the anterior part of the eyeball become exposed (Barahona-Fernandes 1982). Possibly, developmental mechanisms behind pugheadedness could be related to instances of synophthalmia (e.g. Crawford 1948; Honma 1958; Bolker and Thomson 1992).

Sometimes, abnormal pigmentation of the buccal cavity and the tongue is seen, likely associated with exposure to light, as a consequence of the deformity (e.g. Herrick 1885; Sutton 1913; Gudger 1930; Mansueti 1958, 1960; Bortone 1971; Shariff et al. 1986). Chew (1973) noted that, among two Florida bass *Micropterus floridanus* pugheads, only the more severe case showed a highly pigmented tongue, suggesting that tongue pigmentation could be associated with how pronounced the deformation is (Chew 1973). The tongue may also be substantially enlarged (up to 2-3 times the normal size), but it varies from case to case (Pickett 1979; Shariff et al. 1986).

It is common for other (externally visible) deformations, away from the head region, to be absent (noted by e.g. Lowne 1893; Hikita 1955; Talent 1975; Honma and Ishikawa 1978; Leidy 1985; Macieira and Joyeux 2007; Jawad and Ibrahim 2017; Kathan et al. 2020), but such observations could depend on stronger selection against individuals with multiple deformities, making the individual unlikely to survive long enough to be noticed. A case of a slightly pugheaded pandora *Pagellus erythrinus*, which also had saddleback syndrome (deformed dorsal profile, associated with loss of dorsal fin spines and pterygiophores) has been described from marine waters of Turkey (Jawad et al. 2017). Pugheaded common bream *Abramis brama* from the Rhine River area in Europe have been found with a high incidence of deformed fins (40% vs. < 15% in non-pugheaded specimens) and some cases of additionally deformed skeletal structures were also found (Slooff 1982). Frequency of fin deformation in pugheaded bream tended to increase with age (Slooff 1982). Jawad et al. (2018) noted possible deformation of the anterior vertebrae in association with pugheadedness in European hake *Merluccius merluccius*. Al-Harbi (2001) and Hikita (1955) both present cases of common carp *Cyprinus carpio* and chum salmon *Oncorhynchus keta*, respectively, with pugheads and shortened opercula. Another interesting case describe two ventrally conjoined twins of Atlantic salmon *Salmo salar*, where one of the individuals was pugheaded and, in addition, showed a downward curved lower jaw, missing left pelvic fin, abnormally small pectoral fins, and a severely deformed vertebral column with many fused vertebrae (Fjelldal et al. 2016). A similar case of salmonid conjoined twin embryos, where one twin was pugheaded, was described by de Quatrefages (1888; see Gudger 1929).

Some other cephalic and jaw deformities are noted under separate terminology, e.g. sucker-mouth (e.g. Hickey et al. 1977; Barahona-Fernandes 1982), cross-bite (e.g. Hickey et al. 1977), roundheadedness (e.g. Gemmill 1912; Ehrström 1919; Gudger 1933b), and synophthalmia (Crawford 1948; Honma 1958). Sucker-mouth and cross-bite are easily distinguished from pugheadedness, as they relate to lower jaw deformities; however, the latter has been associated with pugheadedness in a few cases (Pickett 1979). Roundheadedness is similar to pugheadedness, but with additional reduction of the lower jaw (Gemmill 1912; Gudger 1933b; Bruno 1990). Roundheadedness is sometimes classified as pugheadedness (e.g. Hellström et al. 2012), and many cases lie between these types of deformity and can be hard to classify into either category, especially if the species have inferior mouth position or subterminal mouth (e.g. Federley 1904; Tornier 1908; Ehrström 1919; Marquard 1936; Rotarides 1941). For instance, in his seminal work on fish diseases, Schäperclaus (1954) presents two Northern pikes *Esox lucius* with reduced foreheads, one of which in addition has a reduced lower jaw which still protrudes past the upper jaws; the latter case is still regarded as pugheaded by the author. The additional reduction of the lower jaw suggests additional disturbance in the development, but both roundheaded and pugheaded fish have shortened and/or deformed parasphenoids (Marquard 1936). Lower-jaw defects without affected cranium have been noted to be less common than pug- or round-headedness, at least in salmonid fish (Bruno 1990). Similarly, Fragkoulis et al. (2018) found few deformities of the lower jaw, while upper-jaw abnormalities were common in offspring from a spontaneous spawn of hatchery gilthead seabream. Elongated lower jaws can lead to an appearance resembling slight cases of pugheadedness, but without deformed bones in the upper part of the head, do not qualify as being classified as pugheads (Ferraresso et al. 2010; see cases in e.g. Noble 1971 and Mazurais et al. 2009).

It needs to be noted that some species exhibit natural head morphologies similar to pugheadedness. For instance, pughead-like phenotypes can be found within populations of three-spined sticklebacks *Gasterosteus aculeatus*, a species with a wide natural variation in head morphology (e.g. Hendry et al. 2013). In some species of cichlids (Cichlidae), mature males also develop humps on the forehead which leads to a head profile very similar to quite severe cases of pugheadedness. Hence, it is vital to know the natural variation of head morphology in a species when assessing whether an individual is pugheaded or not.

As a general phenomenon, *brachygnathia superior* (i.e. abnormally short upper jaws) is not limited to fish but is found also in other vertebrates (e.g. Bateson 1894; Jayo et al. 1987; Hoy et al. 2011). In some vertebrate clades, the bones affected are probably not homologous to fish, since the skulls have different configurations, with different bones forming similar functional structures. For instance, the main bone affected in teleost fish, the parasphenoid, is either lost or only vestigial in mammals and the mammalian vomer (previously considered homologous to the non-mammalian parasphenoid; Gregory 1933) forms the same functional structure (Atkins and Franz-Odendaal 2016). Furthermore, since the parasphenoid appeared first in Placodermi, it has no homolog in chondrichthyan fish (Atkins and Franz-Odendaal 2016). Nevertheless, several cases of pughead-like deformities have been found in chondrichthyan fishes (sharks: Pastore and Prato 1989; Moore 2015; rays: Luther 1961; Templeman 1965; Dahlberg 1970; Ribeiro-Prado et al. 2008; Escobar-Sánchez et al. 2009).

Causation

The causation of pugheadedness was, according to Leonhardt (1906) considered to be caused by damage to the skull until Steindachner (1863) made anatomical investigations and concluded it was pathological. Adaptation to environmental variation by natural selection has been discussed, but also rejected as likely, by Lönnberg (1891). Hybridization between a fish and a bird, a curious hypothesis which seems to have been at least considered by de Réaumur (1752), who noted that the observed specimen of a carp had a head resembling a bird (pugheaded carp often have a beak-like mouth; see Figure 2) but that it lacked feathers, can undoubtedly be ruled out with certainty based on modern biological knowledge.

Pugheadedness as a congenital disorder is well established, although there may be additional causes (e.g. injuries, parasites, or disease). The deformation typically arises in early ontogeny, during embryonical or larval development (Leonhardt 1906; Bruno 1990; Fraser and de Nys 2005). Developmental disorder is not a cause separate from genetic and/or environmental causation. Instead, developmental pathways are likely what genetic and environmental factors are affecting to cause pugheadedness. Genetic mutations can disrupt the developmental pathways of e.g. bone

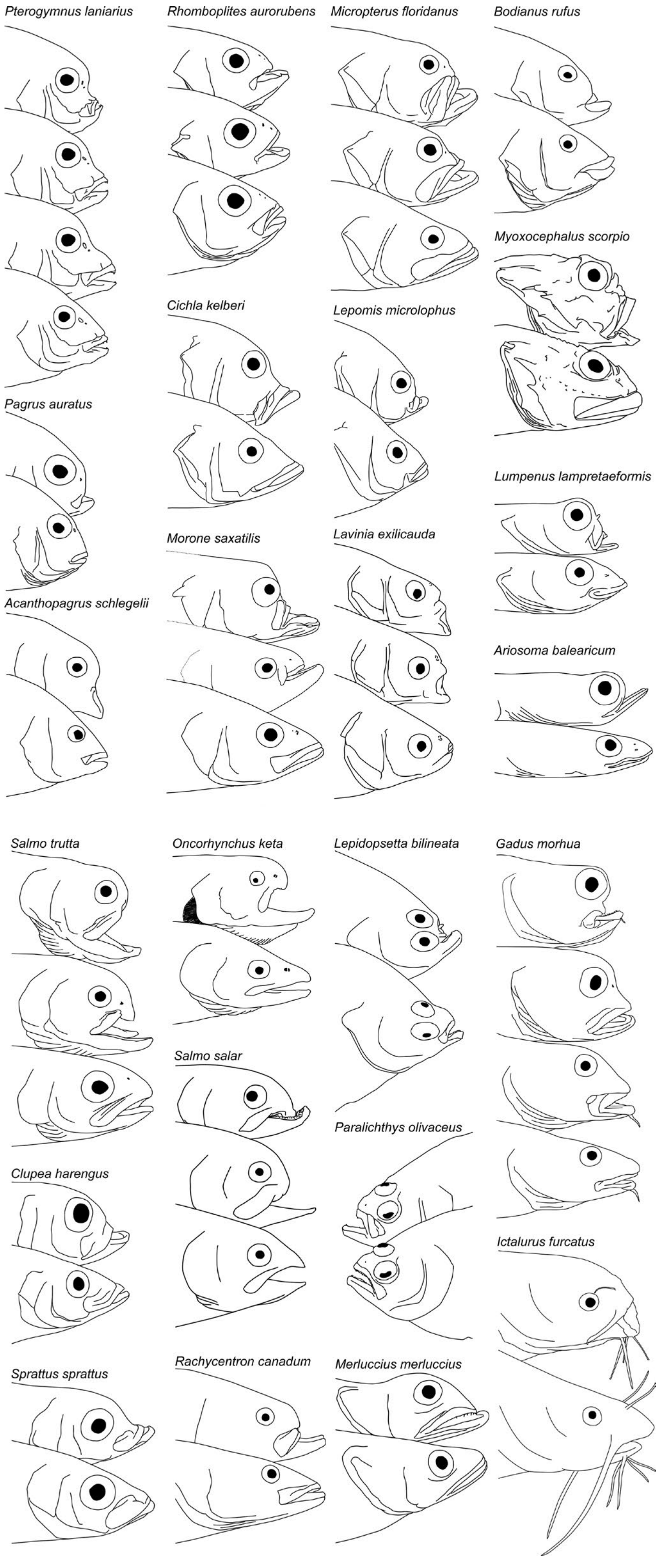

Figure 3. Examples of specimens of fish noted as pugheaded in the literature, redrawn from the original publications. Normal specimens illustrated below the pugheaded ones for each species. *P. laniarius* (Barnard 1935); *P. auratus* (Jawad and Hosie 2007); *A. schlegelii* (Honma and Ikeda 1971); *R. aurorubens* (Bortone 1971); *C. kelberi* (Catelani et al. 2017); *M. saxatilis* (Sutton 1913; Talbot 1967); *M. floridanus* (Chew 1973); *L. microlophus* (Porta and Snow 2019); *L. exilicauda* (ssp. *chi*) (Kathan et al. 2020); *B. rufus* (Macieira and Joyeux 2007); *M. scorpio* (Nyström 1889); *L. lampretaeformis* (Lönnberg 1891); A. balearicum (Lönnberg 1891). *S. trutta* (stream resident phenotype '*fario*') (Gudger 1929); *C. harengus* (Ford 1930); *S. sprattus* (Örey 2017); *O. keta* (Hikita 1955); *S. salar* (Leggett 1969; Jawad et al. 2014); *R. canadum* (Franks 1995); *L. bilineata* (Gudger 1937); *P. olivaceus* (Sawayama and Takagi 2016); *M. merluccius* (Jawad et al. 2018); *G. morhua* (Lundbeck 1928; Marquard 1936; Jawad et al. 2015); *I. furcatus* (Schmitt and Orth 2015). Note that the level of detail differs depending on source material.

formation, hormone expression, or general body-plan morphogenesis during ontogeny and environmental factors are also well-known to affect many different developmental pathways (Barresi and Gilbert 2018). In addition, some developmental disorders may be caused by mere chance (developmental stochasticity) (Oates 2011).

Pugheadedness is likely multifactorially caused, in the sense that many different causing factors exist (e.g. Lang et al. 2018). For any given case of pugheadedness, however, the causation is typically unknown (e.g. Branson and Turnbull 2008; Hellström et al. 2012). This is particularly true for wild specimens (e.g. Möller and Anders 1992; Schmitt and Orth 2015), and in such cases the causation can most often only be speculated upon based on potential factors in the immediate and surrounding capture area.

Genetic causation

Genetics can obviously affect cranial development, as illustrated by the fact that head-shapes can be a target of selection in animal breeding programs, including selection for brachycephalic shapes in dog breeds such as pugs and bulldogs (Schoenebeck and Ostrander 2013) and in the Nãta cattle (Darwin 1868). Selection on cranial deformities also underlie several 'ornamental' varieties of goldfish in the aquarium trade (Herre 2009). Some species naturally exhibit extreme morphological variation in head shape, including pughead-like forms (e.g. three-spined sticklebacks; Hendry et al. 2013).

In Atlantic salmon *Salmo salar*, spinal deformities have been linked to a substantial additive genetic component (Gjerde et al. 2005) and in rainbow trout *Oncorhynchus mykiss* rib and vertebral deformities could be explained by a dominant-mutation mechanism (Gislason et al. 2010). Many different genes are involved in head- and jaw formation through ontogeny (DeLaurier 2019) and several mutants of zebrafish *Danio rerio* with craniofacial deformities similar to pugheadedness have been developed [e.g. *silberblick* (slb) and *dolphin* (dol)] (Piotrowski et al. 1996; Kimmel et al. 2001). Furthermore, a mutation in the gene *osetrix/sp7* have been shown to display the general characteristics of pugheadedness, with delayed osteogenesis and poor mineralization leading to deformed parasphenoids causing midface hypoplasia, domed skull, and protruding mandibles (Kauge et al. 2016). Hence, single-gene mutations can evidently cause pugheadedness, which leads to the conclusion that the deformity can be heritable.

Some experimental indications of inheritance have been found, which lend support for a genetic origin of the deformity. For instance, Knauthe (1893; also see Gemmill 1912) bred anatomically normal sunbleak *Leucaspius delineatus*, derived from pugheaded parents, which themselves produced broods with a pughead incidence of 8% to 28%. However, in bighead carp *Hypophthalmichthys nobilis*, large numbers of offspring from normal-phenotype parents showed pugheadedness, but only 1% of offspring from pugheaded parents showed the deformity (Shariff et al. 1986); whether grand-offspring would show deformities was not investigated, so the experiment is inconclusive with respect to genetic causation. Neither pugheadedness, nor head deformities in general, were found to be significantly heritable in gilthead seabream *Sparus aurata* (Lee-Montero et al. 2015; Fragkoulis et al. 2018), and mouth deformities in general were not found heritable in common carp *Cyprinus carpio* (Kocour et al. 2007).

Inbreeding can also lead to malformations of the cranium, as shown in several vertebrate species, both in captivity (e.g. mice: Kalter 1968) and in the wild (e.g. lizards: Olsson et al. 1996), which also suggests possible genetic causation. In rainbow trout *Oncorhynchus mykiss* there is evidence for vertebral deformities being partially caused by inbreeding (Aulstad and Kittelsen 1971); however, inbreeding was excluded as a factor causing vertebral deformity in Atlantic cod *Gadus morhua* (Gjerde et al. 2005). Inbreeding was also rejected in a study of pugheaded Mediterranean trout S*almo cettii* from a Sardinian stream, based on expected heterozygosity estimates (Palmas et al. 2020). Hybridization can occasionally cause relatively high incidence of pugheadedness, along with other skull and jaw deformities, as seen in white bass *Morone chrysops* × striped bass *M. saxatilis* hybrids and their backcrosses in Hickey et al. (1977).

Evidence for genetic causation of pugheadedness is mixed. While mutations can definitely cause pughead-like deformities, it does not seem to be the only mechanism. Instead it seems reasonable that environmental factors (or randomness) often play a substantial role in incidence. Environmental factors may affect the same developmental pathways that are demonstrably affected by mutations. There may also be gene × environment interactions involved, making heritability detectable only under certain conditions (Kause et al. 2007; Boglione et al. 2013), but studies within this area are rare (Sae-Lim et al. 2016).

Environmental causation

Environmental factors are often hypothesized to cause skeletal deformities, including pugheadedness. Temperature, hypoxia, pH, salinity, water flow rate, light conditions, toxicants, xenobiotics, malnutrition, radiation, etc., acting during the embryonal or larval stages, have also been shown to induce deformities in general in a multitude of studies (e.g. Westernhagen 1970; Hickey 1973; Bengtsson 1979; Boglione et al. 2013). Below a number of environmental factors potentially involved in causing pugheadedness are described in detail.

Temperature affects developmental rate in fish, and it can also influence the incidence of malformations, including pugheadedness. High temperatures appear to be the main problem causing high deformity incidence, although which deformities that emerge varies among species (Hubbs 1959; Bolla and Holmefjord 1988; Lopes et al. 2018). From an experiment incubating striped bass *Morone saxatilis* eggs in a series of temperature treatments (10 – 28 °C; 2 °C increments; species optimum being ~18 °C), Morgan et al. (1981) reported (without quantification) that the three highest temperature treatments (24, 26, 28 °C) resulted in some larvae showing features of pugheadedness, along with small yolk sacs and deformation of internal organs. Temperature may also interact with other factors to cause pugheadedness, like in Atlantic salmon *Salmo salar* where elevated incubation temperature (14 °C; as compared to 8 °C controls) increased jaw deformities (including severely shortened upper jaws), but only when eggs had high vitamin A status (Ørnsrud et al. 2004). Temperature variation during embryogenesis is another potential variable to consider (Bruno 1990), although constant high temperatures have been considered more problematic for deformities in general (Hubbs 1959).

Hypoxia during embryogenesis has been raised as a potential environmental factor behind pugheadedness (e.g. Bruno 1990). Experiments by Garside (1959) revealed that exposing lake trout *Salvelinus namaycush* embryos to low oxygen levels (2.5 – 4.5 p.p.m.) cause reduced development rate and an increase in the incidence of abnormalities of both head and trunk, with head deformations including truncation of either or both jaws and eye-abnormalities. Low oxygen levels have also been shown to associate with spinal deformities (Bengtsson 1979). Hypoxia can occur in natural waters, e.g. due to eutrophication, and was suggested as a plausible cause for a high incidence of pugheaded blue catfish *Ictalurus furcatus* within an area of the tidal Rappahannock River in Virginia, USA, known to suffer from summertime hypoxia (Schmitt and Orth 2015).

Salinity during embryogenesis can be a problem for marine and estuarine species. Suboptimal salinities during embryonic development can cause swollen yolk sacs (yolk edema) (Westernhagen 1970; Doroshev and Aronovich 1974). This in turn may cause pressure on the developing embryo and lead to jaw malformation, as have been observed in European flounder *Platichthys flesus* from the North Sea (Westernhagen 1970). Too high salinity may also affect malformation incidence (Doroshev and Aronovich 1974), but cases related to pugheadedness specifically has not been identified here.

Malnutrition is one of the leading candidate factors for skeletal malformations, including pugheadedness, in aquaculture. Details on general mechanisms behind skeletal malformations due to malnutrition are well-covered elsewhere (Cahu et al. 2003; Lall and Lewis-McCrea 2007; Darias et al. 2011); hence, only some experimental evidence of nutrient effects on the upper jaw of fish are briefly outlined here. Excessive or insufficient intake of several key nutrients have possible effects on skeletal malformation, including minerals (calcium, phosphorus, trace elements), vitamins (A, D, C, E, K), lipids and fatty acids (Cahu et al. 2003; Lall and Lewis-McCrea 2007; Boglione et al. 2013). Vitamins have attracted particular interest in relation to skull deformations. A too high intake of vitamin A can lead to pugheadedness in several species (Villeneuve et al. 2006; Fernández et al. 2008; Mazurais et al. 2009). Retinoic acid (RA), a derivative of vitamin A, is important for specifying the anterior-posterior axis and the formation of the jaw apparatus and deficiency is associated with deformation (Barresi and Gilbert 2018). Temporary increase in RA can activate RA-degrading enzymes, leading to an overall longer-term decrease in RA (Villeneuve et al. 2005; Barresi and Gilbert 2018), a mechanism that may lie behind the observed effects. Synthetic retinoids cause increased jaw malformation in olive flounder *Paralichthys olivaceus*, possibly through disturbing the retinoic acid receptor (RAR) signaling pathway (Haga et al. 2003). High levels of certain dietary lipids may affect the expression of RAR, leading to deficiency and cranial deformation (Villeneuve et al. 2005). Some xenobiotics (e.g. the herbicide glyphosate) also interfere with RA signaling, causing craniofacial disorders in e.g. *Xenopus* frogs (Paganelli et al. 2010), and could hypothetically also cause deformations in fish. Vitamin A regulates thyroid hormone metabolism and high exogenous levels of thyroid hormone have also been experimentally shown to increase pughead incidence (Shkil and Smirnov 2009). Deficiency of vitamins C and D have also been experimentally associated to pugheadedness in fish (Darias et al. 2010, 2011)

In common carp *Cyprinus carpio*, low-phosphorous diets lead to insufficient growth of bones, including the cranial bones (Ogino and Takeda 1976). While the resulting deformity of the head include increased curvature and shortening of the head (which could be taken for slight cases of pugheadedness), it was not consistent with severe pugheadedness (see figures in Ogino and Takeda 1976). Spinal malformations in larval ayu *Plecoglossus altivelis* were reduced by the supplement of lecithin, but only a single case of pugheadedness was noted overall in the study, rendering it inconclusive with respect to this particular deformity (Kanazawa et al. 1981).

In addition to malnutrition of the developing individuals, malnutrition of the broodstock may also cause skeletal malformations (Cobcroft et al. 2004). Such parental effects (dietary deficiency, malnutrition of the mother), however, need further investigation (Fragkoulis et al. 2018).

Diseases and parasites affecting the developmental processes of bone formation may also cause pugheadedness. For instance, whirling disease, caused by a microscopic parasitic myxosporidian *Myxobolus cerebralis*, has been suggested as a possible etiological factor for pugheadedness in salmonid fish (Bruno 1990). Typical symptoms are a whirling swimming pattern, darkened tail-regions, and skeletal deformities; the latter are often located to the spine and cranium, and are caused by cartilage damage and associated inflammation (Elwell et al. 2009). Shortening of the head is seen and depending on the location of the infection, it may cause a pug-headed appearance (Elwell et al. 2009). A variety of myxozoan parasites infect and cause skeletal deformities in other species of fish (e.g. Langdon 1987; Longshaw et al. 2003) and may thereby be related to pughead-like deformities also in non-salmonids.

Pollution is often suspected as a causative environmental factor when pugheads are encountered in nature. Nonlethal doses of developmental toxins can lead to skeletal deformities in general (reviewed in e.g. Sloof 1982; von Westernhagen 1988) and are often the suspected factors leading to pugheadedness in wild fish (e.g. Komada 1980; Berra and Au 1981; Van Der Gaag et al. 1983; Simon and Burskey 2016). Several different kinds of pollutants are candidates for increased occurrences, but anthropogenic pollution cannot be the only causative agent as the deformity was well-known in pre-industrial time (Fjelldal et al. 2015). Nevertheless, evidence indicating pollutants as causing agents of pugheadedness exists, both from correlational and experimental studies.

It is well-known that many pollutants can disturb embryonic development of fish, and many effects are dose-dependent but not pollutant-specific (von Westernhagen 1988). For instance, different types of metals may enter fish eggs and influence the embryo development in several ways, some of which may cause body malformations such as craniofacial malformation and vertebral shortening or curvature (Jezierska et al. 2009). Vertebral deformities are, however, more common than craniofacial deformities after embryonic exposure to pollutants, according to von Westernhagen (1988).

Field studies in the Netherlands indicated that pugheadedness, and several other skeletal deformities, was more common in bream *Abramis brama* in the River Rhine than in Lake Braassem, the former being substantially more polluted than the latter (Slooff 1982). When experimentally incubating rainbow trout *Oncorhynchus mykiss* eggs in polluted water from River Rhine, 14.2% of the hatched individuals showed some level of pugheadedness when exposed to Rhine water directly after fertilization, 9.8% when exposed after water-hardening of the eggs and 4.3% when exposed as eyed ova (with 0% incidence in unchlorinated groundwater) (van der Gaag 1987). Another study in the same experimental system showed an incidence of 6.5% when incubated in Rhine water, 2.7% in flocculated and rapid sand filtrated (RSF) Rhine water, 0.5% in ozonized RSF Rhine water, and 0% in control water (van der Gaag 1987). Hence, it appears that pugheadedness can be caused by polluted water, with early egg stages being most vulnerable. Since river water was used in these studies, the specific pollutant(s) responsible for the effects is unknown.

A variety of toxicants that have been associated with head-deformities in general include polychlorinated biphenyl (PCB) (Hogan and Brauhn 1975), dioxins (Helder 1981; Elonen et al. 1998), heavy metals (Somasundaram et al. 1984; Sfakianakis et al. 2015), selenium (Hamilton et al. 2005; McDonald & Chapman 2007), polycyclic aromatic hydrocarbons (PAH) (Hannah et al. 1982; Kocan and Landolt 1984), petroleum hydrocarbons (PHC) (Lindén 1978; Tilseth et al. 1984; Vignet et al. 2019), and herbicides (Paganelli et al. 2010). This list is non-exhaustive and mainly used to illustrate that many possibly causative agents exists. Different toxicants may cause pugheadedness through different direct or indirect pathways and mechanisms (which can be recognized from other sections of this article), e.g. mutagenesis (e.g.

PAH: von Westernhagen 1988), RA signaling disruption and thyroid hormone disruption (e.g. PCB, PAH, dioxins: Rolland 2000; xenobiotic herbicides: Paganelli et al. 2010), erratic eye development (e.g. selenium: Hamilton et al. 2005), or by causing hydrated swollen yolk-sacs, exerting pressure on the embryo inside the eggs (e.g. PHC: Lindén 1978).

Injuries may also be involved in some cases of pugheadedness, although it does not seem to be the main factor causing this malformation (e.g. Steindachner 1863; Hopewell-Smith 1908; Mansueti 1960). Pinganaud-Perrin (1973) showed that surgical removal of the eye in yolk-sac fry of rainbow trout *Oncorhynchus mykiss* led to pughead deformations (cf. Yung 1901; Antipa 1909; Gudger 1929), which suggests that the pressure from the eyeball on the cartilage during early ontogeny may mechanically stabilize the head formation. Some species may also develop similar deformities associated with cyst formation on the upper jaw during post-hatch development (Wünnemann et al. 2017).

Deformities similar to pugheadedness, which are likely caused by injuries (snouts cut or bitten off) have been observed in several species of teleosts (e.g. Richard 1912; Menzel 1974) and elasmobranchs (Forster 1967; Schwartz 1973). Garstang (1898) noted that “short-nosed” blackspot seabream *Pagellus bogavareo* were “curiously common” at Plymouth, Great Britain, and his hypothesis on causation was that it was caused by fishermen damaging the mouthparts when violently unhooking this unwanted species; however, no illustrations of the deformity were presented. Billfishes (Istiophoridae) can also end up with similar abnormal head morphology when their spear is broken close to the main head region (Morrow 1951). Head deformities caused by thickening of the dermis and formation of subcutaneous adipose tissue in the anterior head region, observed in e.g. scombrids, carangids, clupeids, coregonids and other neritic-pelagic species held in aquaria or certain types of hatchery tanks (Suzuki et al. 1973; Howey 1985; Shimizu and Takeuchi 2002; Stejskal et al. 2018), can lead to a head morphology similar to pugheadedness, likely caused by collisions with walls (Blaxter and Holliday 1963). If walling happens in larval stages, it could probably cause malformations in the cranial bones and hence become actual cases of pugheadedness, as seen in Sawada et al. (2020). One report of pugheadedness in laboratory-reared Pacific herring *Clupea pallasii* notes that the condition developed gradually through ontogeny, suggesting cumulative effects of e.g. walling behavior (Talbot and Johnson 1972).

Early-ontogeny damage in the structures (likely the parasphenoid) that are affected by mutations or disrupted developmental pathways underlying congenital pugheadedness could be hypothesized to lead to a deformation similar to pugheadedness. Not all injury-related deformations of the forehead are equivalent to pugheadedness.

It has also been suggested that mechanical pressure on the embryo inside the egg e.g. from yolk could be a possible cause (Leonhardt 1906; Whitley 1944). While not strictly an injury, the deformation would in such cases still be caused by mechanical force. The parasphenoid is among the first bones to mineralize in the fish skull (Mesa-Rodriguez et al. 2016) and could thereby be vulnerable to mechanical force in early ontogeny, since no other structures surrounding it would relieve the pressure. This hypothesis may be restricted to cases with malformed parasphenoids, not cases where it is shortened.

Overcrowding in aquaculture has also been indicated to affect cranial abnormalities. Roo et al. (2010) found that incidence was more than twice as high when culturing eggs of red porgy *Pagrus pagrus* in intensive rearing systems (100 eggs · L^{-1}; 6.8% incidence), as compared to semi-intensive systems (5 eggs · L^{-1}; 3.1% incidence). Overcrowding in itself is, however, unlikely as a causing factor. Instead, associated environmental alterations, such as oxygen concentration or nutrition, or possibly increased walling behavior, are likely to be the cause behind the increased incidence (Shariff et al. 1986; Roo et al. 2010).

Incidence

In unpolluted natural waters, morphological anomalities in general are relatively rare (often < 1% of individuals: e.g. Whitney 1961; Warlen 1969; Dahlberg 1970; Scherer 1973; Komada 1980; Berra and Au 1981, Nankee 1981), although it can vary substantially among species (Berra and Au 1981) and a few reports suggest that it can sometimes be common in certain populations from presumably unpolluted areas. For instance, Young (1929) noted pugheaded blue cod *Parapercis colias*, of different severity degrees, as common at one of the fishing grounds near the Chatham Islands: “a load of fish from these grounds can be relied on to supply several dozen specimens”. Similarly, panga seabream *Pterogymnus laniarius* were noted to be common enough in South African waters to have a specific name (*dik-bek panga*) among fishermen (Barnard 1935). Hickey et al. (1977) collected records on 14 pugheaded striped bass *Morone saxatilis* from the Hudson River and Long Island area, New York, between 1964 and 1973, in a program that included an information campaign (commenced in 1972) through media and flyers distributed to fishermen. A "population" of pugheaded brown trout *Salmo trutta* is mentioned in Bateson (1894), possibly referring to several specimens caught in Lochdow, near Pitmain in Inverness-shire, Scotland; however, a natural population of mainly pugheaded individuals seem unlikely. Reported incidence estimated from natural environments are summarized in Table 1.

In polluted waters, morphological deformities can become more common (Sindermann et al. 1978; Sloof 1982; Lemly 1993; Klumpp et al. 2002). Several sites from where pugheaded fish have been quantified (Table 1) are polluted. Sindermann et al. (1978) notes that >10% of striped bass were pugheaded in the lower Hudson River estuary, which is located next to New York City and generally polluted. Seine net surveys in 1973, however, only indicated 0.2% incidence in the lower Hudson River (Hickey et al. 1977). Lake El-Temsah in Egypt, where 1% pugheaded ("bird-like head") Nile tilapia *Oreochromis niloticus* were found, was polluted by lead and cadmium (Eissa et al. 2008); however, no unpolluted control site was included in the study, making it hard to assess causation.

Among artificially bred and reared fish pugheads can occasionally be found, with varying incidence: e.g. 48.7% in striped bass *Morone saxatilis* (Grinstead 1971); 0.9% in ayu *Plecoglossus altivelis* (Komada 1980); 1% in bighead carp *Hypophthalmichthys nobilis* (Shariff et al. 1986); up to 9.1% in barramundi *Lates calcarifer* (Fraser and de Nys 2005); up to 0.16% in the well-established AquaGen strain of Atlantic salmon *Salmo salar* (Gjerde et al. 2005); 5.5% in olive flounder *Paralichthys olivaceus* (Sawayama and Takagi 2016); and 6.7% in gilthead seabream *Sparus aurata*

Table 1. Incidence of pugheadedness in fish collected in natural environments. Total number of investigated individuals denoted as N. Incidence specificity depends on level of detail in the original publication. 0% incidence in additional species from these studies are reported in the footnotes.

Species	Incidence	*N*	Locality	Region	Reference
Larvae, 13 spp.	<0.06%[a]	12000	Long Island Sound, Niantic Bay	Connecticut, USA	Nankee (1981)
Abramis brama	1.73% (0.5–2.9%)	6948	Rhine-Meuse catchments	Europe	Slooff (1982)
Bairdiella icistia	0.06% (0–0.9%)	38767	Salton Sea	California, USA	Whitney (1961)
Chasmistes brevirostris	0.34%	1178	Upper Klamath Lake	Oregon, USA	Plunkett and Snyder-Conn (2000)[c]
Chrysichthys nigrodigitatus	0.4%	4511	Cross River estuary	Nigeria	Obiekezie et al. (1988)
Cottus confusus	1.3%*	74	Rock Creek	Washington, USA	Patten (1968)
Ctenolabrus rupestris	0.26%*	381	Loch Sunart	Scotland, UK	Treasurer (1994)
Cynoscion regalis	0.05%*	2021	Georgia estuaries	Georgia, USA	Dahlberg (1970)[d]
Cynoscion regalis	>10%	NA	Lower Hudson River estuary	New York, USA	Sindermann et al. (1978)
Esox lucius	0.03% (0–0.07%)	10494	Heming Lake	Manitoba, Canada	Lawler (1966)
Etropus crossotus	0.24%*	416	Georgia estuaries	Georgia, USA	Dahlberg (1970)[d]
Gadus morhua	0.2% (0%–0.4%)	9592	Wadden Sea	Europe	Möller and Anders (1992)[e]
Gadus morhua	2%[b]	NA	Baltic Sea	Europe	Lang et al. (2018)
Hesperoleucus symmetricus	0.62%*	162	San Lorenzo Creek	California, USA	Leidy (1985)
Hesperoleucus symmetricus	10.0%*	10	Del Puerto Creek	California, USA	Leidy (1985)
Ictalurus furcatus	1.89–3.68%	4357	Rappahannock River	Virginia, USA	Schmitt and Orth (2015)
Lepomis microlophus	0.83%	120	Sparks City Lake	Oklahoma, USA	Porta and Snow (2019)
Limanda	<1%[b]	NA	Baltic Sea	Europe	Lang et al. (2018)
Limanda	<0.5%	17924	Wadden Sea	Europe	Möller and Anders (1992)[e]
Merlangius merlangus	0.1%	6561	Wadden Sea	Europe	Möller and Anders (1992)[e]
Morone saxatilis	0.04%**	4873	San Francisco Bay	California, USA	Talbot (1967)
Morone saxatilis	0.2%	1773	Lower Hudson River	New York, USA	Hickey et al. (1977)
Morone saxatilis	>10%	NA	Lower Hudson River estuary	New York, USA	Sindermann et al. (1978)
Oreochromis niloticus	1%	600	Lake El-Temsah	Egypt	Eissa et al. (2008)
Osmerus eperlanus	<0.5%	35279	Wadden Sea	Europe	Möller and Anders (1992)[e]
Perca flavescens	0.10% (0.06–0.14%)	8987	Heming Lake	Manitoba, Canada	Lawler (1966)
Pimephales notatus	0.65%	2771	Cedar Fork Creek	Ohio, USA	Berra and Au (1981)[f]
Platichthys flesus	<0.5%	19129	Wadden Sea	Europe	Möller and Anders (1992)[e]
Salmo salar	0.09%*	1126	Gambo Pond	Newfoundland, Canada	Leggett (1969)
Salmo trutta	12.5%***	16	Furittu Stream	Sardinia, Italy	Palmas et al. (2019)

*Only one pugheaded specimen.

**Only 2 pugheaded specimens.

***2 specimens considered deformed, but one very slight.

[a] All skull deformities included.

[b] All skeletal deformities, including lordosis, scoliosis and pugheadedness.

[c] 0% incidence in *Deltistes luxatus*.

[d] 0% incidence recorded in 12 other teleost species (5 with N > 1000; 4 with N > 300; 3 with N < 100).

[e] 0% incidence recorded in *Anguilla anguilla* (N = 598), *Zoarces viviparus* (N = 931), *Myoxocephalus scorpio* (N = 305), *Agonus cataphractus* (N = 669), *Pleuronectes platessa* (N = 8739), and *Solea solea* (N = 2574).

[f] 0% incidence recorded in 33 other species (5 with N > 1000; 6 with N > 100; 11 with N > 10; 11 with N < 10).

(Fragkoulis et al. 2018). Extreme cases of very high incidence are also found in the literature, e.g. in Mansueti (1958), where a third of all surviving striped bass *Morone saxatilis* juveniles were pugheaded. It should be noted that there is still typically a low frequency of deformities (e.g. Bruno 1990; Jawad et al. 2014, 2015), and only a few parents may be associated to the bulk of the affected individuals (Sawayama and Takagi 2016). Malformed individuals may have a higher chance to survive early life when fed *ad libitum* in predator-free aquaculture facilities, as compared to natural environments (e.g. Komada 1980), making comparisons of occurrence between natural and artificial environments difficult. Comparative studies between wild and hatchery-reared seabreams (*Sparus aurata* and *Pagrus major*) have indicated that incidence of skeletal malformation (including head deformations like pugheadedness) is much lower in the wild (Boglione et al. 2001; Matsuoka 2003). While the wild fish were sampled at young age, there may still be a survival bias between these environments.

Some comments on incidence records are warranted. It seems likely that recorded frequencies of pugheadedness are overestimates in relation to typical natural frequencies, as there are without doubt a multitude of field studies of fish populations where no pugheaded fish are found, which are not covered in the literature survey. Furthermore, many incidence values based on a single specimen (Table 1), which makes these estimates highly uncertain. Finally, Bengtsson (1979) argues that deformed fish may be easier to capture, causing biased sampling and thereby overestimation of incidence.

Proximate performance implications

Since the premaxillary and maxillary bones may be severely deformed in pugheaded fish, the gape can be restricted, complete opening (Subba 2004; Jawad and Ibrahim 2019) or closure (Mansueti 1960) of the mouth can be hindered, and the protractile function of the jaw can be negatively affected (Nyström 1889; Bortone 1971), with possible severe consequences for feeding efficiency and, hence, growth (Rose and Harris 1968; Shariff et al. 1986; Bruno 1990). When mouthparts are severely affected, the malformed individual may be limited to feed only on suboptimal food items that do not require manipulation with the jaws to be consumed, e.g. algae (Garstang 1898). Some observational studies in culture conditions suggest that no feeding disadvantage is apparent (e.g. Mansueti 1958), and it likely depends on the severity of the condition. Even severely pugheaded individuals have, however, been found to survive for long time in the wild (see below). Possibly, a malformed mouth may also impair ventilation of the gills, so that swimming performance is negatively affected due to limited oxygen uptake (Bortone 1971; Nakamura 1977; Bruno 1990; Lijalad and Powell 2009).

The nostrils can sometimes be situated in an unnaturally narrow space in the anterior lower corner of the eye, and in some cases the olfactory nerve is suspected to be deformed or even missing (Gudger 1937; Al-Hassan and Na'amma 1988; Jawad and Ibrahim 2019; Jawad et al. 2020), suggesting that the development of the olfactory sense organs may be negatively affected, which could also affect performance in terms of foraging, orientation, and ultimately survival. Eyes are typically deformed in more severe cases of cranial compression, clearly visible as exophthalmia or oval-shaped eyes (e.g. Tornier 1908; Berinkey 1959; Bortone 1971; Hickey et al. 1977; Catelani et al. 2017; Jawad and Ibrahim 2019). Eye deformations in aquacultured non-pugheaded hybrid walleyes (*Stizostedion vitreus* × *S. canadensis*) leads to impaired mass gain and reduced body condition, suggesting that general performance may be jeopardized by this effect alone (Garcia-Abiado et al. 2006).

The deformation may also have impacts on the central nervous system due to deformation of the cranial cavity affecting the brain directly (suggested by Yung 1901; Jawad and Ibrahim 2017; Jawad et al. 2020). Nyström (1889) described and depicted the brain of a pugheaded shorthorn sculpin *Myoxocephalus scorpio*; the brain position was anteriorly tilted downwards and the space in the brain cavity was very restricted compared to normal specimens. Morphometric analyses would be necessary to ascertain effects on specific brain subregions, and behavioral studies are required to assess effects of deformities. Yung (1901) presents a drawing of a brain from a pugheaded one-eyed rainbow trout *Oncorhynchus mykiss*, which is clearly abnormally asymmetric. The asymmetry is particularly notable on the right hemisphere of the optic tectum, the same side where the eye was missing. Neurological effects are not yet well investigated, and information on cognitive or behavioral effects is absent from the literature. Since pugheadedness can be induced in hatchery environments, these effects could possibly be investigated experimentally in controlled environments. Zebrafish *Danio rerio* mutants are other potentially useful models for e.g. behavioral studies, but may be of limited use for ecological investigations.

Ultimate performance implications

Most accounts of performance of pugheaded fish in the wild rely on comparing length, mass, body condition, stomach fullness, reproductive status, etc. in a single or a few pughead specimen with that of sympatric conspecifics. Hence, the evidence for ultimate performance issues are not statistically well powered. There is also likely a survivorship bias in the reporting, meaning that individuals that perform poorly are unlikely to survive long enough to get caught and, hence, the reported cases from adults come from individuals that has not been severely affected by the condition. In general, growth impairments leading to small body size or poor condition could make the individual susceptible to death by both starvation and predation, and any substandard functioning of body parts likely increases predation mortality risk (Mesa et al. 1994).

One study has aimed at investigating effects of pugheadedness in a more standardized setting. Utilizing the fact that pugheadedness was exceptionally high in striped bass *Morone saxatilis* hatcheries at the time, Grinstead (1971) conducted a release experiment in Canton Reservoir, Oklahoma, where young-of-the-year pugheads and normal individuals were released in mid-June in two consecutive years. Recaptures were done systematically over summers using mesh-bag seine at six locations in the reservoir. By comparing relative capture frequency and size of pugheads and normal individuals (Figure 4), post-release performance was assessed statistically. Body length of pugheaded bass was consistently lower than in normal individuals (Figure 4B), and a regression analysis suggested that the slope of the pughead-regression was shallower than that of normal fish, indicating generally lower growth rates. Overall, the degree of pugheadedness, as determined by a deformation classification scheme, was reduced over time in recaptured individuals, suggesting selection against individuals with more deformed heads (Grinstead 1971).

From the cases studies, the assessments of performance are largely mixed. One case concerns a floy-tagged pugheaded juvenile brown rockfish *Sebastes auriculatus* which was recaptured 4 times over 15 months (Adams and Ryan 1982). During this time, it grew 6.7 mm in total length; the growth was slower than that of normal conspecifics tagged within the same project during winter, but not during other parts of the year. Bortone (1971) noted that growth of a moderately pugheaded age 0+ pirate perch *Aphedoderus sayanus* did not seem to be seriously affected (the body length was comparable to other age 0+ sympatric conspecifics), possibly due to the non-protractile feeding mode of the species. Similar reasoning was presented in an observational study of a pugheaded Atlantic goliath grouper *Epinephelus itajara*, which appeared to be healthy and in normal body condition and had reached an adult size in a natural environment (Bueno et al. 2015). The ecology of the goliath grouper, being reef-associated and feeding on slow-moving fish and crustaceans, could have facilitated survival according to Bueno et al. (2015). In a case of a pugheaded male landlocked Atlantic salmon from Newfoundland, scale-reading revealed that the 7 year-old specimen had spawned twice and was in the 97th percentile in its year class in length, suggesting that this individual had competed successfully with conspecifics (Leggett 1969).

Comparing two specimens of pugheaded Clear Lake hitch *Lavinia exilicauda chi* with a large number of normal conspecifics, Kathan et al. (2020) found that one had a much lower mass for its length while the

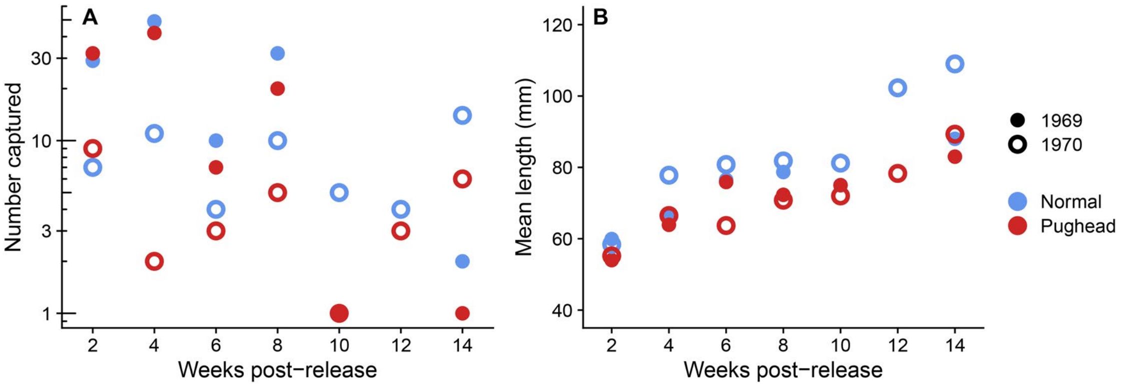

Figure 4. Recapture data from Grinstead (1971), where hatchery-bred pugheaded and normal striped bass (*Morone saxatilis*) were released into Canton Reservoir, Oklahoma, in 1969 (total N = 56000) and 1970 (total N = 44200). A) Relative frequency of recaptured normal and pugheaded bass (relative frequency of released fish not known). B) Mean length of recaptured normal and pugheaded striped bass. Week 12 not sampled in 1969.

other was within the normal range of mass for its length, albeit in the lower part of that range. Similar to the latter specimen, Catelani et al. (2017) found a pugheaded adult peacock bass *Cichla kelberi* to have lower, but not detrimentally reduced, relative body mass than 13 sympatric conspecifics. Even fish with severe head deformities can be found in good condition. Severely pugheaded adult striped bass *Morone saxatilis* have been captured with fish in their stomachs — evidently showing their capacity to hunt down prey (although, the condition of the prey is unknown) (Mansueti 1960; Lyman 1961).

Several studies find that adult pugheaded specimens are in reproductive condition with normal length for their age (Pappenheim 1907; Briggs 1966; Chew 1973; Franks 1995; Bueno et al. 2015; Catelani et al. 2017). It is also sometimes noted that pugheaded specimens appear to be in apparent good health and condition (van Lidth de Jeude 1885; Marlborough and Meadows 1966; Hickey et al. 1977; Jawad and Ibrahim 2017). Several studies note that the growth and/or condition of the fish (mass relative to length) is markedly poorer in pugheads (Rose and Harris 1968; Nakamura 1977; Tilseth et al. 1984; Schmitt and Orth 2015; Jawad et al. 2018; Porta and Snow 2019), typically interpreted as a consequence of poorly functioning jaws and foraging ability. Slow growth has also been observed in aquaculture, where food is abundant (Shariff et al. 1986).

Overall, the performance of pugheaded fish appears to depend both on severity of the deformity, and on the species ecology. Likely, site-specific competition- and predation pressure also influence the performance, but studies are missing on these aspects.

Which species are affected?

To investigate which species are affected by pugheadedness, a literature search was performed. Literature was searched for using several sources with different strength and weaknesses (Falagas et al. 2008). Two standardized scientific literature databases were searched: 1) Web of Science (Clarivate Analytics 2020) and 2) Scopus (Elsevier 2020). The scientific search engine Google Scholar was also used (Google LLC 2020a). Furthermore, all papers found during the searches and previously published bibliographies on fish teratology and pugheadedness (Dawson 1964, 1966, 1971; Dawson and Heal 1976; Leidy 1985) were screened for additional references. The main Google search engine (https://google.com/) was also searched for additional nonscientific records (i.e. photographs). Summaries of the search results are found in Näslund (2021).

All identified publications, ranging from year 1555 to 2020, are summarized and freely available in a digital data spreadsheet deposited in an online repository (Näslund 2021). For each publication, species, family, origin (wild or aquaculture), type of record (photo, illustration, description, osteology, note), number of reported cases, and extent of the publication obtained (full text, abstract, or title) are recorded. Nonscientific sources from websites, blogs, and social media (Twitter, Facebook, etc.) are noted separately. Species names and families were updated to currently valid taxonomy according to Eschmeyer's Catalog of Fishes (Fricke et al. 2020), based on scientific names specified in original publications (i.e. assuming species determination was valid); with the exception of *Sander* spp. which are referred to as *Stizostedion* spp. following Bruner (2021). Deformities described as 'parrot-like head' and similar anomalities (e.g. Michajlowa 1968; Eissa et al. 2008, 2009; Yadegari et al. 2011) were classified as pugheadedness for the literature summary. Cases described as having shortened upper jaws were also included, but not those with extended lower jaws.

From the literature search at least 142 species and 3 hybrids were recorded, with an additional 3 species

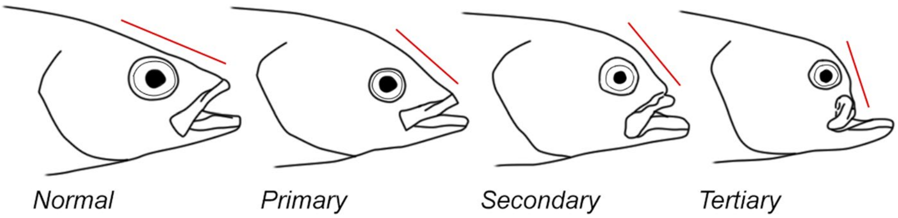

Figure 5. Degrees of pugheadedness as defined by Hickey et al. (1977). Primary pugheadedness: mildly steep forehead. Secondary pugheadedness: moderately steep forehead, slight reduction in size of upper jaw (lower jaw protrudes slightly, but markedly, beyond upper more than normal), possibly malformed maxilla and/or premaxilla, with or without exophthalmia. Tertiary pugheadedness: acutely steep forehead, greatly reduced upper jaw with lower jaw extending far beyond upper, malformation of maxilla and/or premaxilla, incomplete closure of mouth, reduced gape, exposure of tongue, and exophthalmia. Depicted example: striped bass *Morone saxatilis*; note that the exact expression of the deformity will depend on the species' normal head morphology and relative jaw length and position (see Figure 3 for more examples).

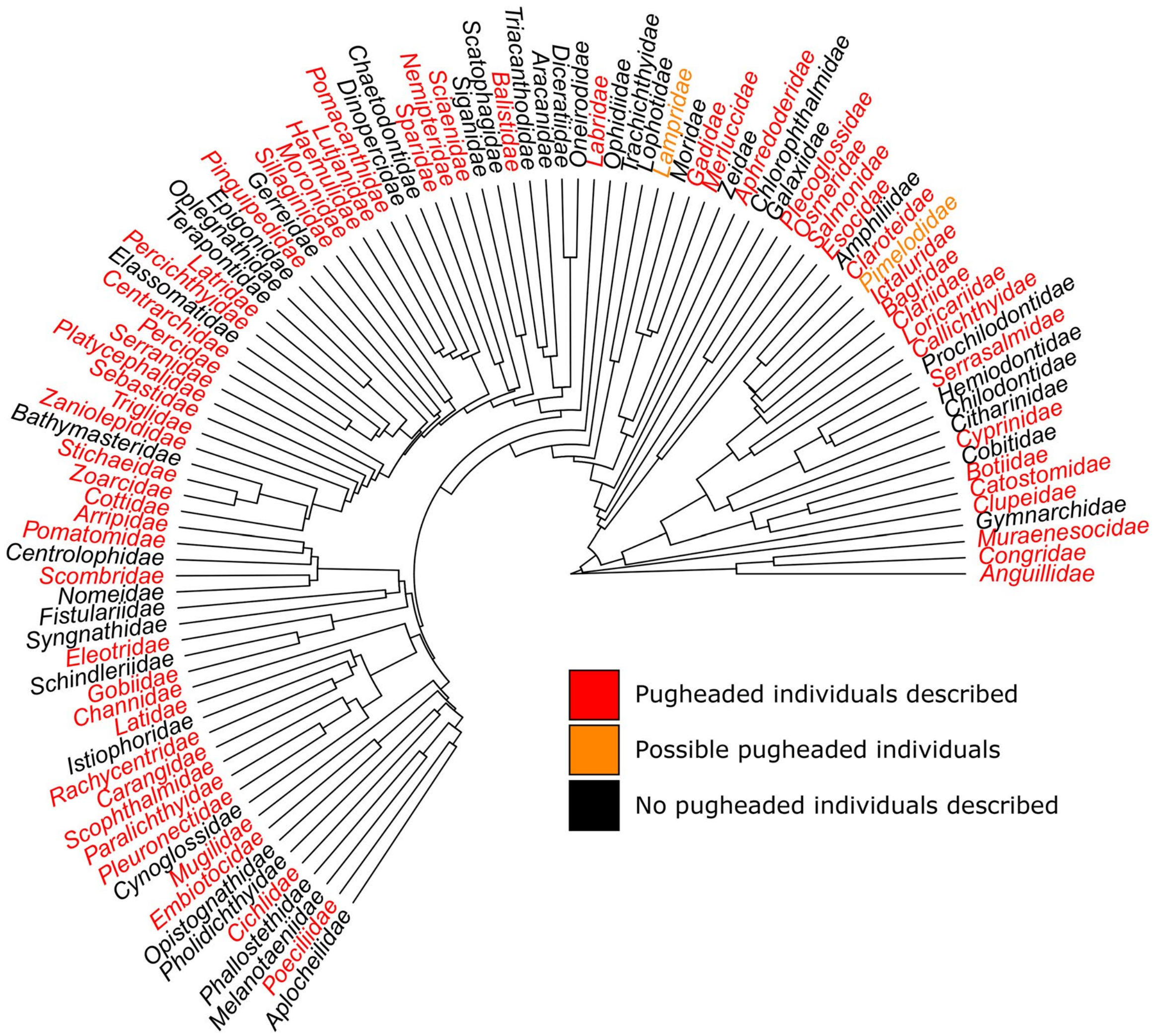

Figure 6. Pughead records mapped onto a phylogeny of fish families. All families with cases of pugheads recorded are mapped, along with 40 randomly selected families where pugheads have not been recorded. The phylogeny is based on data from Rabosky et al. (2018), using the fishtree R-package Chang et al. (2019). See supplemental information in Näslund (2021) for all documented records of pugheaded individuals in each family.

included as possible cases. Six elasmobranch species were recorded with pughead-like deformities, although it is not clear that these represent an equivalent type of deformity as in bony fishes. The nonscientific sources (photographs) revealed 22 additional species, predominantly stemming from angling and aquarist websites and forums. In total, the recorded cases represented 60 different families (excluding the elasmobranchs). These families were well distributed across the actinopterygian phylogeny (Figure 6). Families with more than 10 publications describing cases of pugheadedness were Clupeidae, Cyprinidae, Gadidae, Moronidae, Percidae, Salmonidae, Sciaenidae, and Sparidae. All of these families include species important for commercial fisheries, angling, or aquaculture. Based on these findings, the general conclusion is that pugheadedness likely is a general phenomenon in actinopterygian fish and not specific to certain families or habitats. Certain species being overrepresented in the literature likely reflects bias related to high human exposure to these species (increasing the likelihood of finding pugheaded specimens) and not a particularly high incidence frequency.

Discussion

Descriptive teratology of fishes seems to have progressively fallen out of fashion in the scientific literature over the last century. Many recent cases are not reported scientifically, but instead found in e.g. social media as curiosities (e.g. from aquarium breeders, anglers and aquaculturists). It might be that the condition now is relatively widely recognized, and reporting of additional cases is perceived as unnecessary. Furthermore, most reports pertain to quite severe cases, likely due to slight cases being overlooked as they do not deviate much from normal specimens, as also argued by (Hickey et al. 1977). Hence, there is no good way of assessing the true number of taxa affected by pugheadedness.

Already in 1930s Croker suggested that "nearly all kinds of fish have been observed to be susceptible to the abnormality" (Croker 1931). Based on this review, it can be concluded that a wide range of taxa are indeed susceptible, both in freshwater and marine environments, suggesting that disruption (genetic, environmental, or interactions between these) of one or several common developmental pathway(s) is the underlying mechanism. While additional case reports are indeed interesting, it is advisable to try to focus investigations on incidence and the factors leading to this condition in more detail. This has been the focus in several aquaculture-related projects, but more data are needed from the natural environment, where incidence and causing factors are still mainly speculated upon. Given that observations in the wild are relatively rare, this may be a difficult task which has to rely on opportunistic research conditions. Furthermore, the ecology of pugheaded fishes in the wild, compared to normal individuals, (mortality rates, growth rates, behavior etc.) is still largely based on anecdotal evidence. The occasional high incidence in aquacultured fish could possibly be used for experimental studies (e.g. for behavioral comparisons under controlled conditions, or release-recapture experiments in natural or semi-natural environments). Detailed brain morphology- and cognition studies may also be interesting, given the potential effects the deformity may have on the brain.

Terminology

"Pugheadedness" is a descriptive term covering several different combinations of malformations of the bones in the forehead of fishes (Boglione et al. 2001). Hickey et al. (1977) amended the term with a 3-tiered classification system based on external morphology (primary, secondary, and tertiary pugheadedness; Figure 5; also see Barahona-Fernandes 1982). Prior to that, Gudger (1929) used two degrees of deformation to describe salmonid pugheads (both, however, being relatively severe as compared to classification by Hickey et al. 1977). From the literature review it is clear that even more nuances could be accounted for among the cases, given the fact that the scale of deformity is continuous and that there is substantial variability of the bones affected and secondary effects on e.g. eyes and tongue. A relative jaw-index where the shortening of the deformed specimens is related to normal-specimen jaws could be used to provide a more specific description of the severity degree. Given how commonly used the term is, it seems to be good advice to retain pugheadedness as an overarching term for congenital shortened foreheads, although it likely covers many combinations of bone deformities. The usage of the term should reasonably be restricted to cases with demonstrably shortened or deformed parasphenoid bones, without additionally shortened lower jaws – this definition would align reasonably well with the general consensus through history. The lower-jaw criterion separates pugheadedness from roundheadedness, but there must be a realization that there is a gradient of deformities spanning between these generalized terms and they should mainly be used as heuristic descriptions.

Some authors use a strict definition of pugheadedness, considering only cases with specifically ethmoid and parasphenoid bone malformation as pugheaded (e.g. Sawada et al. 2001). Such strict definitions of pugheadedness do not necessarily match the extensive literature in which a general upper-jaw deformity is typically denoted as pugheadedness, without specific investigations into which osteological elements are affecting the deformities. In recent literature, pugheadedness has also been defined as deformed maxillary and premaxillary elements, without mentioning the parasphenoid (e.g. Daria et al. 2010).

Notes from the literature search

The literature search results indicate that publications on pugheadedness are not particularly well covered by the main scientific databases Web of Science (26 hits) and Scopus (26 hits). The search engine Google Scholar performed substantially better (97 hits), likely due to a wider indexing and searching of whole text documents, rather than being limited to titles, keywords, and abstracts. Nevertheless, searching reference lists in the literature still increased the number of relevant publications with over 100%. For future work on pugheadedness in fish, it is important to know where to find the literature on the subject. Hence, for future reference, an annotated bibliography including all publications found in this study is available in Näslund (2021). Undoubtedly, there are additional descriptive scientific reports on cases of pugheadedness, particularly in non-English literature. There is also a large amount of literature just noting head deformities in general (e.g. in aquaculture and toxicology studies); some of these studies undoubtedly include pugheads, but were either not detected due to lack of relevant key-words in the text, or excluded from the bibliography due to lack of details. There is also undoubtedly more records described in news media, since there are several such news articles noted in the scientific literature [e.g. striped bass *Morone saxatilis* reported in *New York Sun* (December 21, 1919; Gudger 1930), *The Washington Sunday Star* (June 2, 1957; Mansueti 1960), and *Chrisfield Times* (August 5, 1960; Mansueti 1960); a rainbow trout reported in *The Sydney Daily Telegraph* (Nov. 7 1932; Whitley 1944)].

Acknowledgments

Special thanks are directed to the Biodiversity Heritage Library (https://www.biodiversitylibrary.org/) for making old biological literature available online, without this resource this study would not be possible. Two anonymous reviewers are thanked for comments on the manuscript.

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