

## Abnormalities in flatfishes of the south-west Atlantic Ocean

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(Received 26 May 2017, Accepted 2 February 2018)

Five adult paralichthyid specimens with various kinds of abnormalities are reported from the south-west Atlantic Ocean. These abnormal flatfish specimens represent the first records of wholly ambicoloured *Paralichthys orbignyanus* specimens having a deep notch between the eye and dorsal fin and a partially albinistic specimen having skeletal deformities and only the second record of an almost totally ambicoloured specimen. We also report the first observation of reversal in *Paralichthys patagonicus* and an almost totally ambicoloured, reversed *Xystreurus rasile*.

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Key words: abnormalities; ambicolouration; flatfish; Paralichthyidae; reversal; south-west Atlantic Ocean.

The flatfish order Pleuronectiformes is a specialized group of teleosts characterized by highly asymmetrical skulls, with both eyes placed on one side of the head (Brewster, 1987). This extraordinary anatomical specialization arises through migration of one eye during the post-larval stage (Kyle, 1921). Flatfishes can be grouped according to the position of their eyes as sinistral forms, in which the right eye migrates to the left side and dextral forms, in which the left eye migrates to the right side (Ahlstrom *et al.*, 1984). Body pigmentation is also usually asymmetrical, wherein the ocular side is pigmented while the blind side is unpigmented (Norman, 1934).

In some individuals pigmentation anomalies occur on both sides of the body. A frequent anomaly in flatfishes is ambicolouration (*i.e.* the presence of pigmentation on the normally unpigmented blind side of the body). Ambicoloured flatfish specimens have been recorded as being total (Haaker & Lane, 1973), almost total (Forrester & Smith, 1971; Díaz de Astarloa, 1995, 1998) or partial (Taylor *et al.*, 1973; Stickney & White, 1975; Díaz de Astarloa, 1995). Total ambicolouration is always associated

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with head anomalies, such as abnormal positioning of the migrating eye and formation of the anterior dorsal fin into a fleshy hook (Gartner, 1986). Migration of the eye in totally ambicoloured individuals ends on the dorsal crest, under the fleshy hook, whereas in almost totally ambicoloured individuals the eye migrates over the dorsal crest, but does not reach the normal position (Díaz de Astarloa *et al.*, 2006; Macieira *et al.*, 2006). Another anomaly found in flatfishes is called hypomelanosis, also termed pseudo-albinism, which results from a deficiency of pigment cells on the ocular side, with pigment sometimes absent from the entire surface (Venizelos & Benetti, 1999; Bolker & Hill, 2000).

In most flatfish groups, the majority of species have eyes that are either exclusively on the left side (Psettodidae, Citharidae, Bothidae, Achiropsettidae, Scopthalmidae, Paralichthyidae and Cynoglossidae) or the right side (Poecilopsettidae, Pleuronectidae, Samaridae, Achiridae and Soleidae) (Bisbal & Bengston, 1993). However, infrequent anomalous reversals (*i.e.* eyes and colour on the side that is usually eyeless and unpigmented) occur, resulting in sinistral orientation in dextral species and *vice versa* (Díaz de Astarloa, 1997). Such anomalous reversals have been well documented in a wide range of species (Norman, 1934; Gudger & Firth, 1936; Bisbal & Bengston, 1993; Munroe, 1996; Díaz de Astarloa, 1997; da Silva *et al.*, 2007; Macdonald, 2013). In a few species, however, eye migration occurs in either direction with almost equal frequency. For example, studies on the left-sided *Paralichthys californicus* (Ayres 1859) have reported that the incidence of reversal in this species is as high as 40% (Ginsburg, 1952; Kramer *et al.*, 1995).

Specimens analysed in this paper were collected in the field or examined in fish collections. One almost totally ambicoloured *Paralichthys orbignyanus* (Valenciennes 1839) was caught in the Bahía Blanca estuary, Argentina (39° 05' S; 61° 50' W), using a shrimp net in September 2007. The wholly ambicoloured specimen of *P. orbignyanus* with a fleshy hook and the partially albinistic *P. orbignyanus* specimen with skeletal deformities were examined in the fish collections of the Natural History Museum of Vienna (NMW 56464) and the Argentine Museum of Natural Sciences (MACN 5564), respectively. In addition, a reversed specimen of *Paralichthys patagonicus* Jordan 1889, was caught by a commercial bottom-trawler off Mar del Plata, Argentina (38° 10' S; 57° 20' W), in October 2016 and an almost ambicoloured reversed specimen of *Xystreureys rasile* (Jordan 1891) was caught by the R.V. *Eduardo Holmberg* off Chubut province, Argentina (44° 45' S; 65° 23' W), on 20 January 2006.

Counts and measurements were taken with a digital calliper and made on both abnormal and normal specimens ( $n = 10$  for each species). Ten scales from the anterior dorsal area above the lateral line of *P. patagonicus* and *X. rasile* were measured on each side of the body from reversed individuals and compared with those obtained from five normal individuals. Reversed specimens were catalogued in the fish collection of the Instituto de Investigaciones Marinas y Costeras under the following catalogue numbers: UNMdP 4671 (*P. patagonicus*) and UNMdP 4677 (*X. rasile*). The pseudo-albinistic specimen of *P. orbignyanus* with skeletal deformities was x-rayed to determine the presence and extent of osteological deformation.

The almost totally ambicoloured specimen of *P. orbignyanus* had the same colouration pattern on the blind side as on the eyed side except for the right side of the head, which was unpigmented [Fig. 1(a), (b)]. The head of this anomalous *P. orbignyanus* was also shorter compared with normal specimens of the same species, but no differences were observed in other measurements and counts (Table I).

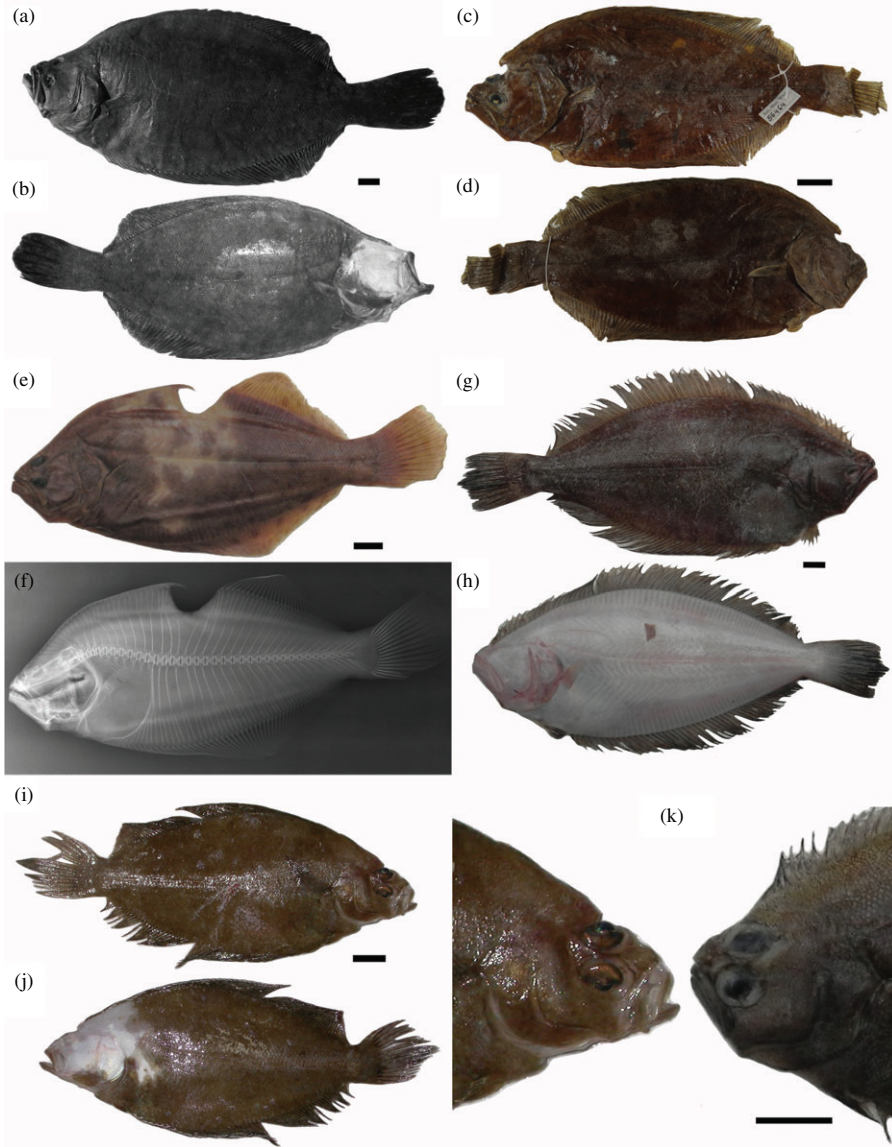


FIG. 1. Abnormal flatfish specimens examined in this study. (a) Ocular side and (b) blind side of an almost totally ambicoloured specimen of *Paralichthys orbignyanus* (322 mm standard length;  $L_S$ ) caught in Bahía Blanca estuary, Argentina. Scale bar = 2 cm. (c) Ocular side and (d) blind side of a totally ambicoloured specimen (NMW 56464) of *Paralichthys orbignyanus* ( $L_S$  202 mm) caught in Pelotas, Rio Grande, Brazil. (e) Specimen (MACN 5564) of *Paralichthys orbignyanus* (243 mm  $L_S$ ) with partial albinism and dorsal surface deformity and (f) radiograph of the ocular side. (g) Ocular side and (h) blind side of a reversed specimen (UNMdP 4671) of *Paralichthys patagonicus* caught off Mar del Plata, Argentina ( $L_S$  311 mm). (i) Ocular side and (j) blind side of a reversed, almost ambicoloured specimen (UNMdP 4677) of *Xystreuryx rasile* caught in central Patagonia, Argentina (192 mm  $L_S$ ). (k) Anterior part of the ocular side of the head of a reversed specimen (UNMdP 4677) of *Xystreuryx rasile* (left) compared to a normal sinistral specimen of the same species (right); N.B. Notch over the incompletely migrated eye. MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Ciudad Autónoma de Buenos Aires, Argentina; NMW, Naturhistorisches Museum, Wien (Vienna), Austria; UNMdP, Universidad Nacional de Mar del Plata, Argentina.

TABLE I. Comparative measurements and counts made from typical and abnormal specimens of *Paralichthys orbignyanus*

	Normal <i>P. orbignyanus</i>			BBE	<i>P. orbignyanus</i> (NMW56464)	<i>P. orbignyanus</i> (MACN 5564)
	Mean	S.D.	Range			
Standard length ( $L_S$ , mm)	273.9	60.7	201.0–354.0	322	202	243
% $L_S$						
Head length	26.8	1.2	25.4–29.0	23.2	27.2	26.4
Pre-orbital length	6.3	0.7	5.4–7.3	5.9	6.4	6.3
Inter-orbital width	2.9	0.4	2.4–3.7	3.6	3.1	2.5
Prepectoral length	26.1	1.3	24.8–28.5	23.9	26.0	25.2
Preventral length	18.3	1.5	16.9–21.7	20.9	20.9	21.2
Predorsal length	5.3	0.8	3.9–6.5	5.6.3	10.3	4.4
Pectoral fin length	12.0	0.9	10.8–13.5	10.0	11.8	12.7
Dorsal–fin rays	76.5	5.1	72.0–90.0	67	76	68
Anal–fin rays	58.2	4.2	54.0–69.0	55	59	60
Pectoral–fin rays	11.0	0.5	10.0–12.00	9	10	11
Gill rakers of 1° arch	4.7 + 15.7	0.7 + 1	4–6 + 15–18	3 + 14	5 + 15	4 + 16
Upper maxilla	10.7	1.0	9.4–12.4	10.9	13.1	11.6
Caudal peduncle depth	11.8	0.6	10.7–12.4	10.4	11.8	12.2

Standard length ( $L_S$ ) is expressed in mm. All other measurements are presented as percentages of  $L_S$ . BBE, Bahía Blanca estuary. MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Ciudad Autónoma de Buenos Aires, Argentina; NMW, Naturhistorisches Museum, Wien (Vienna), Austria.

Another *P. orbignyanus* specimen (NMW 56464) had pigmentation typical of the species on the ocular side [Fig. 1(c)], yet differed from normal specimens by having a totally pigmented blind side [Fig. 1(d)]. The entire blind side was uniformly dark brown and its colouration resembled that of the ocular side. Externally, obvious cranial morphological anomalies were evident; it had anomalous fleshy hook at the anterior end of the dorsal fin and incomplete migration of the right eye. Instead of being situated on the medial region of the head, as is typical for the species, the right eye of this specimen migrated only as far as the dorsal crest under the fleshy hook formed as a result of the obstructed forward growth of the dorsal fin. In this position it was visible from the right side [Fig. 1(d)], which is atypical for this species. Additionally, this totally ambicoloured specimen had a much greater predorsal length (10.3% of standard length;  $L_S$ ) than the range for normal specimens (3.9–6.5%  $L_S$ ). In non-ambicoloured specimens, the posterior part of the maxilla is covered by scales on the ocular side but naked on the blind side, the anus opens on the blind side and the urogenital papilla is located on the ocular side forward and dorsal to the first anal-fin ray. In contrast, the ambicoloured specimen had the posterior part of the blind side maxilla scaly, the anus opening on the ocular side, slightly above the anal-fin origin and the urogenital papilla located on the blind side.

A third *P. orbignyanus* specimen (MACN 5564) had a malformed notch in the middle dorsal region of the ocular side, with this abnormality being surrounded by unpigmented areas (partial albinism) [Fig. 1(e)]. An x-ray taken of this specimen clearly showed that the dorsal pterygiophores were missing from caudal vertebrae 14 and 15 and only one pterygiophore was observed at vertebrae 13 and 16. Thus, a total of four dorsal-fin rays were missing [Fig. 1(f)].

The right-sided (dextral) *P. patagonicus* [Fig. 1(g)] was not a mirror image of a normal individual of this species. Compared with a normal fish of the same size, pre-ventral length and the upper maxilla were longer than is typical (Table II). However, no abnormal colouration and no differences in counts or other morphometrics were recorded [Fig. 1(h)].

The reversed, almost completely ambicoloured *X. rasile* ([Fig. 1(i)] had a pre-ventral length and predorsal length (snout to dorsal-fin origin) much longer than a normal individual. Other measurements and counts fell within the species range (Table II). The blind side of the body was almost completely coloured, with only the head and anterior dorsal area unpigmented [Fig. 1(j)]. There was also a concavity in the anterior cephalic region at the beginning of the dorsal fin, incomplete left eye migration [Fig. 1(k)] and blind side scales that were 20% larger than those of normal specimens.

Presence of abnormalities in various groups of paralichthyid flatfishes are thought to occur more frequently than in other families of the order Pleuronectiformes, (Gartner, 1986). Whereas ambicolouration is well documented and apparently rather common in the Bothidae, Paralichthyidae and Pleuronectidae, few records report such anomalies in the Achiridae, Soleidae and Cynoglossidae. Dawson (1962) summarized results from the literature, listing 27 specimens of bothids and pleuronectids with at least four types of ambicolouration, but noted only two cases of abnormal colouration in other families, including an almost completely ambicoloured *Trinectes maculatus* (Bloch & Schneider 1801) (Achiridae) and a partially ambicoloured *Symphurus plagiusa* (L. 1766) (Cynoglossidae). Gartner's (1986) account of naturally occurring anomalies in *Gymnachirus melas* Nichols 1916 is the first documented report for achirids in the western Atlantic Ocean other than *T. maculatus*. Other cases of anomalous specimens of Achiridae and Cynoglossidae were documented by Moore & Posey Sr. (1974) and Munroe (1996), respectively. The present report adds more records of flatfish abnormalities in specimens of the genus *Paralichthys* Girard 1858 and *Xystreureys* Jordan & Gilbert 1880 (both Paralichthyidae).

Ambicolouration occurs much more frequently in hatchery-reared flatfish. Specimens with nearly 100% ambicolouration have been observed in tank cultured *Paralichthys dentatus* (L. 1766) and *Paralichthys lethostigma* Jordan & Gilbert 1884 (Stickney & White, 1975) and 95% of hatchery reared populations of *P. olivaceus* (Temminck & Schlegel 1846) showed black areas on the blind side of body (Tominaga & Watanabe, 1998). However, blind-side pigmentation is uncommon in wild fish. Three specimens of *P. californicus*, from a total of 1256 have been reported to be ambicoloured (Haaker & Lane, 1973). Dawson (1962) recorded an incompletely ambicoloured specimen of *P. lethostigma* trawled in Calibogue Sound, South Carolina, U.S.A. Two ambicoloured specimens of *Paralichthys isosceles* Jordan 1891 (one almost fully ambicoloured and the other partially ambicoloured) have been reported in Brazilian waters (da Silva *et al.*, 2007). Other reports include a partially ambicoloured *Etropus crossotus* Jordan & Gilbert 1882, captured from coastal waters of Georgia, U.S.A. (Taylor *et al.*, 1973), a totally ambicoloured *P. californicus* collected in Anaheim Bay, California, U.S.A. (Haaker & Lane, 1973) and an almost completely ambicoloured *Eopsetta jordani* (Lockington 1879) with skeletal anomalies taken off the west coast of Vancouver Island, Canada (Forrester & Smith, 1971).

For flatfishes in which blind-side pigmentation is complete or almost complete, this colouration is almost always associated with head or vertebral anomalies or some other morphological variation, such as migration of the eye, scales and associated



TABLE II. Comparative measurements and counts made from typical and reversed specimens of *Paralichthys patagonicus* and *Xystreureys rasile*

	Typical <i>P. patagonicus</i> (n = 10)			Typical <i>X. rasile</i> (n = 10)		
	Mean	S.D.	Range	Mean	S.D.	Range
Standard length ( $L_S$ , mm)	308.9	5.4	301.0–315.0	311	227.5	192.7–253.0
$\%L_S$						
Head length	26.4	0.7	25.5–27.5	27.2	24.8	23.2–26.1
Pre-orbital length	5.4	0.3	5.1–6.1	5.0	4.8	4.1–5.2
Inter-orbital width	1.6	0.2	1.3–1.9	1.3	0.7	0.6–0.9
Prepectoral length	26.1	0.7	25.2–27.2	26.5	24.5	22.7–25.8
Preventral length	17.4	1.4	15.0–19.5	22.1	20.6	17.7–23.7
Predorsal length	4.8	0.7	3.6–5.8	5.4	6.1	4.7–6.8
Pectoral fin length	12.6	0.6	11.6–13.4	12.7	19.7	18.4–21.2
Dorsal-fin rays	81.3	2.6	75.0–84.0	73.0	81.6	79.0–85.0
Anal-fin rays	62.9	2.6	57.0–66.0	57.0	65.3	61.0–70.0
Pectoral-fin rays	11.1	0.6	10.0–12.0	11.0	10.2	9.0–11.0
Gill rakers of 1° arch	2.6 + 10.7	0.5 + 0.7	2–3 + 10–12	3 + 11	5 + 11	4–6 + 9–13
Upper maxilla	11.5	0.4	10.9–12.3	13.1	9.9	9.5–10.6
Caudal peduncle depth	10.0	0.6	9.3–11.2	9.7	11.0	10.6–11.4
						<i>X. rasile</i> (UNMdP 4677)
						192
						25.8
						5.6
						0.7
						25.5
						25.1
						12.4
						20.2
						75.0
						60.0
						10.0
						4 + 10
						9.5
						11.3

All other measurements are presented as percentages of  $L_S$ . UNMdP, Universidad Nacional de Mar del Plata, Argentina.

structures (Norman, 1934; Díaz de Astarloa, 1995, 1998). In normal flatfishes, eye migration is completed before the forward extension of the dorsal fin takes place, but in ambicoloured specimens this migration appears to be arrested or delayed, obstructing growth of the dorsal fin and, as a consequence, a fleshy hook is formed above the eye (Norman, 1934). This hook is present only when pigmentation of the blind side is complete or nearly so (Norman, 1934). Haaker & Lane (1973) reported a totally ambicoloured *P. californicus* with abnormal position of the migrating eye and formation of the anterior dorsal fin into a fleshy hook and an almost totally ambicoloured *Hypsopsetta guttulata* (Girard 1856) with a depression formed in the frontal region of the head. Macieira *et al.* (2006) described an abnormal specimen of *Achirus declivis* Chabanaud 1940 with incomplete eye migration and a hooked dorsal fin. In addition, Díaz de Astarloa *et al.* (2006) reported for the first time the occurrence of a totally ambicoloured *P. patagonicus* with incomplete eye migration and a hooked anterior dorsal fin. Gudger & Firth (1936) offered a hypothesis to explain conditions in which such morphological anomalies occur. They found that when the blind side is completely coloured like the ocular side or when about one-fourth to one-third of the head surface of the blind side is coloured, then the migrating eye will not completely migrate and the dorsal fin will be hooked. For example, the totally ambicoloured *P. orbignyanus* specimen NMW 56464 showed an incomplete migration of the eye along with the formation of a fleshy hook at the anterior end of the dorsal fin [Fig. 1(c)]. The reversed, almost ambicoloured *X. rasile* specimen UNMdP 4677 also featured a clearly notched head at the beginning of the dorsal fin and incomplete left eye migration [Fig. 1(k)].

In many flatfish species, reversals are exceedingly rare. *Pleuronectes platessa* L. 1758 is normally a dextral species, but occasionally sinistral individuals are found (Gudger, 1935). A single case of reversal among 15 859 specimens of *Limanda limanda* (L. 1758) was reported by Bruno & Fraser (1988). Vassilopoulou (1993) reported a small number of occurrences (0.026%) of reversed (dextral) individuals from samples of *Lepidorhombus boschii* (Risso 1810) collected in the Aegean Sea. In the symphurine tonguefish *Symphurus vanmelleae* Chabanaud 1952, right-eyed specimens are also rare (Munroe, 1996). Reversal appears to be rare in the paralichthyid genus *Citharichthys* Bleeker 1862, with only three reported cases (Dawson, 1969; Castillo-Rivera & Kobelkowsky, 1992; da Silva *et al.*, 2007) and in the pleuronectid genera *Microstomus* Gottsche 1835 and *Cleisthenes* Jordan & Starks 1904 (Goto, 2009).

In other flatfish species reversal is more common. Reversed specimens of both the paralichthyid *Xystreurus liolepis* Jordan & Gilbert 1880 (Kramer *et al.*, 1995) and the pleuronectid *Platichthys stellatus* (Pallas 1787) occur more frequently (Policansky, 1982). *Paralichthys californicus* belongs to the left-eyed flounder family, but up to 40% of individuals are reversed (Kramer *et al.*, 1995). Sometimes, reversed specimens are not mirror images of normal individuals of the same species. Díaz de Astarloa (1997) found that the reversed specimen of *P. orbignyanus* had the head, maxilla and prepectoral lengths longer than is typical in a normal fish. Also, da Silva *et al.* (2007) reported meristic differences in a reversed specimen of *Citharichthys macrops* Dressel 1885 compared with normal specimens of the same species. The only case of a reversed individual of *Lepidorhombus whiffiagonis* (Walbaum 1792) was recorded from a survey of 39 072 measured individuals and the reversed individual had a narrower interorbital width and greater caudal peduncle length than non-reversed individuals (Macdonald, 2013). In this study, the right-sided *P. patagonicus* had a pre-ventral length and upper maxilla longer than a normally left-sided specimen. The reversed *X. rasile* specimen

had a lower number of both dorsal and anal-fin rays and longer pre-ventral and pre-dorsal lengths than typical left-eyed specimens. Although no other morphometric differences were found among reversed specimens examined in this paper compared with normal specimens of the same species, multiple traits related to swimming and foraging performance between sinistral and dextral forms might differ in ways that may affect function and ecology, as has been pointed out in the polymorphic pleuronectid *Platichthys stellatus* (Bergstrom, 2007). However, further experimental research is required to test this hypothesis for both *P. patagonicus* and *X. rasile*.

Causes of flatfish abnormalities have been treated or hypothesized by different authors (Gudger & Firth, 1936; Dawson, 1962; Bolker & Hill, 2000; Ulutürk *et al.*, 2015). Effects of light (Houde, 1971), food levels and temperature (Shelbourne, 1964; de Veen, 1969) and availability of suitable substratum (Stickney & White, 1975) have been proposed as possible causes of abnormalities in flatfishes. Gartner (1986) also hypothesized that flatfish abnormalities are most often reported in shallow coastal to estuarine species. The author suggested that shallow-water and estuarine species are more exposed to light intensity and temperature fluctuations that could affect development. Several possible physical and ethological factors have also been suggested to explain abnormalities in hatchery-reared Pleuronectiformes (Kang *et al.*, 2014). However, it is not yet clear if there is a general explanation for why flatfish abnormalities occur in wild. Exposure to light, feeding during the larval stage, genetic factors and environmental stressors have been mentioned as likely causes (Venizelos & Benetti, 1999; Bolker & Hill, 2000; Kang *et al.*, 2014). Norman (1934) indicated that unpigmented areas may be associated with injuries, such as bites. Dawson (1967) suggested that partial albinism occurs as a result of trauma or adverse environmental factors. He suggested that most cases of partial albinism were associated with osteological aberrations. In this study, the occurrence of abnormal pigmentation in the *P. orbignyana* specimen MACN 5564 might have been caused by bites received from a predator, which may have caused both the notch-shaped deformation and the unpigmented areas.

Analysis of the scales of reversed individuals of *P. patagonicus* showed scale sizes on both sides of the body similar to normal specimens. In the right-side specimen of *X. rasile*, however, blind side scales were only 1-4% smaller than the eyed size, whereas in a typical *X. rasile*, blind side scales are 20% smaller. Dawson (1962) mentioned that abnormal individuals may have larger or smaller scales than normal specimens, which may be generally related to ambicolouration.

Studies of flatfish abnormalities are of major taxonomic concern. The description of abnormal individuals as species new to science can sometimes occur. For example, the detailed re-examination of putative *Neotropus macrops* Hildebrand & Schroeder 1928 found that it was a reversed specimen of the previously described species *Citharichthys arctifrons* (Goode 1880) (Hoshino & Munroe, 2004).

The authors wish to thank R. Mazzella for donating the reversed *Paralichthys patagonicus*, S. Mazzella for providing the *P. orbignyana* specimen from the Bahía Blanca estuary. J.M.D.A. is much indebted to Senior Collection Manager A. Palandacic at the Naturhistorisches Museum in Wien, Austria for her kind assistance and support. The technical assistance of G. Chiaramonte (head curator of Ichthyological Division of Museo Argentino de Ciencias Naturales, Buenos Aires) in supplying the specimen of *P. orbignyana* with partial albinism is greatly appreciated. The specimen of *Xystreurus rasile* was collected during the cruise 'EH-01/06' from 11 January to 5 February 2006 on board the R.V. *Dr. Eduardo L. Holmberg*. The crew and researchers of the cruise are acknowledged. Finally, we thank two anonymous reviewers for useful suggestions and comments that really improved the original manuscript. This research was funded by the



Consejo Nacional de Investigaciones Científicas y Técnicas (PIP 11220130100339), Universidad Nacional de Mar del Plata (EXA 767/16), Agencia Nacional de Promoción Científica (PICT 2014–0665).

## References

- Ahlstrom, E. H., Amaoka, K., Hensley, D. A., Moser, H. G. & Sumida, B. Y. (1984). Pleuronectiformes: development. In *Ontogeny and Systematics of Fishes* (Moser, H. G., Richards, W. J., Cohen, D. M., Fahay, M. P., Kendall, W. Jr. & Richardson, S. L., eds), pp. 640–670. Lawrence, U.S.A.: American Society of Ichthyologists and Herpetologists, Special Publication 1.
- Bergstrom, C. A. (2007). Morphological evidence of correlational selection and ecological segregation between dextral and sinistral forms in a polymorphic flatfish, *Platichthys stellatus*. *Journal of Evolutionary Biology* **20**, 1104–1114.
- Bisbal, G. A. & Bengston, D. A. (1993). Reversed asymmetry in laboratory-reared summer flounder. *The Progressive Fish-Culturist* **55**, 106–108.
- Bolker, J. A. & Hill, C. R. (2000). Pigmentation development in hatchery-reared flatfishes. *Journal of Fish Biology* **56**, 1029–1052.
- Brewster, B. (1987). Eye migration and cranial development during flatfish metamorphosis: a reappraisal (Teleostei: Pleuronectiformes). *Journal of Fish Biology* **31**, 805–833.
- Bruno, D. W. & Fraser, C. O. (1988). A case of reversal in the common dab, *Limanda limanda* (L.). *Journal of Fish Biology* **32**, 483–484.
- Castillo-Rivera, M. & Kobelkowsky, A. (1992). First record of reversal in the flounder *Citharichthys spilopterus* (Bothidae). *Copeia* **1992**, 1094–1095.
- Dawson, C. E. (1962). Notes on anomalous American Heterosomata with descriptions of five new records. *Copeia* **1962**, 138–146.
- Dawson, C. E. (1967). Three new records of partial albinism in American Heterosomata. *Transactions of the American Fisheries Society* **96**, 40–404.
- Dawson, C. E. (1969). Three unusual cases of abnormal coloration in northern Gulf of Mexico flatfishes. *Transactions of the American Fisheries Society* **98**, 10–108.
- Díaz de Astarloa, J. M. (1995). Ambicoloration in two flounders, *Paralichthys patagonicus* and *Xystreuris rasile*. *Journal of Fish Biology* **47**, 168–170.
- Díaz de Astarloa, J. M. (1997). A case of reversal in *Paralichthys orbignyanus* a shallow-water flounder from the southwestern Atlantic. *Journal of Fish Biology* **50**, 900–902.
- Díaz de Astarloa, J. M. (1998). An ambicolorate flounder, *Paralichthys isosceles*, collected off Península Valdés, Argentina. *Cybiurn* **22**, 187–191.
- Díaz de Astarloa, J. M., Rico, R. & Acha, M. (2006). First report of a totally ambicoloured Patagonian flounder *Paralichthys patagonicus* (Paralichthyidae) with dorsal fin anomalies. *Cybiurn* **30**, 73–76.
- Forrester, C. R. & Smith, M. S. (1971). Ambicoloration in a petrale sole (*Eopsetta jordani*). *Journal of the Fisheries Board of Canada* **28**, 1672–1674.
- Gartner, J.V. Jr. (1986). Observations on anomalous conditions in some flatfishes (Pisces: Pleuronectiformes), with a new record of partial albinism. *Environmental Biology of Fishes* **17**, 141–152.
- Ginsburg, I. (1952). Flounders of the genus *Paralichthys* and related genera in American waters. *Fishery Bulletin* **52**, 267–351.
- Goto, T. (2009). Reversals in two dextral flounder species, *Microstomus achne* and *Cleisthenes pinetorum* (Pleuronectida: Teleostei), from Japan. *Journal of Fish Biology* **74**, 669–673.
- Gudger, E. W. (1935). Abnormalities in flatfishes (Heterosomata) I. Reversal of sides a comparative study of the known data. *Journal of Morphology* **58**, 1–39.
- Gudger, E. W. & Firth, F. E. (1936). Three partially ambicolorate four-spotted flounders, *Paralichthys oblongus*, two each with a hooked dorsal fin and a partially rotated eye. *American Museum Novitates* **885**, 141–152.
- Haaker, P. L. & Lane, E. D. (1973). Frequencies of anomalies in a bothid, *Paralichthys californicus* and a pleuronectid, *Hypsopsetta guttulata*, flatfish. *Copeia* **1973**, 22–25.

- Hoshino, K. & Munroe, T. A. (2004). *Neotropus macrops* Hildebrand and Schroeder, 1928: a reversed specimen and a junior synonym of *Citharichthys arctifrons* Goode, 1880 (Teleostei; Pleuronectiformes; Paralichthyidae). *Copeia* **2004**, 583–591.
- Houde, E. (1971). Developmental abnormalities of the flatfish *Achirus lineatus* reared in the laboratory. *Fishery Bulletin* **69**, 537–544.
- Kang, D. Y., Byun, S. G., Myeong, J. I., Kim, H. C. & Min, B. H. (2014). Morphological analysis of blind-side Hypermelanosis of the starry flounder, *Platichthys stellatus* during early development. *Development & Reproduction* **18**, 79–87.
- Kramer, D. E., Barss, W. H., Paust, B. C. & Bracken, B. E. (1995). Guide to northeast Pacific flatfishes: families Bothidae, Cynoglossidae and Pleuronectidae. *Marine Advisory Bulletin* **47**, 1–104.
- Kyle, H. M. (1921). The asymmetry, metamorphosis and origin of flatfishes. *Philosophical Transactions of the Royal Society* **211**, 75–129.
- Macdonald, P. (2013). A rare occurrence of reversal in the common megrim *Lepidorhombus whiffiagonis* (Pleuronectiformes: Scophthalmidae) in the northern North Sea. *Journal of Fish Biology* **83**, 691–694.
- Macieira, R. M., Joyeux, J. C. & Chagas, L. P. (2006). Ambicoloration and morphological aberration in the sole *Achirus declivis* (Pleuronectiformes: Achiridae) and two other cases of color abnormalities in achirid soles from southeastern Brazil. *Neotropical Ichthyology* **4**, 287–290.
- Moore, C. J. & Posey, C. R. Sr. (1974). Pigmentation and morphological abnormalities in the hogchoker, *Trinectes maculatus* (Pisces, Soleidae). *Copeia* **1974**, 660–670.
- Munroe, T. A. (1996). First record of reversal in *Symphurus vanmelleae* (Pleuronectiformes: Cynoglossidae), a deep-water tonguefish from the tropical eastern Atlantic. *Cybius* **20**, 47–53.
- Norman, J. R. (1934). Albinism, ambicoloration and reversal. *A Systematic Monograph of the Flatfishes (Heterosomata)*. Trustees of the British Museum, London **1**, 22–29.
- Policansky, D. (1982). The asymmetry of flounders. *Scientific American* **246**, 116–122.
- Shelbourne, J. E. (1964). The artificial propagation in marine fish. *Advances in Marine Biology* **2**, 1–83.
- da Silva, L. C., De Andrade, A. C., de Andrade-Tubino, M. F. & Vianna, M. (2007). Reversal and ambicoloration in two flounder species (Paralichthyidae, Pleuronectiformes). *Pan-American Journal of Aquatic Sciences* **2**, 23–26.
- Stickney, R. R. & White, D. B. (1975). Ambicoloration in tank cultured flounder, *Paralichthys dentatus*. *Transactions of the American Fisheries Society* **104**, 158–160.
- Taylor, G., Stickney, R. R. & Heard, R. III (1973). Two anomalous flounders (Bothidae, *Etropus crossotus*) from Georgia estuarine waters. *Chesapeake Science* **14**, 147.
- Tominaga, O. & Watanabe, Y. (1998). Geographical dispersal and optimum release size of hatchery-reared Japanese flounder *Paralichthys olivaceus* released in Ishikari Bay, Hokkaido, Japan. *Journal of Sea Research* **40**, 73–81.
- Ulutürk, E., Bayhan, B., Filiz, H., Acarlı, D. & Irmak, E. (2015). Abnormalities in the wedge sole *Dicologlossa cuneata* (Moreau 1881) and Black Sea turbot *Scophthalmus maeoticus* (Pallas 1814) from Turkish Seas. *Journal of Aquaculture Engineering and Fisheries Research* **1**, 98–103.
- Vassilopoulou, V. (1993). Orientation anomalies (reversal) of the four-spotted megrim (*Lepidorhombus bosci*) in the Aegean Sea. *Journal of Fish Biology* **45**, 165–166.
- de Veen, J. F. (1969). Abnormal pigmentation as a possible tool in the study of the population of the plaice (*Pleuronectes platessa* L.). *Journal du Conseil International pour l'Exploration de la Mer* **32**, 344–384.
- Venzelos, A. & Benetti, D. D. (1999). Pigment abnormalities in flatfish. *Aquaculture* **176**, 181–188.