

Apistogramma wapisana sp. n.

- Description of a Dwarf Cichlid from Northern Brazil -

by Uwe RÖMER, Ingo HAHN and Anthony CONRAD

Abstract: *Apistogramma wapisana* sp. n. is described on the base of ten specimens collected in two Igarapés in the Boa Vista surroundings, in the upper Rio Branco-System, Brazil. This small species belongs to the *Apistogramma-pertensis*-group, showing only 3 infra-orbital-pores, and is the first *Apistogramma* species described with males generally smaller than females. This species is characterized by its small size, very little and/or revised sexual dimorphism, small mouth, narrow lateral band, big lateral spot, very small but distinct caudal spot as well as by its specific color pattern and behavior, especially during reproduction.

Zusammenfassung: *Apistogramma wapisana* sp. n. wird an Hand von zehn Belegstücken beschrieben, die in zwei Waldbächen in der Umgebung von Boa Vista im oberen Rio Branco-System (Brasilien) gesammelt wurden. Diese kleine Art ist ein Vertreter der *Apistogramma-pertensis*-Gruppe mit nur 3 Infraorbitalporen und die erste beschriebene *Apistogramma*-Art, bei der die Männchen generell kleiner sind als die Weibchen. Die Art ist gekennzeichnet durch ihre geringe Größe, fehlenden bzw. partiell um-

gekehrten Sexualdimorphismus, kleines Maul, schmales Längsband, großen Flankenfleck, kleinen aber deutlichen Schwanzfleck, sowie durch das einzigartige Farbkleid und Verhalten, insbesondere während der Fortpflanzung.

Resumen: *Apistogramma wapisana* sp. n. ha sido descrita en base de diez especímenes, colectado en dos esteros pequeños boscosos (Igarapés) en la región de Boa Vista, superior Rió Branco sistema, Brasil. Esa especie es un representante del *Apistogramma-pertensis*-grupo; tiene solamente tres poros infra-orbitales y es la primera descrita del género *Apistogramma* que tiene los machos generalmente mas pequeños que las hembras. La especie es caracterizada por su menor tamaño, dimorfismo sexual insignificante y revertido, boca pequeña, banda lateral delgada, mancha lateral destinta y muy pequeña, y por su coloración y conducta única, especialmente durante la época de reproducción.

Prefatory remarks: The species described below has been known, as *Apistogramma* sp. "Balzfleck / courtship spot", since as long ago as 1984, but its provenance, by contrast, only since 1993.



photo: J. Eisässer

Apistogramma wapisana sp. n., ♂, adult, slightly aggressive searching for food.



photo: J. Eisässer

Apistogramma wapisana sp. n., ♀, breeding colouration shortly after spawning.

Methods: As already been given for *Apistogramma huascar* sp. n..

Apistogramma wapisana sp. n.

Type material: 10 specimens

Holotypus: A male, 28,0 mm SL (MHNG 2605.68); Brazil; Departamento Roraima, small forest stream (Igarapé), less than 1 km behind the bridge of the road running eastwards from Boa Vista; Oktober 27th 1998, lgt.: Dietmar GOTTWALD, Werner ZUCKER and Antoine SEVA.

Paratypen: Nine specimens: A male, 25,1 mm SL (MHNG 2605.69), three males, 27,8 mm SL, 27,9 mm SL and 28,0 mm SL (SMF 28216 to 28218), a female, 27,5 mm SL (SMF 28219), and a male 24,2 mm SL (SMF 29055); same data as given for the holotype. A female, 29,1 mm SL (IRSNB 821, **topotype**), ein Männchen, 25 mm SL (IRSNB 822) und ein Weibchen, 27,2 mm SL (SMF 29056); Brazil; Departamento Roraima, Igarapé Au au, about 50 km off Boa Vista in the direction of Alto Allegre close to the road BR 205. Oktober 13th 1998, lgt.: Dietmar GOTTWALD, Werner ZUCKER and Antoine SEVA.

Diagnosis: *Apistogramma wapisana* sp. n. differs from all other species of the genus by the combination of the following characters: a small body length (always < 40 mm TL); an almost complete lack of sexual dimorphism - except that

adult females (> 33 mm TL) are somewhat larger than adult males (< 33 mm TL) and have ventral fins that are blackish on the anterior basal portion; 3 infraorbital pores; a small mouth; a distinct, large, elongate roundish lateral spot; a narrow longitudinal band that ends before the clearly separate and strikingly small but distinct caudal-peduncle spot (in females in brood-care coloration the lateral band is partially fragmented); a low dorsal; unpatterned fins with no prolongations or other noticeable modifications; striking courtship behaviour.

Description: Morphological characters: (n=10, 24.2 to 29.1 mm SL); for habitus see the accompanying figures, for biometric data see table.

The **body** is almost cylindrical, moderately elongate and only moderately compressed laterally, slightly oval vertically in cross-section. The upper head profile is uniformly convex, the lower head profile describes a noticeably shallower, uniform curve. The head is relatively short (30.3% SL) and bluntly rounded at the mouth. The mouth is small, the lower jaw relatively long (27.6 % HL), slightly longer than the lower. The snout is likewise relatively long (29.2 % HL). The eye is relatively large (41.8 % HL). The caudal peduncle is relatively long (16.1 % SL). X dentary pores and 3 infraorbital pores apparent.



Apistogramma wapisana sp. n., Holotypus, ♂, MHNG 2605.68 (28,0 mm SL).

Fins: The ventrals (V: 1.5 (n=10)) are short in both sexes, slightly pointed, and barely extend to the genital opening. The pectorals (P: 10 (n=10)) are slightly longer than the ventral fins, milky transparent and unpatterned apart from a few very small (only visible under magnification) dark brown, more rarely black, spots. The dorsal (D: XIV.6 (n=1), XV.5 (n=1), XV.6 (n=7), XVI.5 (n=1)) is low and when folded extends barely past the start of the caudal fin; the length of the spines increases rapidly from D1 to D5 and thereafter hardly at all to the last (usually the longest) spine; in both sexes the fin membranes are rounded and not prolonged beyond the spines. The anal (A: III.4 (n=1), III.5 (n=5), III.6 (n=4)) in both males and females extends, when folded, approximately to the anterior base of the caudal fin. In almost all individuals the soft parts of the dorsal and anal fin are rounded, in some males prolonged slightly to a point. The caudal is rounded in both sexes and in all ten specimens of the type series there are 16 "principal rays" (KULLANDER, 1980).

Scales: Morphology as laid down for *Apistogramma meinkeni* (compare KULLANDER, 1980). Counts of scales see attached table.

Coloration of preserved specimens: (after around 8 years in 75% ethanol.)

Because the accompanying figures clearly illustrate the coloration and pattern of markings in the species, it is mainly diagnostically significant characters that are given here.

The base colour of the **body** is predominantly brownish grey to cream-grey, in males brownish grey, on the lower half yellowish grey, in females also whitish in the ventral region. The straight preorbital stripe is narrow but distinct. The forehead is whitish grey from the upper lip to the interorbital. In some specimens there is a clearly expressed dark band on the nape. In all voucher specimens studied the iris is blackish, the pupil white. The cheeks are light yellowish brown. The cheek stripe is black-brown and runs from the margin of the eye in a straight line



Apistogramma wapisana sp. n., topotype, ♀, IRSNB 822 (29,1 mm SL).

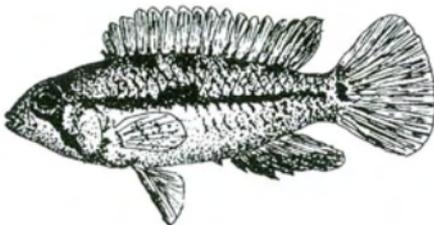


Apistogramma wapisana sp. n., paratype, ♂, IRSNB 821 (27,2 mm SL).

to the posterior lower margin of the operculum; it is barely pupil-width on the orbital and tapers to a point on the edge of the operculum. The operculum usually appears light whitish grey at its centre. The branchiostegal membrane and breast are whitish to (more rarely) whitish grey. Chin spot, throat spot, abdo-

minal stripes, and anal spot are absent in all individuals studied. The breast and the bases of the ventral fins are without markings.

The lateral band is narrow, dark brown in colour, beginning behind the orbital ring below the third foramen of the posterior infraorbital and ending at the sixth crossband, clearly before the small, round caudal spot; it is only around half a scale wide and runs along the scales of the L+1-series. Above the lateral band the body scales have a narrow dark margin, below it their margins are sometimes light. The lateral spot, on crossband 3, is irregular in form and usually clearly higher than



Apistogramma wapisana sp. n.
pattern of typical ♂



Apistogramma wapisana sp. n., paratype, ♂, SMF 29 055 (24,4 mm SL)



Apistogramma wapisana sp. n., paratype, ♂, SMF 28 216 (27,8 mm SL)

the lateral band, roughly longitudinally oval and extending over three L+1 series scales (L+1:6-9) and the adjoining margins of adjacent scales, but not visible in all specimens; in occasional males also enlarged onto the scales of the L+2-series; in females it is sometimes appreciably larger, usually longitudinally oval. Seven unbranched crossbands are only faintly visible in a number of the preserved types; they are around twice as wide as the intervening spaces. The narrow dorsal spots in the area of bands 1 to 6 are no more than faint sooty marks, not extending onto the base of the dorsal. There is no pattern of abdominal stripes, but in preserved (as oppo-

sed to live) individuals occasional fine grey abdominal streaks are apparent on the margins of the flank scales.

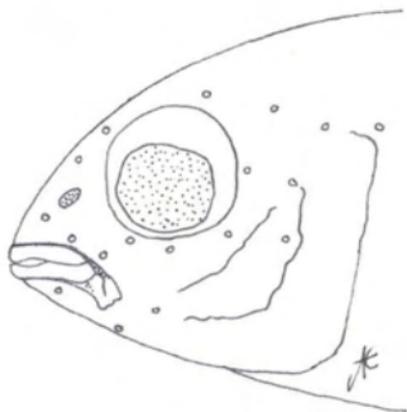
Fins: Pectorals unpatterned transparent, with tiny spots of black-brown pigment visible only under magnification or in very good photos. Ventrals and their bases transparent in males, with no markings but very fine brown-black pigment all over; in females the anterior third of the ventral fins is sooty black. Anal without bands or spots, sooty coloured only at its margin and in the soft-rayed portion. Dorsal transparent unpatterned; only in occasional males are there one or two faint

hyaline bluish rows of dots in the soft-rayed portion of the fin. Caudal generally unpatterned transparent, uniformly pigmented with microscopically fine black or black-brown; however, in a number of individuals one or two fragmentary vertical grey bands are apparent in the centre of the fin.

Coloration of live specimens: Prior to this scientific description, this species has already been depicted several times in photos in CICHLID ATLAS 1 (RÖMER, 1998) and by KOSŁOWSKI (1985, 2002). Hence only a number of supplementary diagnostic colour characters for the identification of live specimens are given here.

The base colour of all sexually inactive individuals is beige-grey. The base colour in reproductively active males changes to a dirty yellowish grey, in the females to a dirty

chrome yellow, often overlain with greenish grey on the upper half of the body. The pattern of regular black crossbands typical of the majority of *Apistogramma* species is absent in *Apistogramma wapisana* sp. n. Only in extreme, exceptional situations (particularly transportation stress!) do occasional - usually female - specimens exhibit a pattern reminiscent of this banding, but very "washed out" and consisting of discontinuous bands of spots. In general all the fins are unpatterned; only females in brood-care coloration exhibit an individually variable black zone in the anterior third of the ventral fins and occasionally a grey to sooty margin to the anterior outer edge of the anal fin. Very rarely female specimens may also be blackish in the area around the genital opening. The dorsal scales mainly have narrow blackish margins, creating a reticulated pattern on the dorsum; occasionally this pattern is restricted to the two series of scales beneath the dorsal, while the lateral band, which is only around half a scale wide, is distinctly marked; in males the section posterior to the lateral spot is usually expressed as a grey-black zig-zag-like line formed by the margins of the scales. In females the inner part of the scales is also glossy black, so the zig-zag effect is lacking. The lateral spot is strikingly large, around five to six scales long and up to three rows of scales high, irregular roundish in shape, usually almost oval, but also - rarely - almost



Apistogramma wapisana sp. n.

pattern of head pores: paratype SMF 28218

drawing: A. CONRAD



Apistogramma wapisana sp. n., paratype, ♀, SMF 28 219 (27,5 mm SL)

rectangular. Depending on mood the normally glossy black lateral spot may also appear "in negative" as a separate, light-coloured, spot in the lateral band; its colour can then vary between metallic silvery and copper-coloured. This colour pattern is particularly frequently

seen in aggressive individuals during the establishing of breeding territories and during the courtship phase. The cheek stripe is narrow - usually not even as wide as the pupil - and runs diagonally backwards to a point on the lower part of the posterior operculum. Males in



Apistogramma wapisana sp. n., ♂, adult, slightly aggressive.



Apistogramma wapisana sp. n., paratype, ♂, MHNG 2605.69 (25,1 mm SL)



Apistogramma wapisana sp. n., paratype, ♀, SMF 29 056 (27,2 mm SL)

territorial mood frequently reduce their pattern elements to this cheek stripe and are otherwise completely without markings. A preorbital stripe is only exceptionally and indistinctly visible; it is grey in colour and only very narrow, usually around 15 to 20 % of the diameter of the pupil. In some moods the iris anterior to the pupil exhibits a distal sooty marginal spot and its upper half is dark grey; in females in brood-care coloration it may be completely black, and then the upper part of the upper lip has a narrow, dark grey or sooty black edging. Ripe females sometimes exhibit a pale whitish-pink abdominal spot, similar to that

also known from *Apistogramma diplotaenia* and the species of the genus *Biotocetus* (cf. RÖMER, 1998, 2000, and this volume). Individuals in fright coloration usually exhibit a brownish base colour and (very rarely) two faint abdominal stripes parallel to the lateral band.

Type locality: The *terra typica* is a small, nameless forest stream, an *igarapé*, the less than 1 km behind the bridge leading east from Boa Vista in the Brazilian federal state of Roraima.

Distribution: As far as is known to date, *Apistogramma wapisana* sp. n. occurs in the north-west of Brazil.



photo: J. Eissässer

Apistogramma wapisana sp. n., ♂, adult, neutral mood.

All confirmed finds originate from the drainage of the upper Rio Branco in the (general) vicinity of the town of Boa Vista. ELSÄSSER caught specimens in three flowing waters, specifically the Igarapés luciniu and Agua Boa, and the Rio Cauamé (RÖMER, 1998). In addition, KOSŁOWSKI (2002) states that ELSÄSSER also caught these fishes in the central Rio Negro drainage in the vicinity of Barcellos do Rio Negro and that a juvenile of this species was imported by STAWIKOWSKI and companions in 1999 from a Guyanan affluent of the Rio Branco. These data apart, the distribution of the species is to date only patchily and inadequately known and urgently requires further field studies.

Ecology: Only a few, but in part carefully recorded, data are available on the biology of *Apistogramma wapisana* sp. n. in the wild, originating from the localities for the type material and three additional collecting sites investigated by ELSÄSSER. Details of his observations at these localities can be found in RÖMER (1998).

Both localities at which the type material was collected were investigated in October 1998. At this time the Igarapé AuAu contained slightly brownish, relatively shallow water (on average 1.0-1.5 metres deep). The pH measured between 5.5 and 6.0, with no measurable (ie practically zero) hardness - similar to in the Rio Branco. The water temperature



Apistogramma wapisana sp. n.
 red: area with confirmed reports
 yellow: area with unconfirmed reports

was more than 30 °C with an air temperature of over 40 °C. Along with the new species the following species were recorded (collected or seen) at this locality: Cichlidae: *Acarichthys heckelii heckelii*, *Acaronia* cf. *vultuosa vultuosa*, *Aequidens* sp., *Apistogramma* sp., *Apistogramma rupununi*, *Cichla* sp., *Chaetobranchopsis* sp., *Crenicichla* cf. *lenticulata*, *Crenicichla* sp., *Crenicichla* cf. *wallaci*, *Heros* sp., *Geophagus* sp., *Hypselecara coryphaenoides*, *Mesonauta Mesonota* cf. *festivus*, *Pterophyllum* sp., *Satanoperca* cf. *lilith*, *Satanoperca* cf. *leucosticta*; Characidae: *Acestorhynchus* sp., *Astyanax* sp., *Hemigrammus* cf. *stictus*, *Moenkhausia* cf. *chrysargyrea*, *Brycon* sp., *Triportheus* cf. *angula-*

tus; Callichthyidae: *Corydoras* sp.; Anostomidae: *Leporinus* sp. (several species); Erythrinidae: *Hoplias malabaricus*; Lebiasinidae: *Nannostomus* cf. *marginatus*, *Copella* sp.; Serrasalminidae: *Metynnis* sp.; Loricariidae: *Ancistrus* sp. (a single specimen); Ctenoluciidae: *Boulengerella* sp.; Gasteropelecidae: *Carnegiella* cf. *strigata*; Rivulidae: *Rivulus* sp..

In the small forest stream (*igarapé*) in the vicinity of Boa Vista the water was likewise light brownish and had a temperature of more than 30 °C. Here the following species were collected or seen together with the new species: Cichlidae: *Aequidens* sp., *Apistogramma* sp., *Apistogramma rupununi*, *Acaronia vultuosa*, *Crenicichla* cf. *lenticulata*, *Crenicichla* cf. *regani*, *Crenicichla* cf. *wallaci*, *Geophagus* sp., *Satanoperca* cf. *lilith*, *Satanoperca* cf. *leucosticta*, *Mesonauta* sp., *Hypselecara coryphaenoides*, *Chaetobranchopsis orbicularis*; Characidae: *Hemigrammus* cf. *stictus*, *Thayeria boehlkei*, *Tetragonopterus argenteus*, *Pristella maxilaris*, *Hypophessobrycon* sp. (several species), *Cestrorhynchus* sp.; Lebiasinidae: *Nannostomus trifasciatus*, *Nannostomus eques*, *Nannostomus beckfordi*; Curimatidae: *Chilodus punctatus*; Anostomidae: *Leporinus nigrolineatus*; Erythrinidae: *Hoplias malabaricus*; Gasteropelecidae: *Carnegiella strigata*.

From the data available to date, *Apistogramma wapisana* sp. n. appears to be in general a species that prefers



For comparison: *Apistogramma* sp. "Chao", ♂, dominant, neutral mood.

smaller, muddy streams, influenced by whitewater, with a thick layer of leaf litter and medium to comparatively high water temperatures.

Etymology: The name *wapisana* is a noun in apposition. The name refers to the Arucan WAPISANA tribe - sometimes also called the Mawayana - who inhabit the region from which the new species described here originates. The numbers of this indigenous people have been decreasing dramatically for a long time, even though after 1810 the ANAISANA people were integrated into their tribal group. In 1988 the latter had no more than 8500 members; no more recent data are available (MÜLLER, 1995). In recent decades large parts of the tribal

area of the WAPISANA have been devastated by excessive gold-mining and deforestation in this region. As a result the WAPISANA have themselves become victims - and at the same time a living symbol - of the destruction of Amazonian ecosystems by "modern Man". All the collecting sites for *A. wapisana* sp. n. known to date lie in the (former) tribal lands of the WAPISANA indians. The name thus relates both directly to the tribe and indirectly to the collecting area.

Captive biology: Detailed discussion of the aquarium biology of *Apistogramma wapisana* sp. n. can be found in CICHLID ATLAS 1 (RÖMER, 2000) and in KOSLOWSKI (2002).



Apistogramma wapisana sp. n., paratype, ♂, SMF 28 218 (28,0 mm SL)

Discussion: *Apistogramma wapisana* sp. n. is one of the smallest members of the genus known to date. The new species is one of the fairly slender forms in the genus, and at first glance apparently a member of the *Apistogramma-pertensis*-supercomplex by virtue of its appearance. This is further supported by the cluster analysis on the systematics of the genus performed by ROMER (2006c). The infra-orbital pores are reduced to three, which is typical of this phylogenetic group and corresponds to the basic format of the forms of the *Apistogramma-iniridae*-subcomplex. The species of the *Apistogramma-iniridae*-subcomplex have a higher dorsal fin, by virtue of which they can be readily differentiated from *Apistogramma wapisana* sp. n.

Apistogramma wapisana sp. n. is readily distinguished from *Apistogramma pertensis*, *A. pulchra*, *A. velifera*, *A. sp.* "double spot", and *A. sp.* "cleaner" by the relatively much smaller caudal-peduncle spot, the appreciably narrower longitudinal

band, the much larger lateral spot, the appreciably smaller size, the strikingly short ventral fins, the lower dorsal fin and the round, unpatterned caudal fin. *Apistogramma wapisana* sp. n. is easily distinguished from other slender members of the genus - for example, the forms of the *Apistogramma-agassizii* and *Apistogramma-uaupesii*-supercomplexes - by the completely different fin form and coloration, and by the lack of sexual dimorphism. The new species is distinguished from *Apistogramma diploaenia* by the completely different lateral markings and the different finnage.

There remains a group of superficially similar species, comprising *Apistogramma meinkenii*, *A. inornata*, and *A. angayuara*, as well as the undescribed forms *Apistogramma* sp. "Chao", *A. sp.* "Parati" and *A. sp.* "white-seam", which share the small size of *Apistogramma wapisana* sp. n.. *Apistogramma meinkenii* can be unequivocally distinguished from *Apistogramma wapisana* sp. n. by



For comparison: *Apistogramma pulchra*, ♂, subdominant, territorial, slightly aggressive.

the invariably banded caudal fin, the wider lateral band, the two lateral spots, the different form of the dorsal, the much larger caudal-peduncle spot and the different brood-care pattern in females. The form *Apistogramma* sp. "Chao" from the Rio Xingú, likewise characterised by an almost complete lack of sexual dimorphism, can be clearly distinguished from *A. wapisana* sp. n. by its particularly large caudal-peduncle spot, the occasional pattern of spots or bands in the caudal fin, the three series of abdominal spots in some motivational states, and the different brood-care pattern in females. *Apistogramma* sp. "Parati" differs from *Apistogramma wapisana* sp. n. in the densely patterned caudal fin, the larger caudal spot,

and the striking pattern sometimes visible on the lower flanks. *A. wapisana* sp. n. differs from *Apistogramma angayuara* and *A. sp.* "white-seam" in the invariably unpatterned caudal fin, and the presence in females during brood care of a lateral band, which in both the forms named is reduced to a single, very rarely two, lateral spots at the positions of crossbands 3 and 4. Both preserved and live *Apistogramma angayuara* also exhibit three series of vertical abdominal streaks, preserved *Apistogramma wapisana* sp. n. at most two, and none at all in life. At present the species most similar to *Apistogramma wapisana* sp. n. are *Apistogramma angayuara* and *A. inornata*; the latter can be unequivocally distinguished from *Apis-*

togramma wapisana sp. n. by the banded caudal, the relatively higher dorsal in males, the distinctly smaller lateral spot, the different brood-care coloration in females (where the longitudinal band is reduced to a single (rarely also a second) lateral spot), and the small pectoral spot.

On the basis of cluster analysis evaluation of the currently available data and observations we assign *A. wapisana* sp. n., together with three further species (*A. meinkeni*, *A. sp.* "Chao", *A. sp.* "Tiquié") to the *Apistogramma-meinkeni*-complex within the *Apistogramma-pertensis*-supercomplex.

However, this finding contradicts the published results of preliminary ge-

netic studies by MILLER & SCHLIEWEN (2005) (for commentary see RÖMER, 2006c), on the basis of which they have placed this species in the phylogenetic vicinity of *Apistogramma steindachneri*. It is true that occasional preserved individuals of *Apistogramma wapisana* sp. n. exhibit a relatively large lateral spot, remotely reminiscent of the lateral spots seen in the *Apistogramma-steindachneri*-complex. However the remaining morphological and ethological characters of the species hardly accord with those of the members of that species complex, hence we assign the species to the *Apistogramma-meinkeni*-complex pending the completion of further research.



photo: J. Elsäßer

Apistogramma wapisana sp. n., ♂, adult, slightly aggressive.

Apistogramma wapisana sp. n.
biometrical data of the type series

| Museum Coll.-Nr. | IRSNB 821 | IRSNB 822 | MHNG 2605.68 | MHNG 2605.69 | SMF 28216 | SMF 28217 | SMF 28218 | SMF 28219 | SMF 29055 | SMF 29056 |
|------------------|-----------|-----------|--------------|--------------|-----------|-----------|-----------|-----------|-----------|-----------|
| Status | PT | PT | HT | PT | PT | PT | PT | PT | PT | PT |
| Sex | ♀ | ♂ | ♂ | ♂ | ♂ | ♂ | ♂ | ♀ | ♂ | ♀ |
| measurements | | | | | | | | | | |
| SL | 27,2 | 29,1 | 28,0 | 25,1 | 27,8 | 27,9 | 28,0 | 27,5 | 24,2 | 27,2 |
| TL | 36,0 | 32,0 | 36,3 | 31,8 | 36,4 | 35,8 | 35,2 | 35,1 | 31,8 | 35,2 |
| TL + Streamer | 36,0 | 32,0 | 36,3 | 31,8 | 36,4 | 35,8 | 35,2 | 35,4 | 31,8 | 35,2 |
| HL | 8,3 | 7,8 | 8,2 | 7,7 | 8,1 | 8,4 | 9,1 | 8,6 | 7,9 | 8,3 |
| HD | 6,0 | 5,5 | 6,4 | 6,1 | 6,3 | 6,1 | 6,6 | 6,9 | 5,9 | 6,4 |
| HW | 4,3 | 3,9 | 4,7 | 3,9 | 4,2 | 4,4 | 4,8 | 4,7 | 4,1 | 4,5 |
| BD | 8,2 | 7,5 | 7,8 | 7,4 | 8,4 | 8,0 | 8,7 | 8,2 | 7,5 | 8,6 |
| PDL | 9,3 | 8,5 | 9,3 | 8,9 | 9,8 | 9,2 | 9,6 | 9,4 | 8,8 | 9,0 |
| TDL | 24,5 | 20,6 | 23,8 | 21,6 | 23,8 | 23,8 | 24,7 | 24,4 | 21,7 | 23,9 |
| PVL | 9,9 | 8,5 | 9,9 | 9,3 | 10,7 | 10,4 | 10,1 | 10,1 | 8,7 | 10,3 |
| PAL | 19,4 | 16,0 | 18,7 | 16,7 | 19,4 | 19,0 | 19,2 | 19,1 | 17,1 | 18,5 |
| TAL | 24,6 | 20,1 | 23,2 | 21,6 | 23,5 | 23,3 | 23,3 | 23,5 | 21,1 | 22,6 |
| Eye | 3,0 | 2,9 | 3,2 | 2,8 | 3,0 | 3,1 | 3,1 | 3,1 | 3,0 | 3,1 |
| SNL | 1,2 | 1,4 | 1,4 | 1,7 | 1,3 | 1,6 | 1,7 | 1,3 | 1,5 | 1,3 |
| CHD | 1,8 | 1,4 | 1,6 | 1,5 | 1,8 | 1,7 | 1,6 | 1,6 | 1,6 | 1,8 |
| POD | 0,6 | 0,6 | 0,7 | 0,7 | 0,7 | 0,7 | 0,7 | 0,8 | 0,8 | 0,7 |
| IOW | 1,9 | 1,8 | 2,0 | 1,8 | 1,9 | 1,9 | 2,0 | 2,0 | 1,8 | 1,9 |
| UJL | 2,5 | 2,2 | 2,5 | 1,8 | 2,6 | 2,6 | 2,3 | 2,3 | 2,3 | 2,5 |
| LJL | 3,4 | 3,0 | 3,4 | 2,7 | 3,3 | 3,3 | 3,2 | 3,3 | 3,2 | 3,5 |
| CPD | 4,1 | 3,6 | 4,1 | 3,7 | 4,3 | 4,0 | 4,2 | 3,9 | 3,8 | 4,1 |
| CPL | 4,5 | 3,8 | 4,4 | 3,7 | 4,1 | 4,4 | 5,5 | 4,1 | 4,0 | 4,4 |
| DFB | 16,4 | 13,4 | 15,6 | 14,5 | 15,0 | 15,1 | 16,2 | 15,9 | 13,7 | 15,2 |
| AFB | 4,7 | 4,0 | 5,0 | 4,8 | 4,3 | 4,2 | 4,5 | 4,8 | 3,9 | 4,2 |
| Pec-L | 7,2 | 6,7 | 7,1 | 6,3 | 7,1 | 7,2 | 7,1 | 7,8 | 6,0 | 7,5 |
| Pel-L | 6,5 | 6,3 | 6,9 | 5,8 | 7,4 | 7,2 | 7,1 | 7,2 | 5,9 | 7,2 |
| PelSL | 3,8 | 3,1 | 3,2 | 2,8 | 3,7 | 3,4 | 3,6 | 4,0 | 2,9 | 4,1 |
| LDS | 3,8 | 3,5 | 3,8 | 3,5 | 3,9 | 4,0 | 4,3 | 4,0 | 3,0 | 4,5 |
| LAS | 4,5 | 3,3 | 4,1 | 3,5 | 4,8 | 4,4 | 4,3 | 4,6 | 3,4 | 4,9 |
| counts | | | | | | | | | | |
| DF | XV.6 | XV.6 | XV.6 | XV.6 | XV.6 | XV.6 | XV.6 | XV.6 | XVI.6 | XV.6 |
| AF | III.5 | III.5 | III.5 | III.6 | III.6 | III.5 | III.6 | III.6 | III.5 | III.5 |
| PF | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 |
| Pec | 12 | 12 | 12 | 12 | 12 | 11 | 12 | 12 | 12 | 12 |
| CF | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 |
| sq.long. | 21 | 21 | 21 | 22 | 21 | 22 | 22 | 22 | 22 | 21 |