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Ecology of River Dolphins and Fish at Confluence Aggregations in the Peruvian Amazon

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Abstract

Amazon River dolphins often form multi-species aggregations at water confluences. This study used a multi-year data set to examine dolphins, fish, and geomorphology at dolphin aggregations. Methods included dolphin transect surveys, dolphin point counts, net and line fish captures, side-scan sonar, and eDNA analyses at five dolphin aggregations and two control sites. Amazon River dolphins (*Inia geoffrensis* and *Sotalia fluviatlis*) are typically found at aggregation sites that occur at water confluences that have greater dolphin numbers than control sites. The confluences had riverbed depressions averaging six metres in depth where fish were concentrated. Pink river dolphins preferred to form aggregations in flooded forest tributaries and large rivers, while grey river dolphins preferred the larger rivers. There were eighty-nine fish species at the confluences within the size of fish consumed by dolphins, and a higher abundance of fish occurred in and around the aggregation sites compared to control sites. The number of dolphins present at the aggregation sites correlated with fish abundance. Dolphin life history, such as fishing, resting, raising calves, and social interactions, occur at the aggregation sites. The aggregation sites are important conservation areas of the endangered pink and grey river dolphins, and through their folklore, Indigenous people living at confluence sites assist in the conservation of the aggregations and have lived with dolphins at confluences for thousands of years, contributing to their survival.

Keywords: pink river dolphin; grey river dolphin; Amazon fish; dolphin aggregations; river confluences

Key Contribution: Amazon river dolphin life history revolves around interspecific aggregations at water confluences that have high fish abundance and diversity.

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1. Introduction

Dolphin populations and their life history depend on fish, both in oceans and rivers, and the abundance and distribution of fish determines dolphin behaviour and habitat use [1]. River dolphins prefer confluences of rivers and areas of riverbed depressions, and they typically gather at these sites, forming aggregations [2]. In the Amazon, river dolphins form groups at confluences in the Bolivian, Amazon, and Orinoco River basins [3–5].

Two sympatric river dolphin species, *Inia geoffrensis* (pink river dolphin) and *Sotalia fluviatilis* (grey river dolphin), inhabit flooded forests and rivers in the Ucamara depression of western Amazonia in Peru [6]. Pink river dolphins, an ancient species, use smaller tributaries and flooded forests, but also use large rivers [7,8]. They have evolved adaptations for the Amazon and flooded forests since the Miocene, around twenty million years ago [9]. Grey river dolphins split from their marine ancestors around two million years ago during the Pleistocene and are less adapted to flooded forest life; they inhabit larger rivers and occasionally smaller tributaries and flooded forests [10,11].

Both species of Amazon River dolphins use confluence areas, including lake–river, channel–river, and river–river confluences where they form aggregations [7]. Fishing behaviour by dolphins is common at these sites, and fish abundance is presumed to be the reason for the dolphins' preference for confluence areas [7,12]. The dynamics of river currents and sediment load might also be a reason for dolphins' preferences for confluence areas [1,13].

River confluences, where two or more rivers or channels meet, often exhibit high fish populations and species richness. This is due to a combination of factors, including increased habitat complexity, diverse water quality conditions, and the confluence acting as a movement corridor for fish [14]. The combination of water flows produces a diversity of habitats, ranging from fast-flowing currents to slower, deeper pools that concentrate nutrients and organic matter for fish diets [15]. Large confluences can have different currents, such as backflow currents and channels that can facilitate fish movements, food availability, and reproduction as spawning and nursery grounds for migratory fish [16]. Consequently, the species' richness and abundance of fish are higher at confluences compared to other river locations [14].

Observations of the fishing behaviour of river dolphins at confluences strongly suggest that they prey on fish in those locations. River dolphins congregate where there is a concentration of fish, and their feeding behaviour demonstrates a clear predator–prey relationship [9]. Grey dolphins feed closer to the surface, chasing fish, while pink dolphins feed deeper in the water [6].

In this study, we used a long-term data set collected monthly over 15 years at multiple areas with dolphin aggregations. This paper analysed the data set to better understand the ecology of Amazon River dolphins in relation to their fish prey and shows how aggregation sites at confluences are central to the life history of dolphins. We used an experimental design that recorded dolphin and fish data at the confluences and at control sites outside of these areas. We studied areas where pink and grey river dolphins aggregate in terms of dolphin numbers and interactions, fish numbers and diversity, and riverbed geomorphology.

The study sites included the aquatic landscape at the confluence of the Ucayali, Maranon, and Amazon Rivers, and the confluences of the Samiria River in the Pacaya–Samiria National Reserve. The Pacaya–Samiria National Reserve, decreed in 1982, is currently co-managed between the Peruvian Protected Area Service (SERNANP) and the Cocama (Kukama) Indigenous people through community-based management groups. The reserve allows sustainable resource use and traditional activities, including artisanal fishing [17]. This area is part of the largest block of várzea flooded forests in western Amazonia and extends over an area of 120,000 km^2 in the Department of Loreto, Peru [18].

The pink river dolphin and the grey river dolphin are both classified as "Endangered" (EN) in the IUCN Red list, which shows their vulnerability to ongoing conservation threats [19]. Dolphin studies in the Pacaya–Samiria National Reserve and adjoining areas span over decades [5,7,20] and the population of both river dolphins is particularly abundant in this region and has been stable over the years [18]. The local Indigenous communities and SERNANP are both important to dolphin conservation at confluence sites. Indigenous communities in this region of the Peruvian Amazon have strong beliefs about not killing the dolphins, and this has been key in maintaining strong dolphin populations, especially at confluence areas where there are dolphin aggregations [21].

2. Materials and Methods

2.1. Study Area

The study area was in the western Amazon in the Loreto Region of Peru. Dolphin research was conducted in the Samiria River basin, and the major Marañon, Ucayali and Amazon rivers in the Pacaya–Samiria National Reserve (PSNR), and a buffer zone situated in the Marañon–Ucayali subsidence area of the Ucamara depression [22] (Figure 1). PSNR and surrounding areas have a predictable annual water level cycle with high water from January to June and low water from July to September. This water level cycle is a result of the winter–summer seasons in the Southern Atlantic, and since water levels slowly rise and fall due to the flatness of the flooded forests. There is an average difference of 9.5 m between peak flooding and the low season trough, ranging from 108.2 to 117.7 m.a.s.l. [18].

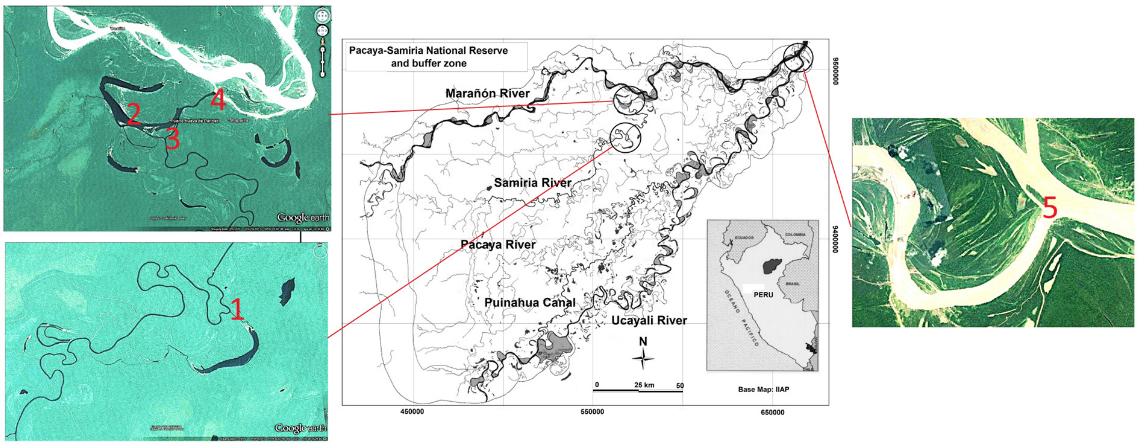

Figure 1. Map of the study area and aggregation sites: (1) the Samiria River and Atun Lake (Samiria–Atun), (2) Samiria River and Tapischa Lake (Samiria–Tapischa), (3) Samiria River and Shiringal Channel (Samiria–Shiringal), (4) Samiria River and Maranon River (Samiria–Maranon), and (5) the confluence of the Ucayali, Maranon, and Amazon Rivers (UM–Amazon).

We studied dolphin aggregations with a variety of methods to estimate dolphin and fish populations, dolphin behaviour, and age structure. Between 2010 and 2024, we completed a total of 1341 dolphin surveys covering 6705 km of transect and over 50,000 sightings of individuals. In addition, 1290 fish surveys conducted over the same period at the same locations measured over 40,000 fish. Dolphin and fish surveys were performed throughout the year, in all seasons and months.

2.2. Dolphin Surveys

Dolphin surveys included population size, age structure and behaviour. We estimated abundance and density using standard methods for river dolphins [23–25]. Surveys involved 5 km aquatic transects placed at aggregation and control sites. Transects began before the aggregation site, progressed through the core area, and ended after the site.

We used motorboats between 8 and 14 m long for dolphin surveys, and we drifted downriver if there was sufficient river current. The boat engine was used at minimum speed if there was insufficient current, especially in the lakes and channels. The transect velocity was between 2 and 4 km/h. A Garmin GPS was used to measure the position and length of transects.

We also studied dolphin aggregations using point counts. Data were collected for one hour from an anchored boat at the aggregation site. The point counts recorded the same data as the 5 km aquatic transects with the addition of distance and angle from the boat of dolphin sightings.

Visual records of dolphins breaching the water surface allowed for species identification, pod size, and composition. The pod size was the number of dolphins present, and the pod composition was recorded as infant, juvenile, sub-adult, adult, and large male. The composition used the dolphins' relative size, with infants being the smallest, juveniles notably smaller than adults, sub-adults being slightly smaller than adults, and large males exceeding the average adult size. Pod numbers and composition were determined by observing the individuals for multiple breaches of the dolphins and care was taken not to double count individuals. We did not perform individual recognition of dolphins, except during the observation period.

Behavioural data included feeding, moving, resting, playing, and mating. Pink and grey river dolphins feed differently. Pink river dolphins use their heterodont dentition to feed on catfish that are usually deep in the water near the riverbed and typically stay submerged for several minutes and surface actively, whereas grey river dolphin fish near the surface, chasing fish and often feeding in pods [6].

Moving (displacement) behaviour was a consistent movement of dolphins either upstream or downstream. Dolphins often breach in unison whilst moving. Dolphins stay close to the bank where the currents are weaker when travelling upstream. When dolphins rest, they face upstream against the currents, or in slow-moving whirlpools, often close to the bank and they breach the water slowly.

Play behaviour was when dolphins become excited and display rolling, tail wagging, fin slapping, and they can jump completely out of the water, sometimes with flips or twirls. Spy hopping occurred in pink river dolphins when individuals protrude their beak out of the water and twirl it vertically in circles. Mating behaviour was also recorded.

We determined dolphin abundance by counting the number of individuals at aggregation and control sites during 5 km surveys as individuals/survey, which permitted statistical comparisons. The data spanned 2010–2019 and 2022–2024. We calculated annual means per site for each species. Seasonal analysis divided the data between high-water (Jan–June) and low-water (July–Dec) seasons. Analysis during peak flooding, when dolphins had greater access to the flooded forests, used the months of April and May.

2.3. Fish Catch per Unit Effort Surveys

We surveyed fish to obtain catch-per-unit-effort (CPUE) data during 2012–2019 and 2022–2024 using both gill net and rod-and-line methods at the same locations as dolphin surveys. CPUE was used as a measure of fish abundance. The effort was a standard gill net of green nylon measuring 30 m long, 3 m deep with a 2–3-inch mesh, set for 1 h. Nets were set in rivers, channels, lake habitats, and flooded forest habitats, and a GPS point was noted for each net location. We recorded data on species, weight, and standard length. Fish were returned into the water after measuring.

Hook and line fishing had a mean of 5 people fishing per hour. Traditional poles with simple fish lines and hooks were baited with meat. We recorded measurements on species, weight, and standard length, and fish were released after measuring.

We measured fish abundance as individuals captured per one-hour survey, or fish/hour-survey. The control sites used the same method, and the variables were the same (fish/hour), allowing for a comparative analysis between aggregation and control sites.

2.4. Side-Scan Sonar Surveys

We studied geomorphology of the riverbed and counted fish numbers using a StarFish Seabed Imaging System which is a high-definition side-scan sonar. The sonar produces near-photographic quality images of the riverbed. Fish are visualized as white dots which are caused by gas in their swim bladders and stomachs, or through direct reflection. The StarFish side-scan sonar was placed on the bow or side of a 10 m boat, and line surveys were performed at 4–6 km/h for 5 km. Images were used to determine fish numbers by adding all fish spots and direct images of fish and discounting floating vegetation. Although side-scan sonar generates images from both sides, only the side with less interference was used for counting fish.

2.5. eDNA

Species richness and abundance at the Maranon–Ucayali–Amazon confluence site used environmental DNA (eDNA) of water samples because it was not possible to conduct CPUE studies at this location due to the size of the merging rivers. eDNA sample collection and analysis were performed with Nature Metrics. Water collection, filtering, and storage of aquatic kits followed the sampling protocol of the Standard Aquatic eDNA Kit (https://www.naturemetrics.com). Each water sample used four sub-samples collected around the centre of the aggregation and control site at 100 m intervals.

2.6. Statistical Analysis

We used ANOVA tests to analyse differences between variables at aggregations and control sites, including dolphin species, dolphin numbers, fish CPUE, side-scan sonar, seasons, years, river type, and river size. For the Samiria sites, ANOVA tests of means were used because of the large sample sizes. Correlations were used for fish–dolphin relationships.

A MANOVA evaluated differences in aggregation size based on the combination of fish CPUE and side-scan sonar fish numbers across sites and years. The relationships were analysed between the dependent variable of aggregation size, as number by year, and the factors of fish CPUE and side-scan sonar numbers, by site (1–5) and years (2010–2018).

Ethical approval was authorized by SERNANP and the Peruvian Forestry and Wildlife Service (SERFOR) for biological surveys, with approval code RD-000116-2022-DGGSPFFS-DGSPFS.

3. Results

Five dolphin aggregations and two control sites were studied, representing the main waterscape types of the Ucamara basin in western Amazonia. We found mixed species aggregations on the Samiria, Maranon, Ucayali, and Amazon Rivers, all at confluences of rivers, lakes, and channels.

The aggregation sites were located at confluences of lakes and rivers (n = 2), at the confluences of two rivers (n = 2), and at the confluence of a channel and a river (n = 1). The confluence aggregation sites included: the Samiria River and Atun Lake (Samiria–Atun), Samiria River and Maranon River (Samiria–Maranon), Samiria River and Tapischa Lake (Samiria–Tapischa), Samiria River and Shiringal Channel (Samiria–Shiringal), and the confluence of the Ucayali, Maranon, and Amazon Rivers (UM–Amazon). The Samiria–Atun aggregation was in a tributary river, while the other sites connected to one of the larger rivers (Maranon, Ucayali, and Amazon) (Figure 1). The Samiria–Tapischa, Samiria–Shiringal, and Samiria–Maranon aggregations were in the wetland habitats at the mouth of the Samiria River.

Dolphins studied in areas outside the aggregations were used as control sites, one on the Samiria River (Samiria Control), and another on the Amazon River and Yarapa Channel (Amazon Control).

3.1. Dolphin Aggregations

Both the pink and grey river dolphins used the same aggregation sites, and both species were common. At the aggregations, pink river dolphins were present 99.8% of the time. Grey river dolphins were not always present, and the interior river site (Samiria–Atun) had the lowest presence of grey river dolphins, with both species present 62.7% of the time. The two dolphins formed mixed-species aggregations more frequently at sites linked to major rivers, with both species present 84% of the time, and mixed-species aggregations were greater in the major rivers than in the tributary river (ANOVA, df 15, F 7.77, $p = 0.015$). The UM–Amazon site had the largest rivers and the greatest mixed-species aggregation, with both dolphins present 98.8% of the time.

3.2. Pink River Dolphin

Pink river dolphins had an overall mean of 16.9 ind/survey (SD 3.5, range 13.1–21.0) per aggregation site. At the control sites outside of aggregation sites, pink river dolphins had a mean of 7.0 ind/survey (SD 0.5, range 6.7–7.4) (Table 1).

Table 1. Number of pink river dolphins and grey river dolphins (ind/survey) at aggregation and control sites. Values are individuals per 5 km aggregation survey or control survey.

Sites	Minimum	Maximum	Mean (Ind/Survey)	Std. Deviation
Pink River Dolphin				
Samiria–Atun	8.86	17.00	13.15	2.60
Samiria–Tapishica	9.57	24.25	18.49	5.42
Samiria–Shiringal	13.86	36.20	21.01	7.40
Samiria–Maranon	12.60	34.50	18.88	6.78
UM–Amazon	5.00	29.00	13.25	7.04
Samiria Control	3.60	10.40	7.44	2.06
Amazon Control	0.00	27.00	6.78	5.91
Grey River Dolphin				
Samiria–Atun	1.62	11.55	4.45	3.27
Samiria–Tapishica	4.40	12.33	8.10	2.92
Samiria–Shiringal	4.95	17.16	9.72	4.21
Samiria–Maranon	5.22	8.50	6.91	1.42
UM–Amazon	7.00	47.00	19.10	11.05
Samiria Control	1.60	4.02	2.47	0.93
Amazon Control	1.00	30.00	7.23	7.02

All the aggregation sites had greater numbers of pink river dolphins than the control areas (Table 2). The pink river dolphin numbers at the control sites were similar to each other and were about half of the pink dolphin numbers found at aggregations (ANOVA, $p = 0.75$). The dolphin aggregations at the mouth of the Samiria River had the largest number of pink river dolphins, with a mean of 19.5 (SD 1.35) ind/survey. The number of dolphins between aggregation sites differed (ANOVA, df 43, F 2.95, $p = 0.032$), with the number of dolphins at the Samiria–Atun and UM–Amazon aggregations being smaller than those at the mouth of the Samiria River.

Table 2. ANOVA analysis of differences in pink and grey river dolphin numbers between aggregation and control sites. Due to the large sample sizes for the Samiria sites, analyses were on annual means.

Site Comparison	df	F Value	*p* Value
Pink River Dolphin			
Samiria–Atun vs. Samiria Control	1, 14	23.6	<0.001
Samiria–Tapischa vs. Samiria Control	1, 14	29.0	<0.001
Samiria–Maranon vs. Samiria Control	1, 14	20.8	<0.001
Samiria Shiringal vs. Samiria Control	1, 14	24.9	<0.001
UM–Amazon vs. Amazon Control	1, 80	11.5	<0.001
Samiria Control vs. Amazon Control	1, 77	0.1	0.75
Grey River Dolphin			
Samiria–Atun vs. Samiria Control	1, 14	2.6	0.123
Samiria–Tapischa vs. Samiria Control	1, 14	26.8	<0.001
Samiria–Maranon vs. Samiria Control	1, 14	22.5	<0.001
Samiria Shiringal vs. Samiria Control	1, 13	51.7	<0.001
UM–Amazon vs. Amazon Control	1, 50	18.1	<0.001

3.3. Grey River Dolphin

Grey river dolphins had an average of 18.9 ind/survey (SD 9.2, range 11.5–34.5) at aggregation sites, compared with a mean of 5.6 ind/survey (SD 2.2, range of 4.0–7.2) at control sites (Table 1).

All the confluence aggregation sites had greater numbers of grey river dolphins than control areas outside the confluences, except the interior river site (Samiria–Atun) (Table 2). Aggregation sites connected to large rivers had a greater number of grey river dolphins than control areas. The Samiria–Atun aggregation site, inside a tributary river and not linked to a large river, had similar grey river dolphin numbers as control sites, and was not an aggregation for grey river dolphins. Grey dolphin aggregations increased in numbers with the size of the river, with the greatest being at the UM–Amazon aggregation site (mean 19.1 ind/survey) and the lowest at the mouth of the Samiria (mean 8.24 ind/survey).

3.4. Dolphin Behaviour at Aggregations

The behaviours observed were fishing, resting, moving, and playing. At the confluence aggregations, both species of dolphins had greater point counts of fishing than other behaviours. In both species, there were also greater counts of fishing behaviour at the aggregations than at control sites, indicating that dolphins often feed at the sites (Table 3). Contrary, at the control sites, displacement behaviour (moving) had the greatest counts, indicating that dolphins often move between confluence areas when on the main river channel.

Table 3. Frequency of pink and grey river dolphin behaviours at aggregation sites and controls. The values are counts of behavioural categories per survey (counts/survey).

Behaviour	Sites	Minimum	Maximum	Mean (Counts/Survey)	Std. Deviation
Pink River Dolphin					
Fishing	Aggregations	0.00	68.00	15.16	15.80
	Control	0.00	37.00	13.14	13.86
Resting	Aggregations	0.00	51.00	9.64	12.34
	Control	0.00	15.00	4.70	6.46
Moving	Aggregations	0.00	8.00	1.08	1.81
	Control	0.00	6.00	1.98	2.73
Playing	Aggregations	0.00	54.00	1.80	7.52
	Control	0.00	2.00	0.38	1.32
Grey River Dolphin					
Fishing	Aggregations	0.00	80.00	16.62	16.34
	Control	0.00	74.00	14.62	23.31
Resting	Aggregations	0.00	82.00	2.73	10.87
	Control	0.00	25.00	2.50	6.72
Moving	Aggregations	0.00	17.00	2.59	4.14
	Control	0.00	9.00	1.56	2.42
Playing	Aggregations	0.00	85.00	3.38	11.4
	Control	0.00	6.00	0.75	1.77

Pink river dolphins displayed a greater amount of resting and play behaviours at aggregation sites than the controls, and calves displayed these behaviours more than adults. Grey river dolphins displayed play behaviour with greater frequency at the aggregations.

3.5. Seasonal Differences in Site Usage

The pink river dolphins used aggregations throughout the year without seasonal differences in the abundance of individuals at these sites between the high-water season (January–June) and the low-water season (July–December) (ANOVA, $p = 0.71$). However, during the peak flood pulse months of April–May, pink river dolphins decreased at the aggregation sites and moved into the small tributaries and lakes that were not accessible to them during the rest of the year. At the UM–Amazon confluence, their numbers went down to 5 ind/survey during the peak flood pulse in April from an average of 13 ind/survey during the rest of the year. In the Yarapa Channel, there were no dolphins in the low-water season, whereas in the peak flood months, there were 6 ind/survey. The control sites outside the aggregations had a greater number of pink river dolphins in the low-water season (9.3 ind/survey) than in the high-water season (6.2 ind/survey) (ANOVA, df 11, F 5.12, $p = 0.04$).

The grey river dolphins showed no difference in numbers at the UM–Amazon aggregation site, the most used aggregation by this species, between the high- and low-water seasons (ANOVA, $p = 0.31$). Grey river dolphins were rare in flooded forests, and, in the high-water season, they used the larger rivers.

Seasonal aggregation sites occurred. For example, the confluence at the Yarapa Channel and Amazon River had a mixed-species aggregation during the high-water season of

11 ind/survey, but in the low-water season, when water stops flowing from the channel and the confluence ceases, dolphin numbers decreased and were similar to the control sites.

3.6. Channel Geomorphology of the Riverbed at Dolphin Aggregations

We evaluated the riverbed geomorphology at aggregation sites using side-scan sonar. The Samiria River control site had a depth of around 10–12 m during the high-water season and 2–4 m during the low-water season, which fluctuates between flood and drought years [26]. The control site on the main channel of the Amazon had a depth of 30–40 m in the high-water season and 20–30 m in the low-water season. The secondary channel at the UM–Amazon confluence had a depth of 10 m in high water and 2 m in low water outside of a depression caused by a reverse current, with a high-water depth of around 18 m and a low-water depth of around 12 m. All the confluence aggregation sites had a depression in the riverbed that averaged 6.3 m deep (SD 1.6, range from 5 to 9 m) (Table 4, Figure 2). On the Samiria River, the riverbed depth at the confluence aggregations outside the depressions were similar to the Samiria control depths.

Table 4. Riverbed depressions at the aggregation sites in metres from the surrounding riverbed.

Confluence Sites	Depression Depth (m)
Samiria–Atun	6.0
Samiria–Tapishca	5.0
Samiria–Maranon	6.5
Samiria–Channel	5.0
UM–Amazon	9.0

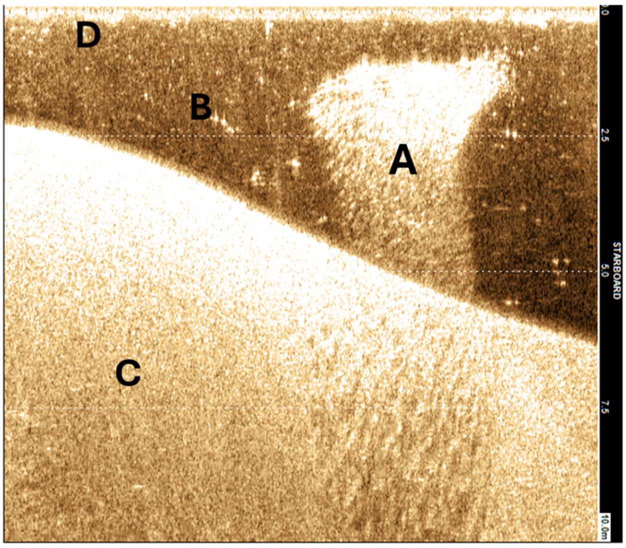

Figure 2. Fish captured on side-scan sonar at the Samiria–Tapishca depression. The letter A is a school of fish, B is individual fish, C is the riverbed, and D is the water surface.

The geomorphology of the UM–Amazon site, formed from the merging of the Ucayali and Maranon Rivers, is important for dolphin and fish populations. The size of the Maranon (16,175 m^3/s) and Ucayali (11,415 m^3/s) Rivers results in a complex hydrogeomorphology consisting of fast-flowing deep channels, stagnation zones, and secondary currents [27]. The Ucayali River determines the bed formation at the confluence, and there is a secondary current that is counterclockwise on the left bank and has a riverbed depression separate from the main channel and bordered by a stagnant zone [27]. Dolphin and fish aggregations were located at this secondary current zone (Figure 3).

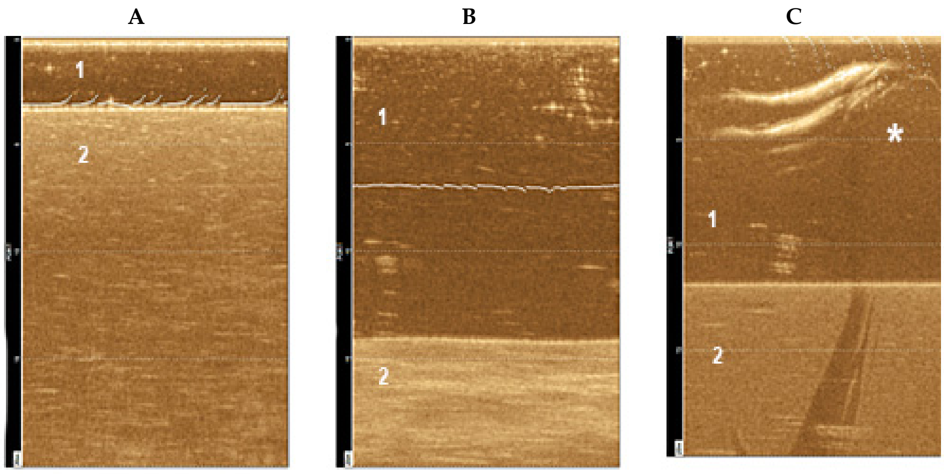

Figure 3. Side-scan sonar images of the depression of the secondary current zone of the Ucayali–Maranon River confluence, which makes up the UM–Amazon aggregation site, (**A**) on the periphery of the depression, (**B**) in the depression, and (**C**) two dolphins (*) at the edge of the depression. The water area is darker (1), and the riverbed lighter (2) in colour. The left vertical axes are the depth, and the white dots are the fish.

3.7. Fish Numbers

Fish numbers at the confluence sites were determined using side-scan sonar and had a greater abundance of fish than the control sites (ANOVA, df 107, F 9.5, $p = 0.003$). The control sites had the lowest fish numbers (4.2–8.7 fish/image), whereas the confluence aggregation had greater fish numbers (14.6–33.6 fish/image). The interior tributary aggregation had fewer fish numbers (14.6 fish/image), and the UM–Amazon aggregation site had the greatest fish numbers (33.6 fish/image) (Table 5).

Table 5. Fish numbers (fish/image) at dolphin aggregation sites and control sites as individuals per side-scan sonar image.

Site	Minimum	Maximum	Mean (Fish/Image)	Std. Deviation
Samiria–Atun	1.00	47.00	14.60	10.11
Samiria–Tapishca	3.00	137.00	30.81	33.88
Samiria–Maranon	5.00	76.00	25.93	19.41
UMA-Amazon	20.00	56.00	33.57	8.74
Control Samiria	1.00	88.00	8.77	14.12
Control Amazon	0.00	15.00	4.27	4.40

3.8. Fish Species and Abundance

The Samiria River aggregation sites had a total of eighty-nine species of fish. The CPUE used one hour net and one hour rod fishing to calculate abundance as ind/hour. The occurrence measured a 1–0 capture per season per year of the species, with a maximum of 24 occurrences over the 12-year sample. The most frequently observed species were *Astronotus ocellatus*, *Liposarcus pardalis*, *Pygocentrus nattereri*, *Prochilodus nigricans*, *Serrasalmus humeralis*, and *Serrasalmus rhombeus* (Table 6). The CPUE method recorded fish in the weight range eaten by dolphins, with a mean of 136.5 g/fish. The amount actually eaten by dolphins of each fish species was not measured and is likely to be related to the preference of dolphins and abundance of fish. The fish abundance at the aggregations was lower during the high-water season (6.1 fish/h (SD 4.1)) and greater in the low-water season (14.7 fish/h (SD 8.4)) (ANOVA, df 21, F 9.1, $p = 0.007$; Figure 4).

Table 6. The most common fish species caught at aggregation sites using both gill net and rod-and-line methods. The occurrence measured a 1–0 capture per season per year of the species, with a maximum of 24 occurrences over the 12-year sample.

Species	Occurrence
Astronotus ocellatus	23
Pterygoplichthys pardalis	20
Pygocentrus nattereri	20
Prochilodus nigricans	18
Serrasalmus humeralis	17
Serrasalmus rhombeus	15
Aphanotorulus emarginatus	14
Mylossoma albiscopum	14
Ancistrus sp.	12
Heros efasciatus	12
Hoplerythrinus unitaeniatus	12
Hoplias malabaricus	12
Aequidens tetramerus	11
Triportheus angulatus	11
Chaetobrachus flavescens	10
Mesonauta festivus	10
Metynnis sp.	10
Piaractus brachypomus	10
Oxydoras niger	10
Cichlasoma amazonarum	9
Tetragonopterus argenteus	9
Brycon cephalus	7
Satanoperca jurupari	7
Schizodon fasciatus	7

The composition of fish species at the UM–Amazon site was determined through eDNA analysis. The common genera/species that had over 1000 DNA fragments included *Leporinus*, *Schizodon*, *Ctenobrycon hauxwellianus*, *Cyphocharax*, *Prochilodus lineatus*, *Pellona flavipinnis*, *Trachelyopterus galeatus*, *Megalechis picta*, *Pterodoras granulosus*, *Trachydoras steindachneri*, *Calophysus macropterus*, *Pinirampus pirinampu*, and *Zungaro zungaro*. The diversity of fish was greater at the UM–Amazon aggregation site with a species richness of 57-73 OTU's, compared to the control site in the main river channel that had a lower species richness of 26-33 OTU's.

3.9. Dolphin–Fish Correlation

The numbers of fish and dolphins were positively correlated at all the aggregation and control sites (Pearson 2-tailed, N = 7, $p < 0.001$). However, the proportion of pink and grey river dolphins varied, with grey river dolphins having greater numbers than pink river dolphins where fish populations were largest (Figure 5).

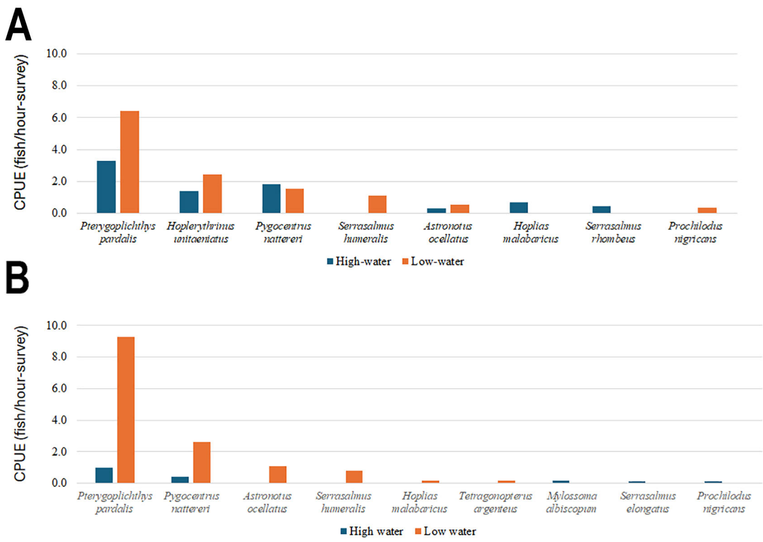

Figure 4. The catch-per-unit-effort (CPUE) of fish at the aggregation sites: (**A**) Samiria–Atun, and (**B**) Samiria–mouth. CPUE was used as a measure of abundance as ind/survey, which includes both net, and hook and line methods.

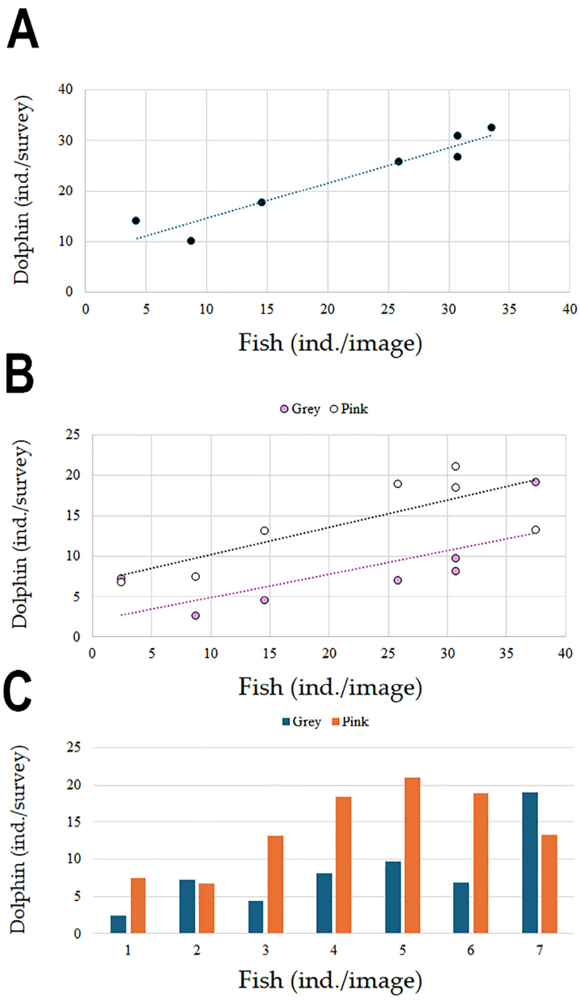

Figure 5. Relationship between river dolphin numbers (as individuals/survey) and fish numbers (as fish/image) in the seven study sites: (**A**) relationship between both dolphin species and fish numbers, (**B**) relationship between pink and grey dolphin species and fish numbers, and (**C**) relationship between the pink and grey river dolphins at sites and fish abundance as a non-parametric ranking. Sites 1 and 2 are the controls.

MANOVA showed that the pink river dolphin aggregations were determined by both fish abundance and waterscape type. The abundance of fish (df 2, f 10.6, $p < 0.001$) and the aggregation site (df 2, f 25.4, $p = 0.001$) were the main factors determining dolphin numbers. There were no differences between the years 2012 and 2023, with dolphins having stable populations at the confluences during the study period (df 2, f 0.89, $p = 0.418$) (Supplementary Material). The control sites, outside of confluences, had the lowest numbers of dolphins and fish. The interior tributary river (Samiria–Atun) had significantly larger dolphin and fish numbers than the control sites, but smaller numbers of dolphin and fish than those found in the aggregations at the confluences of major rivers. Confluence sites connected to the major rivers were the most important for dolphins.

3.10. Dolphin Demographics at Aggregations

Dolphin groups in areas of mixed species aggregations had greater numbers of young individuals, including infants and juveniles, than adults of both species (Figure 6). A high proportion of young individuals indicates a dolphin nursery, and aggregation sites were areas where dolphins raised their calves. Young dolphins were in sub-groups at the centre of the aggregation, with mature female-sized dolphins around the edge and larger males on the outskirts.

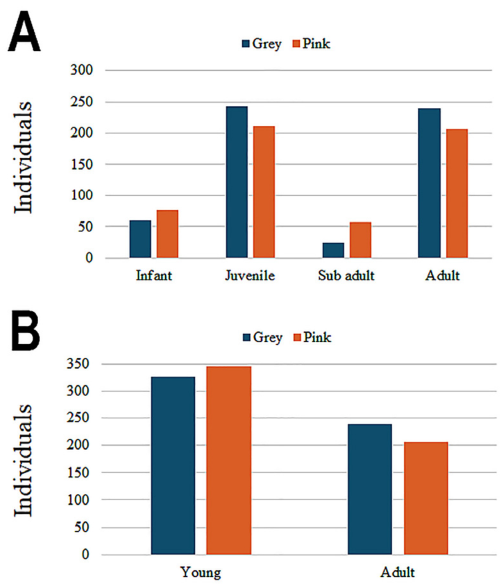

Figure 6. Demographics of river dolphins in aggregation sites. Counts of total recorded compositions during surveys for (**A**) grey river dolphins and (**B**) pink river dolphins. The age classes include infants, juveniles, sub-adults, and adults are shown in the top graphs, and young and adults in the bottom graphs.

At aggregation sites, the pink river dolphin calves made up 62% of the individuals, the rest being adults, whereas the grey river dolphin calves made up 57% of the individuals. The aggregations had greater proportions of young individuals, which resulted in inter-specific nurseries. At times, the nurseries had young individuals of both species in proximity, and, at other times, they used different areas of the confluence.

4. Discussion

Our study shows that all aggregation sites of pink and grey river dolphins were located at water confluences. The aggregations had statistically higher numbers of dolphins than the control sites, and both dolphin species used these areas, albeit to different degrees.

Dolphin aggregations occurred at areas with the highest fish abundance. Fish and dolphins converged at confluence areas of rivers, channels and lakes that form the aggregation sites. At the aggregation sites, both fish and dolphin abundance were greater than at control sites, dolphin abundance was positively correlated with the abundance of fish, and fishing was the most frequent dolphin behaviour. These findings suggest that fish are important for the formation of dolphin aggregations and that fish predation by dolphins is greater than in areas away from the confluences.

The dolphin aggregation in the tributary river at the Samiria–Atun site was not connected to a major river, and this site had a pink river dolphin aggregation, but not a grey river dolphin aggregation. Other studies have also shown that pink river dolphins use the smaller rivers, lakes, and flooded forests more than the grey river dolphins, who prefer larger rivers and lakes [5,28,29].

The largest grey river dolphin aggregation was at the confluence of the Ucayali, Maranon, and Amazon Rivers (UM–Amazon), which was four-fold greater in water surface area than confluence areas at the mouth of the Samiria River (Samiria–Tapishca, Shiringal, and Maranon). Grey river dolphins at UM–Amazon had greater numbers than Pink dolphins; while at the mouth of the Samiria River, the species distribution reversed, with a greater abundance of pink river dolphins.

Habitat preferences showed that pink river dolphins are more inclined to use smaller water bodies and flooded forest habitats, whilst grey dolphins are more inclined to larger open waters [4,30]. Differences in preferences lead to similar total dolphin numbers at gatherings, but with varying proportions of species. The different preferences may result from competition, since dolphins could reduce competition by having proportional differences in numbers between different confluences. Feeding behaviour differs between the species and this can also reduce competition, since grey river dolphins feed near the surface, while pink river dolphins feed deeper in the water [6].

Aggressive behaviour between the two dolphin species was rare and consisted of short chasing interactions. In contrast, the two species were frequently observed fishing together and having mixed-species nurseries, and observations of the two species in mixed pods at the aggregations were common. These findings suggest that fish availability in the aggregations was sufficiently high that both dolphin species did not need to compete with aggressive behaviour for food resources.

Shorebirds, including herons, egrets, and cormorants, consume greater quantities of fish than dolphins and are a main competitor of dolphins, with similar fish diets [26]. Indeed, occasionally, pink river dolphins would drown egrets that were floating on vegetation by rapidly pulling them under, but they did not eat the birds. This might have been a game for the dolphins, or a result of direct competition.

Fish numbers at the aggregations sustained dolphins year-round. Pink dolphins travelled to smaller streams, lakes, and channels during peak flood months, as they do throughout the Amazon [29]. However, dolphin aggregation sites had similar numbers present throughout the year, serving as important feeding sites in all seasons.

Fish abundance at the aggregation sites was greater during the low-water season and decreased during the high-water season. The continental weather systems from the southern Atlantic result in the inundation of the flooded forests during the rainy season from January to June [31]. In the Ucamara depression, the volume of water increases by up to four times, causing one-third of the Loreto Region to flood, the size of an inland sea. The inundation of the forests usually lasts for two months during peak flooding. This increase in water volume and water surface area results in fish dispersing throughout the flooded forests with a lower fish abundance compared to the low-water season when fish concentrate in lakes, rivers, and channels, and the forests are dry land.

While the fish abundance was correlated to the size of dolphin aggregations, the study cannot determine which species of fish dolphins ate. Notably, the fish species observed in the confluences are all known to occur in other areas of the Amazon floodplain, including flooded forest, lakes, and their connected channels [32] and many of the fish genera and species have been observed to be dolphin food [9,10].

The methods used to estimate fish abundance included CPUE, side-scan sonar and eDNA. The CPUE yielded species richness and an abundance of fish that were consumed by dolphins. The side-scan sonar yielded the numbers of fish but not species, whereas the eDNA gave a measure of abundance and species richness of all species, including smaller and larger sizes than the size of fish eaten by dolphins. eDNA abundance, as measured by the number of DNA fragments in a sample, can be a useful indicator of fish abundance, but needs to be interpreted with caution due to variations in DNA shedding rates between species. While more DNA fragments suggest a larger population, factors like species-specific shedding rates and environmental conditions can influence the relationship between eDNA and actual fish numbers [33,34].

Both river dolphin species have home ranges from two to 25 km [20,35]. Dolphins may move between aggregation sites at confluences, which are around 10 km apart, and would allow a home range of 25 km to encompass confluence areas [34]. The composition of the aggregations appears to consist of a core pod that is frequently present, and other individuals that are at the aggregation for shorter multi-day periods.

Confluences are areas of high biological activity within the floodplain system of Amazonia [16]. Often the mixing waters differ in their velocity, temperature, and density resulting in a complex 3-dimensional flow dynamic with boundary zones over which water velocities can rapidly change with back eddies, up- and down-welling, and areas of slack water. The river flow influences bed morphology, creating deep areas attractive to fish seeking to avoid bird predation. The mixing waters frequently differ in their chemical and biological characteristics and promote enhanced fish productivity [36]. Small organisms, such as fish eggs and larvae and planktonic crustaceans, together with allochthonous forest inputs, tend to become concentrated in boundary zones, and these attract small fish. In flowing waters with velocities lower than their sustainable swimming speeds, fish orientate with the flow, tend to hold station, and let their food flow towards them [37]. The smaller fish form aggregations in water of suitable velocity and depth and these are attractive to large fast swimming predators who are better able to swim in currents, such as apex predators such as dolphins. In fast-flowing water, a small fish is a sitting target for a dolphin.

At confluence sites, the higher fish densities during the low-water season suggest that these areas offer deeper water refuges in which to feed and reduce predation during the dry season. Oxygen concentration and elevated temperatures can also be limiting factors for fish in floodplain lakes during the low-water season, where fish die-offs are frequently observed [38]. Confluences, with their turbulent flows and vertical mixing, allow fish to utilize deeper, cooler waters because of the increased oxygen availability. These mixing zones may be key ecological regions for the maintenance of aquatic diversity within the floodplain ecosystem.

The life history of Amazon River dolphins revolves around aggregation sites, which are key for feeding, raising young, social behaviours, and interspecific interactions. The high proportion of young dolphins and greater displays of playing and resting behaviours strongly suggest that the aggregation sites serve as nurseries. These areas are important for the survival and development of young river dolphins, providing abundant food, protection, and opportunities for learning essential social and fishing skills [29,39]. The aggregation sites are important for the long-term survival of dolphin populations. They provide abundant food and a safe environment for vulnerable young dolphins to develop vital skills, including the ability to interact with the conspecific species.

The conservation of river dolphins is particularly important at confluences that host dolphin aggregations. People usually live at confluence sites, and these villages use fish resources for subsistence and market sales. For example, at the Samiria confluence site, four local communities from the Kukama Indigenous people harvest 1740 tons of fish annually [17]. Campbell et al. [19] found that 89% of dolphin home ranges overlap with human fishing areas. People use shallow areas along the shore for fishing at confluences since gill nets do not work in deep water. Shallow areas are habitats where shorebirds fish, whereas the deeper pools of the confluence areas are where dolphins feed, and this separation decreases direct overlap of human and dolphin fishing areas.

The dolphin aggregations at confluences are of special conservation interest and are important for the survival of both river dolphin species. The large dolphin numbers and stable populations in the study sites are in large part due to the local Kukama Indigenous peoples who live at the confluences. The Kukama people living close to the Samiria and UM–Amazon confluences have strong folklore and traditional stories surrounding dolphins, which drive positive conservation attitudes and behaviours, including a strong belief in not harming or killing dolphins [21].

Indigenous Amazonians and dolphins have co-existed at the same confluences for thousands of years, and Indigenous beliefs have helped conserve the dolphins throughout this time and continue to do so today. The Pacaya–Samiria National Reserve's co-management strategy supports conservation efforts of the Kukama communities and, together with SERNANP, they are helping the dolphins to survive at their natural aggregation sites.

5. Conclusions

Confluences of rivers, channels, and lakes are areas were pink and grey river dolphins form aggregations. These aggregation sites are important for the life history of the dolphins and are important sites for dolphin conservation. All of the confluences had riverbed depressions harboring large fish populations. Dolphin fished at the confluences but also had nurseries with a high percentage of young dolphins, showing the importance of the aggregation sites for raising young in areas of abundant fish. The dolphin aggregations increased with fish numbers, and the highest dolphin and fish populations were found on the largest rivers. Local Indigenous people have villages at confluence areas and fishing is an important activity, resulting in overlap between people and dolphin aggregations. Strong taboos that the Indigenous people have about not killing dolphins have helped in the conservation of dolphin aggregations at confluence sites.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/fishes10100495/s1, Table S1: MANOVA statistics.

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Informed Consent Statement: Not applicable.

Data Availability Statement: Data supporting reported results are achieved at the Museum of Indigenous Cultures, Iquitos, Peru, and on the database of the Rio Amazonas Research Station, and access can be requested at Fundamazonia, www.fundamazonia.org.

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Conflicts of Interest: Peter Henderson was employed by the company PISCES Conservation Ltd., UK. Peter Henderson was responsible for Conceptualization, methodology, writing—original draft preparation, and writing—review and editing the manuscript during the research. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Abbreviations

The following abbreviations are used in this manuscript:

CPUE	Catch per unit effort
UM–Amazon	Ucayali, Maranon, Amazon Rivers confluence
SERFOR	Peruvian Forestry and Wildlife Service
SERNANP	Peruvian Protected Area Authority

References

1. Rai, A.; Bashir, T.; Lagunes-Díaz, E.G.; Shrestha, B. The effect of physiographic and hydrologic complexities and their alterations on the distribution of obligate freshwater dolphins. *Ecol. Evol.* **2023**, *13*, e10106. [CrossRef]
2. Shostell, J.; Ruiz-García, M. An introduction to River Dolphin species. In *Biology, Evolution, and Conservation of River Dolphins Within South America and Asia*; Nova Science Publishers Inc. Ed.: New York, NY, USA, 2010; pp. 1–28.
3. Gravena, W.; Hrbek, T.; da Silva, V.M.F. Boto (Inia geoffrensis—Cetacea: Iniidae) aggregations in two provisioning sites in the lower Negro River—Amazonas, Brazil: Are they related. *PeerJ* **2019**, *7*, e6692. [CrossRef]
4. Martin, A.R.; da Silva, V.M.F.; Salmon, D.L. Riverine habitat preferences of botos (*Inia geoffrensis*) and tucuxis (*Sotalia fluviatilis*) in the Central Amazon. *Mar. Mamm. Sci.* **2004**, *20*, 189–200. [CrossRef]
5. Bélanger, A.; Wright, A.J.; Gomez, C.; Shutt, J.; Chota, K.; Bodmer, R. River dolphins (*Inia geoffrensis* and *Sotalia fluviatilis*) in the Peruvian Amazon: Habitat preferences and feeding behavior. *Lat. Am. J. Aquat. Mamm.* **2022**, *17*, 2–9. [CrossRef]
6. Rosas-Ribeiro, P.F.; Rosas, F.C.W.; Amaral, R.S.; Fettuccia, D.C.; Brum, S. Amazonian Aquatic Mammals: Existing Knowledge, Current Threats and Future Studies. In *Amazonian Mammals: Current Knowledge and Conservation Priorities*; Spironello, W.R., Barnett, A.A., Lynch, J.W., Bobrowiec, P.E.D., Boyle, S.A., Eds.; Springer Nature: Cham, Switzerland, 2024; pp. 181–213. [CrossRef]
7. McGuire, T.L. Ecology and conservation status of tucuxi (*Sotalia fluviatilis*) in the Pacaya-Samiria Reserve, Peru. *Lat. Am. J. Aquat. Mamm.* **2010**, *8*, 103–110. [CrossRef]
8. Mintzer, V.J.; Lorenzen, K.; Frazer, T.K.; da Silva, V.M.F.; Martin, A.R. Seasonal movements of river dolphins (*Inia geoffrensis*) in a protected Amazonian floodplain. *Mar. Mamm. Sci.* **2016**, *32*, 664–681. [CrossRef]
9. Best, R.C.; da Silva, V.M.F. *Inia geoffrensis* . *Mamm. Sp.* **1993**, *426*, 1–8. [CrossRef]
10. Da Silva, V.M.F.; Best, R.C. *Sotalia fluviatilis* . *Mamm. Sp.* **1996**, *527*, 1–7. [CrossRef]
11. Ruiz-García, M.; Mejia, D.; Escobar-Armel, P.; Tejada-Martínez, D.; Shostell, J.M. Molecular Identification and Historic Demography of the Marine Tucuxi (*Sotalia guianensis*) at the Amazon River's Mouth by Means of Mitochondrial Control Region Gene Sequences and Implications for Conservation. *Diversity* **2013**, *5*, 703–723. [CrossRef]
12. Duran, L.G.; Aliaga-Rossel, E. Abundance of the Bolivian River Dolphin (Inia boliviensis) in Mamore River, Upper Madeira Basin. *Aquat. Mamm.* **2016**, *42*, 330–338. [CrossRef]

13. Yuan, S.; Xu, L.; Tang, H.; Xiao, Y.; Gualtieri, C. The dynamics of river confluences and their effects on the ecology of aquatic environment: A review. *J. Hydrodyn.* **2022**, *34*, 1–14. [CrossRef]
14. Yuan, S.; Jiajian, Q.; Tang, H.; Xu, L.; Xiao, Y.; Liu, M.-Y.; Rennie, C.; Gualtieri, C. Fish Community Traits near a Large Confluence: Implications for Its Nodal Effects in the River Ecosystem. *J. Hydrology.* **2023**, *626*, 130335. [CrossRef]
15. Qiu, J.; Yuan, S.; Tang, H.; Deng, Y.; Gualtieri, C. Hydrodynamic Responses of Fish Community Dynamics in Large-Scale Morphologically Complex River Systems. *Water Resour. Res.* **2025**, *61*, 7. [CrossRef]
16. Henderson, P.A.; Hamilton, W.C. Evolution and Diversity in Amazonian Floodplain Communities. In *Dynamics of Tropical Communities*; Newbery, D.M., Prins, H., Brown, N., Eds.; Blackwell Science: Oxford, UK, 1998; pp. 385–419.
17. Kirkland, M.; Eisenberg, C.; Bicerra, A.; Bodmer, R.; Mayor, P. Sustainable Wildlife Extraction and the Impacts of Socio-economic Change Among the Kukama-Kukamilla People of the Pacaya-Samiria National Reserve, Peru. *Oryx* **2018**, *54*, 260–269. [CrossRef]
18. Bodmer, R.; Mayor, P.; Antunez, M.; Chota, K.; Fang, T.; Puertas, P.; Pittet, M.; Kirkland, M.; Walkey, M.; Rios, C.; et al. Major shifts in Amazon wildlife populations from recent intensification of floods and drought. *Con. Bio.* **2018**, *32*, 333–344. [CrossRef]
19. Trujillo, F.; Crespo, E.; Van Damme, P.A.; Usma, J.S. *The Action Plan for South American River Dolphins 2010–2020*; Fundación Omacha: Bogotá, Colombia, 2010; p. 249. ISBN 978-958-8554-10-5.
20. Campbell, E.; Alfaro Shigueto, J.; Mangel, J.; Mena Alvarez, J.L.; Thurstan, R.; Godley, B.; March, D. Satellite-monitored movements of the Amazon River dolphin and considerations for their conservation. *Oryx* **2023**, *57*, 769–779. [CrossRef]
21. Spence, C. Conservation Stories: How Indigenous Traditional Stories Can Influence the Conservation of Amazonian Aquatic Mammals. Master's Thesis, School of Anthropology and Conservation, University of Kent, Canterbury, UK, 2023; p. 26.
22. Zulkafli, Z.; Buytaert, W.; Manz, B.; Veliz, C.; Willems, P.; Lavado-Casimiro, W.; Guyot, J.; Santini, W. Projected increases in the annual flood pulse of the Western Amazon. *Environ. Res. Lett.* **2016**, *11*, 014013. [CrossRef]
23. da Silva, V.M.F.; Freitas, C.E.C.; Dias, R.L.; Martin, A.R. Both cetaceans in the Brazilian Amazon show sustained, profound population declines over two decades. *PLoS ONE* **2018**, *13*, e0191304. [CrossRef]
24. Aliaga-Rossel, E.; Duran, L.G. Four decades of research on distribution and abundance of the Bolivian river dolphin *Inia geoffrensis* boliviensis. *Endang. Species Res.* **2020**, *42*, 151–165. [CrossRef]
25. Gomez-Salazar, C.; Trujillo, F.; Portocarrero-Aya, M.; Whitehead, H. Population, density estimates, and conservation of river dolphins (Inia and Sotalia) in the Amazon and Orinoco river basins. *Mar. Mamm. Sci.* **2012**, *28*, 124–153. [CrossRef]
26. Bodmer, R.; Fang, T.G.; Puertas, P.; Antúnez, M.; Chota, K.; Bodmer, W. *Cambio Climático y Fauna Silvestre en la Amazonía Peruana: Impacto de la Sequía e Inundaciones Intensas en la Reserva Nacional Pacaya Samiria*; FundAmazonia/Sernanp: Lima, Peru, 2014; p. 254.
27. Guerrero, L.; Abad, J.D.; Ortals, C.; Valderde, H.; Estrada, Y.; Chicchon, H.; Marin, J.; Canas-Alva, C. Hydrogeomorphology of the origin of the Amazon River, the confluence between the Marañón and Ucayali rivers. *Earth Surf. Process. Landf.* **2024**, *49*, 3949–3967. [CrossRef]
28. McGuire, T.L. Distribution and Abundance of River Dolphins in the Peruvian Amazon. Ph.D. Thesis, Texas A & M University, College Station, TX, USA, 2002.
29. da Silva, V.M.F.; Brum, S.M.; Mello, D.M.D.; Amaral, R.S.; Gravena, W.; Campbell, E.; Gonçalves, R.S.; Mintzer, V.J. The Amazon River dolphin, *Inia geoffrensis*: What have we learned in the last two decades of research? *Lat. Am. J. Aquat. Mamm.* **2023**, *18*, 139–157. [CrossRef]
30. Faustino, C.; da Silva, V.M.F. Seasonal use of Amazon floodplains by the tucuxi *Sotalia fluviatilis* (Gervais 1853), in the Central Amazon, Brazil. *Lat. Am. J. Aquat. Mamm.* **2006**, *5*, 95–104. [CrossRef]
31. Espinoza, J.C.; Ronchail, J.; Frappart, F.; Lvavdo, W.; Santini, W.; Guyot, J. The major floods in the Amazonas River and tributaries (western Amazon basin) during the 1970–2012 period: A focus on the 2012 flood. *J. Hydrometeorol.* **2013**, *14*, 1000–1008. [CrossRef]
32. Cuesta, F.; Calderon, M.; Rosero, P.; Calispa, M.; Zisling, H.; Perez Castillo, Y.; Echevarría, G.; Rios-Touma, B. Seasonally Flooded Landscape Connectivity and implications for fish in the Napo Moist Forest: A High-Resolution Mapping Approach. *Glob. Ecol. Conserv.* **2024**, *56*, e03257. [CrossRef]
33. Qiu, S.; Ooi, J.L.S.; Chen, W.; Poong, S.W.; Zhang, H.; He, W.; Su, S.; Luo, H.; Hu, W.; Affendi, Y.A.; et al. Heterogeneity of Fish Taxonomic and Functional Diversity Evaluated by eDNA and Gillnet along a Mangrove-Seagrass-Coral Reef Continuum. *Animals* **2023**, *13*, 1777. [CrossRef]
34. Mosquera-Guerra, F.; Trujillo, F.; Oliveira-da-Costa, M.; Marmontel, M.; Van Damme, P.A.; Franco, N.; Córdova, L.; Campbell, E.; Alfaro-Shigueto, J.; Mena, J.L.; et al. Home range and movements of Amazon river dolphins *Inia geoffrensis* in the Amazon and Orinoco river basins. *Endanger. Species Res.* **2021**, *45*, 269–282. [CrossRef]
35. Martinelli, M.D.; Lasso, C.A.; Caballero, G.S. eDNA metabarcoding: An effective tool for vertebrate diversity studies in the Colombian Amazon and Orinoco basins. *Front. Ecol. Evol.* **2024**, *12*, 1409296. [CrossRef]
36. Bouchez, J.; Moquet, J.S.; Espinoza, J.C.; Martinez, J.M.; Guyot, J.L.; Lagane, C.; Pombosa, R. River mixing in the Amazon as a driver of concentration-discharge relationships. *Water Resour. Res.* **2017**, *53*, 8660–8685. [CrossRef]
37. Webb, P. Control of Posture, Depth, and Swimming Trajectories of Fishes. *Integr. Comp. Biol.* **2002**, *42*, 94–101. [CrossRef]

38. Agostinho, A.A.; Alves, D.C.; Gomes, L.C.; Dias, R.M.; Petrere, M., Jr.; Pelicice, F.M. Fish die-off in river and reservoir: A review on anoxia and gas supersaturation. *Neotrop. Ichthyol.* **2021**, *19*, e210037. [CrossRef]
39. Tardin, R.; Espécie, M.; Lodi, L.; Simão, S. Parental care behavior in the Guiana dolphin, Sotalia guianensis (Cetacea: Delphinidae), in Ilha Grande Bay, southeastern Brazil. *Zoologia* **2013**, *30*, 15–23. [CrossRef]