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Original Article

A decade of Philippine freshwater goby research (2010–2022): a systematic review and meta-analysis of ichthyofaunal surveys

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ABSTRACT. Freshwater goby (Family *Gobiidae*) is one of the diverse and widespread fish species in rivers and lakes, with economic values ranging from ornamental and subsistence provisions. Several ichthyofaunal surveys have been conducted in the Philippines; however, no systematic review and meta-analysis was performed to analyze freshwater goby species richness over fish species richness. Following the PRISMA Protocol, twenty–three (23) studies were assessed and statistically analyzed using JASP Version 0.18.3. Each paper was reviewed to identify study sites, goby genera, diversity indices (Shannon, Pielou's evenness, and Simpson), and physicochemical parameters, with correlations analyzed across fish species, goby species richness, and diversity indices. Results revealed that most freshwater goby studies take place in Luzon, and the genus *Glossogobius* is the prevalent goby species at most study sites. The diversity index for introduced fish species ranged from low to medium, as indicated by the enriched biodiversity index score from Guerrero (2014). In terms of physicochemical parameters, all values generally met the standards set by DAO 2016-08. However, the forest plot revealed that the effect size was entirely on the positive side of zero, with a combined effect size of 0.46, suggesting a moderate impact. The funnel plot indicated an asymmetrical pattern among studies, suggesting potential publication bias. Analysis suggests that goby diversity in the Philippines is high in terms of species richness, with a moderate effect size when compared to overall fish species richness based on the collated studies. Taking into account the high publication bias observed, we recommend including more studies from Southeast Asian countries. Researchers are encouraged to prioritize biodiversity studies in the Visayas and Mindanao regions to mitigate study bias. A comparative analysis of native and introduced fish species richness would also be beneficial in determining their potential impact on the overall effect size of species richness.

Keywords: freshwater gobies, *Gobiidae*, Philippines, PRISMA, systematic review, meta-analysis

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1. Introduction

Freshwater gobies (Family *Gobiidae*) play a crucial ecological role in tropical freshwater ecosystems, particularly in insular streams where they dominate due to the absence of primary freshwater fishes. However, approximately 20% of their populations are increasingly threatened by habitat degradation, pollution, climate change, and human activities such as deforestation, agricultural runoff, and dam construction, which disrupt their migratory routes and breeding grounds (Millenium Ecosystem Assessment [MEA], 2005). Recent estimates indicate that 25% of evaluated freshwater fish species worldwide face extinction (Vié et al., 2009). Despite their widespread distribution and ecological importance, many freshwater gobies remain understudied, and their conservation status is largely unknown, particularly in the Philippines and other Southeast Asian regions. The conservation status of freshwater gobies (Family *Gobiidae*) varies globally, with many species facing population declines due to habitat degradation, invasive species, pollution, and

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climate change, particularly in Southeast Asia and the Pacific. While conservation efforts in regions like Japan and Hawaii have led to improved habitat protection, many goby species remain understudied, highlighting the need for further research and sustainable management strategies (Guo et al., 2013).

As key players in maintaining the ecological stability of island environments, these small but significant fish species help regulate ecological processes and provide multiple ecosystem services in freshwater ecosystems (Benstead et al., 2003; N'Guyen et al., 2018). Many species exhibit amphidromous life cycles, requiring both freshwater and marine habitats to complete their development. In oceanic islands, such as some islands in the Philippines, there are no primary freshwater fishes, but instead peripheral freshwater fishes are typically found with the dominant *Gobiidae* group (Herre, 1953; Leveque et al., 2008). Smith et al. (2003) added that many freshwater fish species are phylogenetically derived from marine ancestors such as gobies, sleepers, and eels because their planktonic larvae drift long distances among islands in oceanic currents. These species, found in insular streams, also support fewer freshwater species than continental streams since multiple factors (i.e., island age, length, and geographical location) shape their biodiversity. Insular streams, found mostly in Southeast Asian countries, possess a complex combination of species dispersal from multiple continental sources and other islands, inter-island migration, and the evolution of new endemic species (Covich, 2006; Reichenbacher et al., 2020).

In the Philippines, despite their ecological and economic significance, freshwater gobies face numerous threats that jeopardize their populations and the livelihoods of communities dependent on them (Herre, 1953). Overfishing affects subsistence fisheries such as '*ipon*' fisheries, which has led to declining stocks due to unsustainable harvesting practices and the lack of strict regulations) (Herre, 1927; Blanco, 1956). Human-mediated activities have resulted in sedimentation, water pollution, and the destruction of critical breeding and nursery grounds. Additionally, the rapid expansion of urbanization, dam construction, and river channelization disrupts the natural migratory patterns of amphidromous goby species, leading to population fragmentation and genetic bottlenecks. The ornamental fish trade threatens goby populations due to high demand and unregulated collection, while the lack of comprehensive research and conservation efforts further leaves many species understudied and vulnerable (Kornis et al., 2013). Without immediate intervention through habitat conservation, sustainable fisheries management, and stricter policy enforcement, the future of goby populations in the Philippines remains at risk, along with the ecological balance of the freshwater ecosystems they support.

Several ichthyofaunal surveys have been conducted in the Philippines, but yet no comprehensive systematic review and meta-analysis have been performed to quantify the effect size of goby species richness relative to overall fish species richness. Understanding the abundance and diversity of goby species is crucial for assessing their ecological significance and conservation status. This study aims to bridge this research gap by conducting a systematic review and meta-analysis of ichthyofaunal surveys in the Philippines from 2010 to 2022. Specifically, the study seeks to: (1) assess the existing goby species documented in the Philippines up to the genus level, (2) analyze diversity trends over time and across different freshwater ecosystems, and (3) generate forest and funnel plots to statistically determine the effect size of goby species richness in relation to total fish species richness in these studies. Synthesizing data from various surveys provides a more comprehensive understanding of goby biodiversity patterns, which can serve as a foundation for future conservation and management efforts.

2. Materials and Methods

PRISMA Protocol: We developed a search strategy that minimized bias when identifying the cohort of studies for our review. The study utilized the Preferred Reporting Items for Systematic Reviews (PRISMA) (Page et al., 2021) to review the occurrence of Freshwater goby species (Family *Gobiidae*) in the recently conducted Ichthyofaunal surveys from January 2024-June 2024. Using the literature search software *Publish or Perish* (Version 7.26; https://harzing.com/pophelp/index.htm). We conducted searches across multiple academic databases, including Google Scholar, Scopus, and Web of Science (ISI) for articles related to Gobi richness and fish species richness in freshwater ecosystems in the Philippines, with no restrictions on language and publication year. Using the search term "Freshwater Fish Diversity Philippines", we initially identified 980 articles from Google Scholar and Web of Science (ISI) while 34 articles from Scopus. After applying screening criteria to assess quality and relevance, we narrowed the selection to 45 articles, ensuring that only high-quality and pertinent studies were included in our review. This systematic approach allowed us to compile a robust dataset for analyzing goby species diversity and their ecological significance in Philippine freshwater ecosystems. (Fig. 1)

Data collection and extraction

We compiled a comprehensive list of 23 articles that were included in our systematic review and meta-analysis, synthesizing research on goby species richness and overall fish species richness in Philippine freshwater ecosystems. For each study, key details were documented, including the province where the survey was conducted, the specific location, and the corresponding scientific references from ichthyofaunal surveys in the Philippines. To ensure efficient organization and management of sourced literature, Zotero was utilized, a widely used reference management tool that facilitates the storage, citation, and retrieval of academic materials. This systematic approach allowed us to maintain accuracy, streamline data handling, and ensure transparency in our analysis of goby diversity trends across the country.

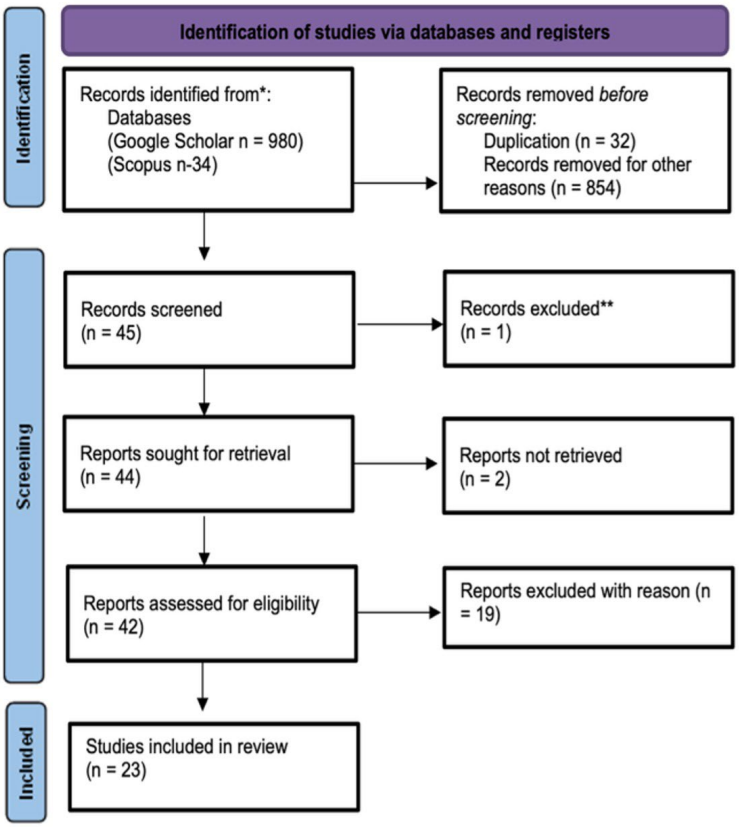

Fig.1. The study utilized the PRISMA flow diagram to showcase the plotted systematic review that comes from published articles.

Inclusion and exclusion criteria: To ensure the rigor and reliability of our meta-analysis on goby species richness relative to overall fish species richness, we established a set of a priori inclusion criteria for selecting published articles (van Rhee et al., 2015). These criteria were designed to filter studies that provided comprehensive and comparable ecological data from ichthyofaunal surveys in the Philippines. Specifically, a study was included only if it reported goby species richness and total fish species richness, ensuring that the data were relevant to our analysis. Additionally, the study must have been conducted within Philippine freshwater ecosystems and provided key biodiversity metrics, such as species richness, relative abundance, and diversity indices, including Shannon, Evenness, and Simpson indices. To account for changes in biodiversity over time, if multiple studies were conducted at the same location, only the most recent reassessment study was considered. This approach prevented data redundancy while capturing the most up-to-date trends in goby diversity.

Only studies with active and passive random sampling, which are standard for ichthyofaunal assessments, were included to ensure consistent methodology. Additionally, studies had to report critical physicochemical parameters such as water temperature, pH, and dissolved oxygen, as these factors significantly influence freshwater fish distribution and diversity. By enforcing these strict inclusion criteria, we ensured that our meta-analysis incorporated only high-quality, standardized data, allowing for robust statistical comparisons and reliable insights into the patterns of goby species richness in Philippine freshwater ecosystems. This meticulous selection process was crucial in reducing bias and enhancing the validity of our findings, ultimately contributing to a more comprehensive understanding of goby diversity and its ecological implications.

Data analysis: We extracted data for 17 key categories from each article to ensure a comprehensive and standardized dataset (Table 1 and Table 2). Given that a single publication could report abundance data for multiple goby species, we structured our dataset by article, ensuring that each observation recorded was associated with a specific publication. Each goby species documented within a study was assigned to a separate row in our database, and its abundance statistics were recorded along with the presence or absence of other measurements of fish species richness within the same study (Table 2). This systematic approach allowed us to capture species-specific trends while maintaining consistency in data organization (Hak et al., 2016).

The extracted data included publication characteristics such as (1) publication year, (2) title of the study, (3) author(s), (4) province, (5) municipality, (6) freshwater ecosystem type (lake or river), (7) survey year, (8) protection status (protected or unprotected area), (9) seasonality, and (10) survey method (see Table 2). Additionally, we gathered information on (11) dissolved oxygen, (12) pH, and (13) water temperature at each study site. Key biodiversity metrics were also recorded, including (14) goby species richness, (15) total fish species richness, and three diversity indices: (16) Shannon Diversity Index, (17) Pielou's Evenness Index, and (18) Simpson's Dominance Index (see Table 2). To determine whether a study was con-

Table 1. Final list of publications included in the systematic review and meta-analysis.

Publication No.	Site	Province	References
1	Minalin Channel-Pampanga River Basin	Pampanga	Baysa et al., 2022
2	Ambuklao Dam, Karao River, Eddet River, Adaoay River, Agno River, Galiano River, Sab-dang River, Amburayan River, Payay-Asin River, Poblacion River, Asin-Lewen River Dopi River	Benguet	Bestre et al., 2018
3	Lake Taal River System (Looc, Magapi {Inlets} and Pasipit {Outlet})	Batangas	Corpuz et al., 2015a
4	Lake Bato, Agos River, Bagacay Falls, Lake Baao-Bula, and Pawili River	Camarines Sur	Corpuz et al., 2015b
5	Lake Oro and Lake Dakong Napo, Esperanza	Agusan Del Sur	Cuadrado et al., 2019
6	Santa Cruz River System	Laguna	Cui et al., 2022
7	Tigum River	Iloilo	Denusta et al., 2020
8	Candaba Wetland	Pampanga	Garcia, 2010
9	Tablas Island Wetlands	Romblon	Gonzalez et al., 2023
10	Eight Floodplain Lake in Agusan Marsh (Panlabuhan, Mihaba, Tugno, Kasawangan, Mambagongon, Sabang-Gibong, Kilobidan, and Tikgon)	Agusan Del Sur	Jumawan and Seronay, 2017
11	Tikub Lake	Quezon	Labatos and Briones, 2014
12	Sawaga River	Bukidnon	Lubos et al., 2020
13	Pajo-Sto. Domingo River System	Catanduanes	Masagca et al., 2022
14	Daniog River	Surigao Del Sur	Mercado, 2018
15	Ihawan Spring Community Watershed	Surigao Del Sur	Ojao et al., 2021
16	Ilog-Hilabangan River System	Negros Occidental	Pacalioga and Peralta, 2016
17	Bago River	Negros Occidental	Pacalioga et al., 2010
18	Watersheds of Mt. Makiling Forest Reserve	Laguna	Paller et al., 2011
19	Tayabas River	Quezon	Paller et al., 2013
20	Lake of San Pablo (Yambo, Sampalok, Pandin, Palakpakin, Mohicap,Calibato, & Bunot)	Laguna	Paller et al., 2017
21	Danao Lake	Leyte	Romero et al., 2023
22	Talabaan River Sytem	Misamis Oriental	Vedra et al., 2022
23	Bega Watershed	Agusan Del Sur	Visto et al., 2015

ducted on an island or the mainland, we relied on information provided within each article and used it to contextualize goby species richness and fish species richness in relation to geographical location.

To assess effect size and standard deviation, we utilized the web-based Campbell Collaboration Effect Size Calculator (https://www.campbellcollaboration.org/research-resources/effect-size-calculator.html). Meta-analysis was conducted using JASP statistical software, focusing on freshwater species richness and goby species richness. Our analysis revealed that Shannon Diversity, Pielou's Evenness, and Simpson's Dominance indices showed no strong correlation with goby species richness. However, due to missing data in some articles, diversity indices were manually calculated when species richness and relative abundance were available.

Descriptive statistical analysis was applied to the physicochemical parameters, including water temperature, pH, and dissolved oxygen, to identify patterns and variations across study sites. The final dataset was analyzed to ensure thematic consistency among the selected research articles, reinforcing the validity of this systematic review and meta-analysis in evaluating goby diversity and its relationship with freshwater fish communities in the Philippines.

Risk bias assessment: To ensure the reliability and validity of the included studies, we conducted a rigorous risk of bias and quality assessment using the Risk of Bias In studies of Temporal Trends in Ecology (ROBITT) framework, developed by Boyd et al. (2022). This framework consists of a 17-question assessment designed to evaluate potential biases within ecological studies, particularly those analyzing temporal trends in biodiversity and species richness. The ROBITT tool allows for a systematic and standardized evaluation of study quality, helping to identify methodological limitations such as incomplete data reporting, inconsistencies in sampling techniques, and the potential influence of external environmental factors. By implementing this framework, we aimed to minimize the inclusion of

Table 2. Summary of study details, locations, and biodiversity indices of freshwater goby species in the Philippines (2010–2022).

Author	Year	Province	Municipality	Lake/River	Survey year	Method	Species richness	No. of goby species
Uy et al.	2015	Surigao Del Norte & Agusan Del Norte		Mainit Lake and Kalinawan River	2007	sampling survey	41	4
Gonzalez et al.	2023	Romblon	Alcantara, Calatrava, Ferrol, Looc, Odiongan, San Agustin, San Andres, Sante Fe, & Santa Maria	Tablas Island	2019	sampling survey	44	12
Corpuz et al.	2015	Batangas	Taal Lake	Taal Lake (Inlet Looc and Magapi) (Outlet; Pansipit)	2011	sampling survey	37	7
Dantis and Lacap	2021	Pangsaninan		Agno River	2018	sampling survey	23	1
Labatos and Briones	2014	Quezon	Tiaong	Tikub Lake		sampling survey	9	1
Opiso et al.	2014	Bukidnon		Alanib River		sampling survey	2	1
Cui et al.	2022	Laguna	Santa Cruz	Santa Cruz River System	2016–2017	sampling survey	12	3
Corpuz et al.	2015	Camarines Sur			2010	sampling survey	29	8
Quimpang et al.	2016	Davao Oriental	Mt. Hamiguitan	River	2015	sampling survey	33	9
Paller et al.	2017	Laguna	San Pablo	Lake	2013–2014	sampling survey	10	1
Dapar et al.	2021	Davao Oriental	Mt. Hamiguitan	River	2019–2021	sampling survey	25	9
Baysa et al.	2022	Pampanga	Minalin	River	2018	sampling survey	16	3
Cuadrado et al.	2019	Agusan Del Sur	Ezperanza	Lake	2017	sampling survey	12	2
Mercado	2018	Surigao Del Sur	Lanuza	River	2016–2017	sampling survey	13	2
Masagca et al.	2022	Catandauanes		Pajo-Sto. Domingo River	2017–2018	sampling survey	20	3
Lubos et al.	2020	Bukidnon	Malaybalay	Sawaga River	2018–2019	sampling survey	8	0
Yagos et al.	2022	Zamboanga Del Sur	Bayog	Sibugay River	2018	sampling survey	19	2
Romero et al.	2023	Leyte	Ormoc City	Danao Lake	2021–2022	sampling survey	8	1
Paller et al.	2013	Quezon		Tayabas River	2010	sampling survey	15	6
Visto et al.	2015	Agusan Del Sur	Prosperidad	Bega Watershed	2014	sampling survey	6	1
Roque et al.	2019	Bataan		Bagac River Systems		sampling survey	17	5
Quimpang et al.	2020			Matingao River and Marbel River	2012–2013, 2015	sampling survey	6	2
Macalisang et al.	2023	Romblon	San Agustin	Wetland	2016–2017	sampling survey	31	9
Paller et al.	2011	Laguna		Watershed		sampling survey	16	3
Vedra et al.	2022	Misamis Oriental		Talabaan River System	2021	sampling survey	12	4
Ojao et al.	2021	Surigao del Sur	Tandag	Ihawan Spring Community	2018	sampling survey	23	1
Quimpang et al.	2018	Northwestern Mindanao, Philippines		Lake Duminagat	2013	sampling survey	6	0

studies that may introduce bias into our meta-analysis, ensuring that our findings reflect accurate and unbiased trends in goby species richness relative to fish species richness in Philippine freshwater ecosystems.

Each study was critically assessed based on multiple criteria, including study design, data collection methods. Factors such as whether the study provided sufficient details on sampling protocols and included robust statistical analyses were considered in the quality assessment. Additionally, we evaluated whether the studies adhered to standardized ecological survey methodologies, which is crucial for ensuring comparability across different research works. Studies that scored low in ROBITT's risk assessment were either excluded from the meta-analysis or noted as having potential biases that could influence interpretation. This rigorous assessment process allowed us to refine our dataset, ensuring that our systematic review and meta-analysis were built upon high-quality research, ultimately strengthening the reliability of our conclusions regarding goby biodiversity and its ecological significance in Philippine freshwater habitats. All data were analyzed using JASP Software (Goss-Sampson, 2019).

3. Results

Location of the study: Among the studies included in our systematic review and meta-analysis, the majority were conducted on Luzon Island, with significantly fewer studies focusing on freshwater ecosystems in Mindanao and the Visayas (see Table 1 and Table 2). This geographic disparity highlights a research gap in goby species assessments outside Luzon, where ecological studies on freshwater fish diversity appear to be more concentrated. The scarcity of research in Mindanao and the Visayas suggests their potential underrepresentation in ichthyofaunal studies, possibly resulting in unaddressed critical biodiversity patterns and conservation concerns. Given the unique ecological characteristics of freshwater ecosystems on these islands, further research is necessary to provide a more comprehensive understanding of goby species richness and distribution across the Philippine archipelago.

In terms of habitat type, most studies were conducted in river systems, while only a smaller portion focused on lakes. This trend may be attributed to the fact that riverine environments, particularly those with direct connectivity to marine waters, serve as critical habitats for amphidromous goby species, which require both freshwater and marine environments to complete their life cycles. Rivers also provide more accessible sampling sites for researchers, making them the preferred study areas for ichthyofaunal surveys. In contrast, lake ecosystems, though equally important for fish diversity, are less frequently studied, possibly due to logistical challenges or differences in research priorities. This uneven distribution of studies suggests the need for more focused efforts in assessing goby populations in lake ecosystems to ensure a holistic understanding of their ecological roles and conservation needs.

Goby species richness: Overall, this study documented a total of twenty-nine (29) genera of freshwater gobies from the family *Gobiidae*, highlighting the rich diversity of goby species in Philippine freshwater ecosystems (Fig. 2). Among these, the most prevalent genus recorded was *Glossogobius* sp., which appeared in seventeen studies, indicating its widespread distribution and ecological significance. Additionally, other frequently documented genera included *Sicyopterus* sp., *Redigobius* sp., *Rhinogobius* sp., and *Awaous* sp., which were consistently observed across multiple study sites (Table 2; Fig. 2). The dominance of these genera suggests their adaptability to various freshwater habitats, particularly in riverine systems with direct connectivity to marine environments. Their frequent occurrence across different studies underscores their potential role as ecological indicators and emphasizes the need for further research on their population dynamics, habitat preferences, and conservation status.

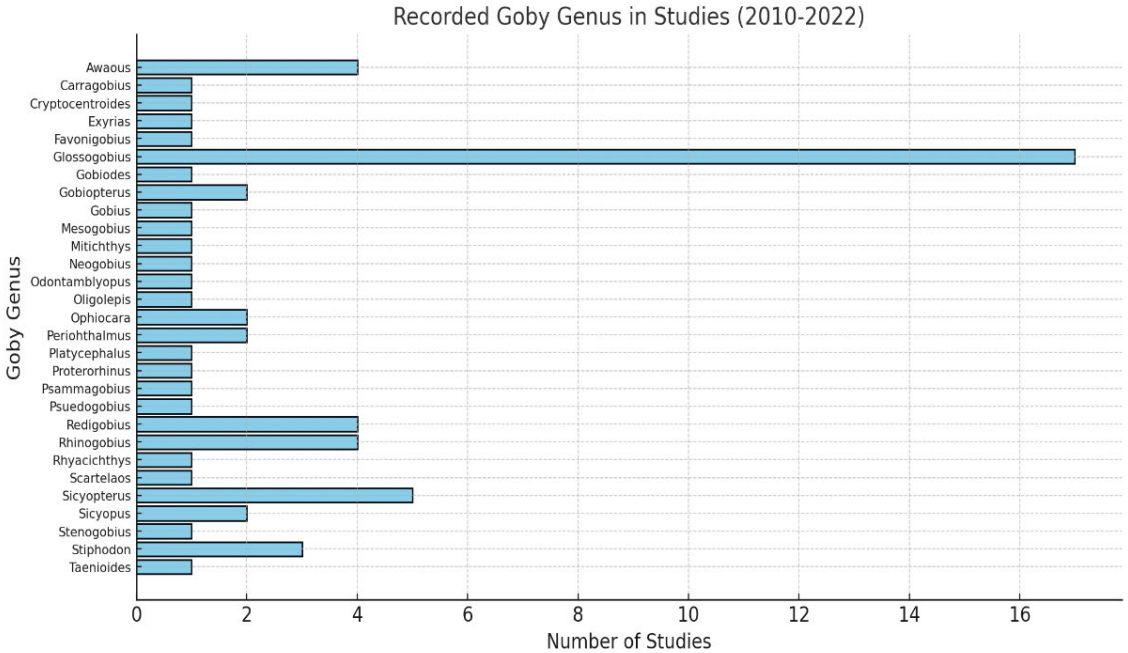

Fig.2. Recorded Goby Genus across studies between 2010 and 2022.

Diversity indices: The diversity indices computed from the analyzed studies reveal considerable variation in goby species richness and distribution across different freshwater ecosystems in the Philippines. H' = 2.657 to 0.19 indicated a wide disparity in species diversity among study sites (Table 3). Higher H' values suggest more evenly distributed and diverse goby communities, whereas lower values reflect dominance by a few species or low overall species richness. This variation may be attributed to differences in habitat conditions, environmental disturbances, or anthropogenic impacts such as pollution, habitat fragmentation, and overfishing. Additionally, variations in sampling effort and methodologies may have also influenced the recorded diversity levels across studies.

Similarly, differences in how uniformly goby species are distributed within the studied freshwater systems (PE = 0.918–0.12). A higher PE Index suggests a more balanced species composition, whereas lower values indicate dominance by certain species, potentially due to ecological competition or environmental stressors. The Simpson's D values ranged from 0.788 to 0.10, further reinforcing the disparity in community structure across the surveyed sites (Table 3). Higher Simpson's D values indicate a more evenly distributed goby community, while lower values suggest the dominance of a few resilient species that outcompete others in specific environments. These findings underscore the complexity of goby assemblages in Philippine freshwater ecosystems and emphasize the importance of conservation efforts to protect habitats that support high species diversity and evenness.

Physicochemical analysis: Out of the 23 studies reviewed, only 11 provided data on key physicochemical parameters, namely dissolved oxygen (DO), pH, and water temperature, which are crucial in assessing the environmental conditions of freshwater ecosystems (Table 4). The recorded DO indicated varying oxygen availability across different study sites (DO = 10.00 mg/L–5.42 mg/L). Higher DO values suggest well-oxygenated waters that support diverse aquatic life, while lower values may indicate potential stressors such as organic pollution or eutrophication. pH levels observed across study sites revealed slightly alkaline to near-neutral conditions (pH = 8.54 to 7.73), which are generally suitable for freshwater gobies and other fish species. Meanwhile, water temperature (31.50°C to 24.22°C) varied significantly, with the highest temperatures recorded in studies such as Mercado (2018) and the lowest in Paller et al. (2013). These temperature fluctuations may influence metabolic rates, breeding behaviors, and species distribution within these freshwater habitats.

Table 3. Goby species richness and biodiversity indices (Shannon H', Evenness-PE, and Simpson D).

No.	References	Species richness	Goby species	H'	PE	D
1	Baysa et al., 2022	24	3	1.63	0.56	0.38
2	Bestre et al., 2018	13	3	1.54	0.45	0.22
3	Corpuz et al., 2015a	37	7	2.68	0.78	0.1
4	Corpuz et al., 2015b	29	8	1.65	0.62	0.33
5	Cuadrado et al., 2019	12	2	1.45	0.52	0.34
6	Cui et al., 2022	12	3	1.38	0.73	0.69
7	Denusta et al., 2020	8	1	1.2	0.58	0.62
8	Garcia, 2010	21	2	2.16	0.79	0.85
9	Gonzalez et al., 2023	44	12	1.7	0.65	0.29
10	Jumawan and Seronay, 2017	16	2	1.9	0.69	0.788
11	Labatos and Briones, 2014	9	1	1.87	0.21	0.18
12	Lubos et al., 2020	8	0	1.9	0.2	0.84
13	Masagca et al., 2022	20	3	2.66	0.89	0.92
14	Mercado, 2018	13	2	1.6	0.72	0.78
15	Ojao et al., 2021	23	1	1.88	0.6	0.42
16	Pacalioga and Peralta, 2016	56	11	2.41	0.733	0.85
17	Pacalioga et al., 2010	55	7	1.71	0.45	0.22
18	Paller et al., 2011	16	3	1.04	0.36	0.4
19	Paller et al., 2013	15	6	1.55	0.74	0.26
20	Paller et al., 2017	10	1	1.56	0.68	0.3
21	Romero et al., 2023	8	1	0.19	0.12	0.08
22	Vedra et al., 2022	12	4	1.21	0.74	0.59
23	Visto et al., 2015	6	1	1.22	0.65	0.65

Note: H' = Shannon Index, PE = Pielou's Evenness Index, D = Simpson Index

Table 4. Physicochemical variables found across 23 articles.

No.	References	Water Temperature	pH	DO
1	Baysa et al., 2022	27.765	7.6	27.765
3	Corpuz et al., 2015a	28.14	7.62	28.14
4	Corpuz et al., 2015b	28.178	7.976	28.178
13	Masagca et al., 2022	28.73	7.91	28.73
14	Mercado, 2018	31.503	7.68	31.503
15	Ojao et al., 2021	28.873	7.367	28.873
17	Pacalioga et al., 2010	24.971	7.699	24.971
18	Paller et al., 2011	26.287	8.539	26.287
19	Paller et al., 2013	24.225	7.315	24.225
20	Paller et al., 2017	27.755	7.825	27.755
23	Visto et al., 2015	25.625	7.375	25.625

Table 4 highlighted site-specific variations in water quality, which can be influenced by factors such as seasonal changes, geographic location, and anthropogenic activities. For instance, studies conducted in urbanized or disturbed environments may exhibit higher temperatures and lower DO levels due to increased runoff, reduced vegetation cover, and pollution. Conversely, sites in relatively undisturbed areas with stable riparian vegetation and minimal human impact tend to maintain more favorable water quality parameters. The variations observed emphasize the need for continued monitoring and assessment of freshwater ecosystems, as physicochemical factors play a vital role in maintaining the health and stability of goby populations. Understanding these environmental parameters can provide valuable insights into habitat suitability, species adaptability, and potential threats to freshwater biodiversity in the Philippines.

Relationship among variables from the pool of publications: A strong positive relationship was observed between goby species richness and overall fish species richness, suggesting that areas with higher fish diversity also tend to support a greater number of goby species ($r = 0.846$, $p < .001$; Table 5). This finding indicates that gobies, as a taxonomic group, thrive in ecologically rich freshwater systems where fish communities are more diverse, possibly due to favorable environmental conditions such as habitat complexity, resource availability, and stable water quality parameters. The significant correlation also suggests that gobies may serve as an important ecological indicator of freshwater biodiversity, with their presence reflecting overall ecosystem health. Furthermore, since gobies exhibit amphidromous life cycles requiring both freshwater and marine environments, the observed correlation may highlight the importance of hydrological connectivity in sustaining both goby and broader fish assemblages.

Apart from the strong goby-fish species richness correlation, additional positive relationships were observed between fish species richness and H', indicating that higher fish species richness contributes to greater species diversity and evenness in freshwater ecosystems ($r = 0.487$, $p = 0.019$). Similarly, PE showed significant correlations with both H' and Simpson D, reinforcing the idea that ecosystems with a balanced distribution of species tend to exhibit greater overall diversity ($r = 0.611$, $p = 0.002$; $r = 0.657$, $p < 0.001$, Table 5). This implies that in areas where fish species are more evenly distributed, goby species also benefit

Table 5. Pearson correlation (r) of variables from the final selection of studies.

Variable		Goby species richness	Fish species richness	Shannon Index	Simpson Index	Evenness Index
1. Goby species richness	Pearson's r	—				
	p-value	—				
2. Fish species richness	Pearson's r	0.846	—			
	p-value	< .001	—			
3. Shannon Index	Pearson's r	0.327	0.487	—		
	p-value	0.128	0.019	—		
4. Simpson Index	Pearson's r	-0.170	-0.098	0.330	—	
	p-value	0.438	0.656	0.124	—	
5. Evenness Index	Pearson's r	0.161	0.118	0.611	0.657	—
	p-value	0.462	0.591	0.002	< .001	—

from reduced interspecific competition and more stable ecological conditions. The presence of strong evenness and diversity relationships further highlights the role of habitat conservation in maintaining the structural integrity of fish communities, as disturbances such as habitat fragmentation and pollution can disrupt these ecological balances.

Conversely, the Simpson D in Table 5 displayed weak and non-significant correlations with goby species richness ($r = -0.170$, $p = 0.438$) and fish species richness ($r = -0.098$, $p = 0.656$), due to the dominance by several species that does not necessarily correspond with higher goby or fish diversity. This may indicate that in some freshwater habitats, a few dominant species outcompete others, leading to lower overall diversity despite relatively high species richness. Such findings highlight the complexity of species interactions in freshwater ecosystems, where diversity indices alone may not fully capture the ecological dynamics at play. Ultimately, these results emphasize the importance of taking into account multiple biodiversity metrics when assessing freshwater fish communities, as well as the need for conservation strategies that maintain both species richness and community evenness to support long-term ecological stability.

Meta-analysis, forest plot, and residual heterogeneity across study sites and publications: The forest plot analysis revealed that all studies included in the meta-analysis are positioned entirely on the positive side of zero, indicating a consistent trend in the relationship between goby species richness and overall fish species richness (Fig. 3). Among the studies, Study 16 exhibited the highest effect size (0.69), suggesting that goby richness in this dataset has a relatively strong association with fish species richness. This may be due to favorable environmental conditions, such as well-preserved freshwater habitats, optimal water quality parameters, or higher habitat complexity, which support diverse goby and fish populations. Conversely, Study 12 recorded the lowest effect size (0.0), indicating little to no measurable relationship between goby richness and overall fish species richness in that study (Fig. 3). This could be attributed to various ecological factors, such as habitat degradation, pollution, or methodological inconsistencies in species sampling and identification.

The combined effect size across all studies falls within the range of a low but statistically significant effect ($g = 0.46$; 0.34–0.57). This suggests that although goby species richness d positively correlates with total fish species richness, this association is not very substantial. Several factors could contribute to this low effect size, including ecological niche differentiation, varying habitat preferences among fish species, or site-specific environmental conditions that influence community structure. Additionally, differences in survey methodologies, seasonal variations, and geographical distribution may also play a role in moderating the observed relationship. Despite the relatively low effect size, the positive direction of the results reinforces the idea that freshwater ecosystems with greater fish diversity tend to support higher goby richness, albeit to varying degrees.

Furthermore, a low heterogeneity index was recorded across publications (Fig. 3), indicating minimal variability among the included studies ($I^2 = 14.74\%$; $H^2 = 1.173$). This suggests that the relationship between goby species richness and fish species richness is consistent across different research locations, with little variation associated with methodological differences or external environmental factors. A low heterogeneity value strengthens the reliability of the meta-analysis findings, implying that outliers or conflicting results from individual studies do not significantly influence the observed trend. However, the relatively low effect size highlights the need for further investigations into additional ecological factors that may influence goby species distribution, such as hydrological connectivity, competition, and habitat fragmentation. Future research should consider a broader range of environmental variables and explore potential interactions that may contribute to variations in goby and fish diversity patterns across different freshwater ecosystems.

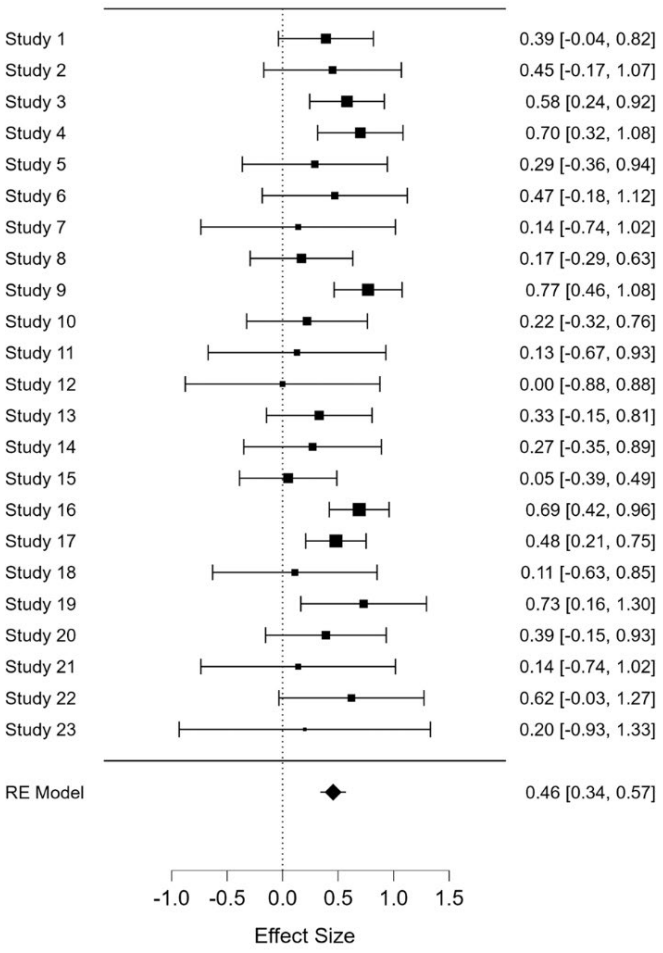

Fig.3. Forest plot.

Table 6. Residual heterogeneity estimates.

	Estimate
τ^2	0.010
τ	0.102
I^2 (%)	14.737
H^2	1.173

The funnel plot in Figure 4 provided a visual assessment of potential publication bias among the studies included in the meta-analysis of freshwater goby species from recent ichthyofaunal surveys in the Philippines (2010–2022). Ideally, in the absence of publication bias, the data points representing individual studies should be symmetrically distributed around the central effect size, forming an inverted funnel shape. This symmetrical pattern indicates that studies with both large and small effect sizes are equally reported, reducing the likelihood of selective publication and ensuring a more balanced representation of available data.

However, the observed funnel plot displays noticeable asymmetry, suggesting a significant deviation from the expected distribution. This pattern demonstrates the potential presence of publication bias, where studies with smaller effect sizes or non-significant results may be underreported or unpublished. Several factors could contribute to this asymmetry, including selective reporting, variations in sampling methodologies, or geographical disparities in research focus. Additionally, differences in study quality, sample sizes, or ecological conditions across study sites may also influence the distribution of effect sizes. Taking into account this deviation, further statistical analyses, such as Egger's regression test, are necessary to quantitatively assess the extent of publication bias and evaluate its potential impact on the overall findings of the meta-analysis.

Publication bias in freshwater goby studies: Egger's regression test for funnel plot yielded a statistically strongly significant result, indicating the presence of publication bias (sei = –2.749, p = 0.006). A p-value below 0.05 suggests that smaller studies with non-significant or negative findings may be underreported or unpublished, leading to an overestimation of the overall effect size in the meta-analysis.

The result of the funnel plot in Figure 4 revealed an asymmetrical pattern among studies' standard error over effect sizes, indicating a strong publication bias. Moreover, the Egger's test further confirmed a publication bias (p = 0.006). The presence of publication bias in this study may stem from multiple factors, including selective reporting of studies with significant findings, variations in survey methodologies, or regional biases in freshwater goby research across the Philippines. Given these findings, sensitivity analyses such as the trim-and-fill method or fail-safe N tests could be explored to adjust for bias and assess the robustness of the meta-analytic conclusions. While publication bias does not invalidate the primary conclusions, it underscores the need for cautious interpretation of the results. Future ichthyofaunal surveys should aim for comprehensive reporting, including non-significant findings, to ensure a more balanced representation of freshwater goby diversity in the region.

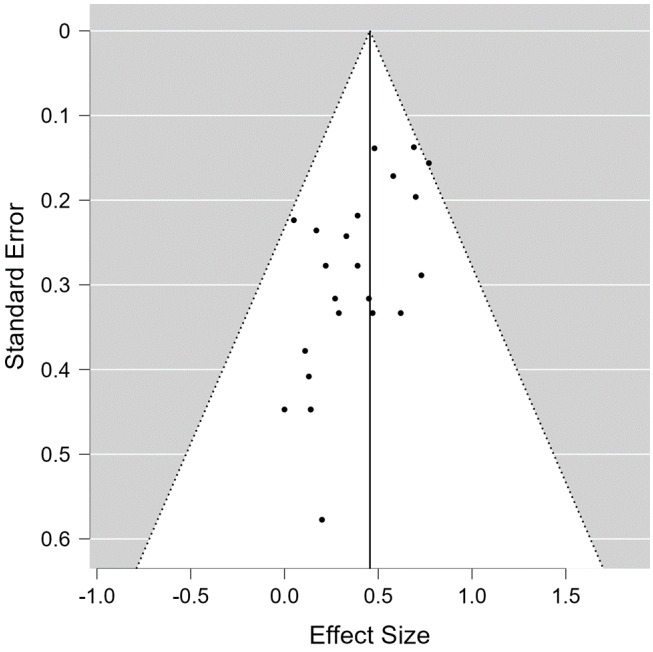

Fig.4. Funnel plot asymmetry.

Table 7. Regression test for funnel plot asymmetry ("Egger's test").

	z	p
sei	–2.749	0.006

4. Discussion

Across 23 studies, Luzon emerges as the predominant locus of research on Philippine freshwater gobies, corroborating earlier evidence that it is the country's most intensively studied freshwater region (Magbanua et al., 2017). This concentration of effort has yielded a comparatively coherent picture of gobiid diversity and assemblage structure in Luzon's riverine systems, but it also risks entrenching a geographic bias in our national understanding of freshwater fish ecology. Although the available is sufficient for robust inferences about Luzon, it also emphasizes the limited generalizability of these insights to the rest of the archipelago.

By contrast, freshwater systems in the Visayas and Mindanao remain poorly studied, creating a significant knowledge gap in goby species distributions, assemblage composition, and biodiversity processes in these regions. The observed disparity mirrors the broader pattern identified by Magbanua et al. (2017) for freshwater ecosystem research in the Philippines, reinforcing the need for spatially balanced sampling. Targeted, stratified ichthyofaunal surveys—designed to capture habitat gradients, hydrological seasonality, and watershedlevel landuse pressures—are therefore essential to develop a comprehensive, archipelagowide baseline.

Taxonomically, the compiled records converge on the prominence of *Glossogobius*, with *Glossogobius* spp. as the most prevalent gobies across studies, which is consistent with the genus's recognition as one of the most speciose gobioid lineages (Agorreta et al., 2013). Comparative biogeographic work supports ongoing species radiation within *Glossogobius* across Papua New Guinea, Sulawesi, Madagascar, and the Philippines (Hoese and Allen, 2009). Within the Philippines, eight

Glossogobius spp. have been documented to date, with *G. aureus* as the most abundant and commercially salient, a pattern aligned with the genus's ecological versatility and capacity to occupy a range of lowland freshwater habitats.

Across studies reporting community metrics, diversity indices (Shannon, Evenness, and Simpson) normally fall within low to medium ranges (Magurran, 2021). This is consistent with theory and empirical patterns, demonstrating that insular tropical rivers typically support lower fish diversity than their continental tropical counterparts (Smith et al., 2003). Insular stream fish assemblages are shaped by dispersal from multiple sources, including adjacent islands, producing species pools constrained by overwater colonization and habitat connectivity (Covich, 2006). Notably, introduced species were recorded in all studies; while their ecological impacts warrant focused assessment, they have—at least numerically—contributed to higher local species counts in some Philippine freshwater systems (Guerrero, 2014).

Physicochemical data from 11 studies indicate that dissolved oxygen, pH, and water temperature generally meet thresholds that were established by the Department of Environment and Natural Resources Administrative Order (DAO) No. 201608 on Water Quality Guidelines and General Effluent Standards. These conditions are broadly suitable for sustaining freshwater fish communities, including gobiids, which often exhibit finescale microhabitat specialization. Nevertheless, maintaining water quality is critical: fluctuations in oxygen dynamics, thermal regimes, and acidity can reshape trophic interactions, alter recruitment, and precipitate shifts in community composition. Sustained, watershedscale monitoring is therefore warranted to detect and mitigate degradation arising from pollution, deforestation, sedimentation, and landuse change under DAO 201608 compliance frameworks.

Correlation analyses reveal a strong positive relationship between goby species richness and overall fish species richness, reinforcing the ecological expectation that in oceanic islands—where diadromous and amphidromous lineages frequently dominate—peripheral freshwater fishes such as Gobiidae are naturally prevalent (Leveque et al., 2008). Concordantly, fish species richness is positively associated with the Shannon Index, which integrates both richness and evenness; as richness rises, Shannon entropy typically increases, provided dominance does not intensify. By contrast, the strong positive correlation between Simpson and Evenness indices, coupled with the absence of a direct richness–Simpson correlation, underscores Simpson's sensitivity to dominance structure rather than to richness per se, highlighting the importance of balanced relative abundances for community stability.

The metaanalysis (Forest Plot) places all studies on the positive side of zero, yielding a combined effect size of 0.46, indicative of a moderate yet statistically meaningful association between goby richness and total fish richness. Low heterogeneity ($I^2 = 14.74\%$) suggests broadly comparable methodologies across studies, with only minor differences in sampling gear, effort, or habitat coverage. Two caveats deserve attention. First, introduced species in total richness may inflate effect sizes by adding taxa independent of native community assembly processes; sensitivity analyses excluding nonnative species would clarify this influence. Second, the funnel plot shows asymmetry, and Egger's test indicates potential publication bias—an unsurprising outcome given the topic's specificity and a literature base that already emphasizes gobiid dominance in Philippine freshwaters (Herre, 1953; Leveque et al., 2008). Addressing these biases will require broader geographic coverage and systematic inclusion of gray literature and null results.

These findings motivate a forward agenda grounded in geographic rebalancing, methodological standardization, and data transparency. Priorities include (i) expanding surveys in the Visayas and Mindanao with stratified designs across watershed types and disturbance gradients; (ii) coupling morphology with molecular barcoding to resolve cryptic *Glossogobius* lineages (cf. Hoese and Allen, 2012); (iii) harmonizing protocols for effort, gear, and index calculation to reduce residual heterogeneity; (iv) conducting sensitivity analyses that partition native versus introduced assemblage components (Guerrero, 2014); and (v) integrating longterm waterquality monitoring within the DAO 201608 framework to link community responses with environmental change (DENRBMB, 2016). Such steps will strengthen inference on gobiid biogeography and community ecology, enhance the robustness of future metaanalyses, and generate the evidence base needed to identify endemism, assess ecosystem health, and design effective, regionappropriate conservation strategies (Herre, 1953; Smith et al., 2003; Leveque et al., 2008; Covich, 2006; Magbanua et al., 2017).

5. Conclusion

Goby diversity in the Philippines, as measured by species richness, remains notably high, with *Glossogobius* sp. emerging as the most prevalent genus across the studies. However, a significant geographical disparity exists in ichthyofaunal surveys, as most studies were conducted in Luzon, while freshwater systems in the Visayas and Mindanao remain underrepresented in published literature. This research gap underscores the need for further exploration in these regions to obtain a more comprehensive picture of goby species distribution and diversity. The diversity index scores from the studies revealed low to medium diversity, which is consistent with the general understanding that tropical insular streams have fewer fish species compared to continental rivers. Additionally, the presence of introduced fish species contributed to an increase in overall biodiversity scores, although their ecological impacts on native goby populations require further investigation. Understanding whether these introduced species compete with, displace, or coexist with native gobies is critical for future conservation and management strategies (Patzner et al., 2011).

The strong positive correlation between goby species richness and total fish species richness suggests that gobies are a dominant and ecologically significant group within Philippine freshwater habitats. Meta-analysis results further supported this finding, with a combined effect size of 0.46, indicating a moderate but notable influence of goby richness on overall fish diversity. This highlights the ecological importance of gobies in structuring freshwater communities, particularly in insular environments where they thrive as peripheral freshwater species. Given their adaptability and prevalence, gobies may serve as reliable indicators of freshwater ecosystem health. However, publication bias, as detected in the funnel plot and Egger's test, suggests that existing studies may not fully capture the diversity and ecological roles of gobies across all freshwater systems in the Philippines. Addressing these gaps through expanded research efforts in understudied regions, along with standardized methodologies, will enhance our understanding of goby diversity and its broader ecological implications.

Taking into account the high publication bias observed in this study, future research studies should expand their focus beyond the Philippines to include goby diversity across Southeast Asian nations. A broader regional approach will provide a more comprehensive understanding of goby distribution patterns, reduce bias, and allow for comparisons between different freshwater ecosystems. Moreover, there is a critical need to increase ichthyofaunal surveys in the Visayas and Mindanao regions, as these areas remain underrepresented in published literature. Expanding research efforts in these regions will not only help address publication bias but also contribute valuable data on goby diversity and freshwater fish assemblages in lesser-studied habitats.

Furthermore, a meta-analysis comparing native fish species richness with introduced fish species richness would be highly beneficial in assessing the ecological impact of non-native species on freshwater biodiversity. This analysis could determine whether introduced species significantly influence overall species richness and whether their presence alters native fish communities, including goby populations. Understanding these effects is crucial for developing informed conservation and management strategies aimed at preserving native biodiversity while mitigating the potential ecological disruptions caused by introduced species.

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Conflict of Interest

The authors declare no potential conflict of interest regarding the publication of this work. In addition, the ethical issues including plagiarism, informed consent, misconduct, data fabrication and, or falsification, double publication and, or submission, and redundancy have been completely witnessed by the authors.

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Original Article

LIMNOLOGY FRESHWATER BIOLOGY

Assessment of water quality and zooplankton community structure in the Gambhiri River (Chittorgarh, Rajasthan, India)

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ABSTRACT. This study examines water quality parameters and zooplankton community structure in the Gambhiri River, Chittorgarh district of Rajasthan, India, to assess the ecological health and trophic state of this vital freshwater ecosystem. Seasonal sampling was conducted from January to December 2023 at six sampling sites to observe spatial and temporal variations in physicochemical parameters and zooplankton communities. Key water quality parameters, including water temperature, pH, total dissolved solids, turbidity, electrical conductivity, total hardness, chloride, alkalinity, dissolved oxygen, and biological oxygen demand, were measured using standard analytical techniques. Zooplankton samples were collected with a plankton net, preserved, and identified to the lowest possible taxonomic level, following standard keys. In the study period, 65 species of zooplankton were analyzed, of which 26 species of Rotifera, 25 species of Cladocera, 8 species of Copepoda, and 6 species of Ostracoda were recorded. Cladocera appeared as the dominant group of zooplankton with a higher density (38.67%), followed by Rotifera (35.72%), Copepoda (18.57%), and Ostracoda (7.03%). The season-wise zooplankton analysis revealed that Cladocera and Rotifera were the dominant groups across all seasons, while Copepoda and Ostracoda contributed comparatively less to the total density. Cladocera showed higher density than Rotifera during summer and post-monsoon seasons, whereas during monsoon and winter, Rotifera slightly dominated over Cladocera. Copepoda consistently remained the third dominant group in all seasons, while Ostracoda recorded the lowest density throughout the study period. The study highlights the importance of zooplankton as sensitive bioindicators for evaluating the health of freshwater ecosystems and recommends routine monitoring and pollution control measures to preserve the ecological integrity of this crucial water resource in Rajasthan's semi-arid region.

Keywords: Gambhiri River, zooplankton diversity, physicochemical parameters, seasonal variation

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1. Introduction

Water is the essential factor for the emergence, development, and protection of life. Rivers are crucial for the progress of any community or country, fulfilling needs in various sectors, including domestic, agricultural, aquatic, industrial, and hydroelectric. Freshwater ecosystems, particularly rivers, are among the most vital natural resources on Earth, providing essential ecosystem services, including water supply, nutrient cycling, and support for aquatic biodiversity (Dudgeon et al., 2006). Despite covering less than 1% of the Earth's surface, freshwater ecosystems harbor approximately 10% of all known species, making them biodiversity hotspots of global significance (Strayer and Dudgeon, 2010). In the Indian subcontinent, rivers have long played a central role in shaping human civilization by sustaining large populations and acting as hubs of economic activity as well as cultural and traditional practices (Gopal and Chauhan, 2006). However, rapid urbanization, industrialization, and agricultural intensification have led to severe deterioration of water quality in rivers across the country, with developing regions facing particularly acute challenges (Vörösmarty et al., 2010; Singh et al., 2004).

The diversity and seasonal variation studies of zooplankton are of great importance in water bodies because they are the intermediate link between phyto-

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plankton and fish. It has been reported that zooplankton are predators of phytoplankton and are very sensitive to changes in environmental conditions (Xiong et al., 2016). Zooplankton are an integral component of the food chain; they occur in all waterbodies and are important to nutrient recycling and regeneration of primary production. According to Dudgeon et al. (2006), factors such as anthropogenic activities and climate change are obstructing the stability of most freshwater ecosystems, thereby causing a loss in the diversity of zooplankton (Alahuhta et al., 2019). A lot of research has been carried out on the diversity of various types of plankton, many of which are associated with far-ranging ecological and economic impacts (Anyanwu et al., 2023).

Plankton thrive in diverse environmental conditions but are highly responsive to changes in the physicochemical properties of their habitats. Research indicates that factors such as dissolved oxygen, temperature, salinity, and other physicochemical variables influence various zooplankton species (Anyanwu et al., 2023).

The ecological integrity of riverine systems depends on complex interactions between physical, chemical, and biological components. Among these, zooplankton communities form a crucial link in aquatic food webs, serving as primary consumers that convert phytoplankton and detrital matter into biomass available to higher trophic levels, including fish (Dutta et al., 2025). Beyond their ecological role, zooplankton have emerged as effective bioindicators of water quality due to their sensitivity to environmental changes, short generation times, and differential species-specific tolerances to pollution (Jeppesen et al., 2011; Gannon and Stemberger, 1978). Studies across Indian freshwater systems demonstrated strong correlations between zooplankton diversity metrics and physicochemical parameters such as dissolved oxygen, nutrients, conductivity, and temperature (Roychoudhury et al., 2013; Thakur et al., 2013).

Like many rivers in rapidly developing regions of India, the Gambhiri faces multiple anthropogenic pressures, including discharge of untreated or partially treated sewage from Chittorgarh city and smaller towns, agricultural runoff containing fertilizer and pesticide residues, potential small industrial effluents, water abstraction for irrigation and domestic use, and sedimentation from land use changes (Rodell et al., 2009). In the present study, we attempted to assess water quality and investigate the species composition, distribution, and seasonal variation of zooplankton at the Gambhiri River, Chittorgarh District, Rajasthan.

2. Materials and methods

2.1. Location of the study area

Chittorgarh is an important city of Rajasthan in western India. The city lies between the Berach and Gambhiri rivers and is situated at an average elevation of approximately 394 m (1292 ft) above mean sea level. It occupies a location in the southern region of Rajasthan and the northwestern part of India. Chittorgarh is situated adjacent to a prominent hill, on which the historic Chittorgarh Fort is located, near the Gambhiri River. Geographically, the area extends between latitudes 23°32′ and 25°13′N and longitudes 74°12′ and 75°49′E, falling within the southeastern part of Rajasthan (Fig. 1) (Loth and Panchal, 2023).

2.2. Collection of water samples

Water samples were collected from January to December 2023 from the effluent discharge points into the Gambhiri River in Chittorgarh district of Rajasthan, India. Sampling was carried out at six designated sites along the river. The samples were gathered in 1-liter plastic bottles that had been thoroughly pre-cleaned and rinsed, adhering to standard safety and contamination prevention protocols.

Fig.1. Map showing sampling sites at the Gambhiri River.

2.3. Analysis of water samples

The physicochemical parameters of water were analyzed following standard procedures recommended by the Indian Standards (IS) and the American Public Health Association (APHA). Water temperature was recorded using a mercury thermometer (℃) (IS 3025 pt-9, 1984). The hydrogen ion concentration (pH) was measured in situ with a calibrated digital pH meter in accordance with IS 3025 pt-11 (1983). Total dissolved solids (TDS), turbidity, and electrical conductivity (EC) were determined using standard instruments as prescribed under IS 3025 guidelines. Total hardness was estimated by the EDTA titrimetric method, employing Eriochrome Black T as an indicator (IS 3025 pt-21, 2009). Chloride content was analyzed through argentometric titration using a standard silver nitrate solution with potassium chromate as an indicator, following IS 3025 pt-32 (1988) procedures. Alkalinity was determined by titration with standard sulfuric acid using phenolphthalein as an indicator (IS 3025 pt-23, 1986). Nitrate concentration was measured by the UV spectrophotometric method (APHA 4500-NO_3^-, 1992), with absorbance recorded at 220 nm and correction applied at 275 nm. Dissolved oxygen (DO) was estimated by Winkler's iodometric method in accordance with IS 3025 pt-38 (1989). Biochemical oxygen demand (BOD) was calculated from the difference in DO values measured initially and after a five-day incubation period, following standard IS 3025 pt-44 (1993) protocols. Phosphorus was analyzed using a colorimetric technique based on the formation of a molybdate complex, as described in APHA Method 4500-P (1992). Sulphate concentration was determined by the turbidimetric method, wherein sulphate was precipitated as barium sulfate and measured at 420 nm using a spectrophotometer, in accordance with APHA Method 4500-SO_4^{2-} (1992).

2.4. Collection and identification of zooplankton

For the zooplankton study, samples were collected from surface waters. Quantitative samples were obtained by towing a Hensen standard plankton net at a constant speed. The net was made of nylon with a mesh size of 50 μm. Immediately after collection, plankton samples were transferred to a polyethylene bottle (100 mL) and preserved in 70% ethyl alcohol for further analysis. For quantitative estimation, 50 L of surface water were filtered through a small plankton net made of nylon with a mesh size of 50 μm. The concentrated samples were thoroughly mixed, and 10 mL was withdrawn for counting. Zooplankton enumeration was carried out using a counting chamber under a compound microscope (Olympus CH20iBIMF). Zooplankton abundance was expressed as the number of individuals per liter of water. Zooplankton taxa were identified using standard identification keys, reference books, and relevant monographs (Edmondson, 1992; Battish, 1992; Tonapi, 1980; Khan, 2003; Sharma et al., 2012; Horne et al., 2019).

2.5. Statistical analysis

The statistical methods to analyze data were as follows: mean, standard deviation, one-way ANOVA, two-way ANOVA, and Karl Pearsons's Coefficient of Correlation. The R software was used for data analysis (https://www.r-project.org/about.html).

3. Results and discussion

Table 1 shows season-wise physicochemical parameters of water samples collected. Most of the test results revealed significant differences in water quality parameters across seasons. Seasonal variation in water temperature regarding each sampling site demonstrated a highly significant difference in electrical conductivity, hardness, chloride, alkalinity, nitrate, and sulfate. A significant difference was found for TDS and turbidity. At the same time, a non-significant difference was found for pH, dissolved oxygen, BOD, and phosphorus.

In river ecology, water temperature is the most critical environmental parameter influencing aquatic organisms as well as the biological and chemical processes in water. Natural variations in water temperature are commonly governed by several environmental factors, including seasonal changes, water depth, wave activity, latitude, solar radiation, wind patterns, and heat exchange in near-shore zones (Saad et al., 2017). Statistical analysis revealed a highly significant variation in water temperature ($F = 128.73$; $p < 0.001$). As shown in Table 1, surface water temperature in the Gambhiri River varied from 21.15 ± 1.07 ℃ to 30.50 ± 1.07 ℃ during different seasons of the study period.

The ecological performance of aquatic environments is strongly influenced by pH, as it regulates metabolic activity and the availability of nutrients. In the present investigation, river water pH showed moderate seasonal variation, which can be attributed to the combined influence of domestic sewage, surface runoff, and occasional industrial effluent inputs. Throughout the study period, pH values remained within a narrow range of 7.71 ± 0.40 to 7.94 ± 0.51 (Table 1). The lowest pH values were recorded during winter, whereas higher values were observed in the post-monsoon period. The increase in pH during post-monsoon may be linked to intensified photosynthetic activity, resulting in greater assimilation of dissolved CO_2 and a subsequent rise in pH (Islam et al., 2025). Comparable seasonal patterns were also reported by Islam et al. (2025) for the Kangsabati River, West Medinipur, and Khairy et al. (2015) for the Mediterranean Lakes in Egypt.

Total dissolved solids (TDS) consist primarily of inorganic ions, including calcium, magnesium, sodium, potassium, bicarbonate, chloride, and sulphate, which accumulate in aquatic systems through natural and anthropogenic processes (Adimalla et al., 2018). The overall concentration of dissolved solids serves as a general indicator of water suitability for various purposes. In the present study, total dissolved solids (TDS) ranged from 408.67 ± 43.78 to 510.83 ± 48.83 mg/L, with the lowest concentrations recorded during winter and the

Table 1. Season-wise physicochemical parameter

Parameter	Season				Sig.
	Winter	Summer	Monsoon	Post-Monsoon	
Water Temp. (°C)	27.62 ± 0.57	30.50 ± 1.07	29.07 ± 0.75	21.15 ± 1.07	F = 128.73 p = 0.000 ***
pH	7.71 ± 0.40	7.81 ± 0.57	7.77 ± 0.64	7.94 ± 0.51	F = 0.21 p = 0.889 NS
TDS (mg/L)	408.67 ± 43.78	510.83 ± 48.83	485.67 ± 36.48	421.50 ± 111.39	F = 3.24 p = 0.044 *
Turbidity (NTU)	4.12 ± 2.43	12.83 ± 8.28	5.43 ± 4.20	2.87 ± 2.41	F = 4.90 p = 0.010 *
EC (μS cm^{-1})	691.33 ± 125.04	995.17 ± 84.53	933.50 ± 109.66	840.67 ± 86.35	F = 9.92 p = 0.000 ***
Hardness (mg/L)	251.67 ± 23.17	175.00 ± 36.74	156.67 ± 42.74	173.33 ± 24.22	F = 10.07 p = 0.000 ***
Chloride (mg/L)	102.80 ± 14.8200	48.43 ± 10.67	60.75 ± 10.55	70.57 ± 11.48	F = 22.55 p = 0.000 ***
Alkalinity (mg/L)	281.02 ± 25.04	148.33 ± 38.69	153.33 ± 47.61	195.00 ± 48.89	F = 13.35 p = 0.000 ***
Nitrate (mg/L)	19.18 ± 6.82	13.33 ± 2.97	6.54 ± 4.80	6.30 ± 2.96	F = 10.46 p = 0.000 ***
DO (mg/L)	6.47 ± 2.19	4.65 ± 1.15	7.10 ± 0.85	6.68 ± 2.02	F = 2.57 p = 0.083 NS
BOD (mg/L)	4.12 ± 2.22	4.92 ± 4.40	4.65 ± 1.22	6.28 ± 2.97	F = 0.59 p = 0.628 NS
Phosphorus (mg/L)	0.17 ± 0.17	0.19 ± 0.01	0.25 ± 0.06	0.14 ± 0.10	F = 1.20 p = 0.334 NS
Sulphate (mg/L)	28.19 ± 4.58	33.74 ± 1.65	39.99 ± 3.49	47.64 ± 3.91	F = 32.82 p = 0.000 ***

Note: NS = $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

highest during summer. A comparable seasonal result in TDS was also reported by Chauhan et al. (2020).

Turbidity showed a statistically significant seasonal variation ($F = 4.90$; $p = 0.010$) (Table 1), with maximum values recorded during summer (12.83 ± 8.28 NTU). A similar seasonal trend in turbidity was also reported by Chauhan et al. (2020). Elevated turbidity during this period is likely associated with increased runoff and a higher sediment load. Turbidity showed a positive relationship with water temperature ($r = 0.468$; $p < 0.05$) and strong correlations with TDS ($r = 0.658$; $p < 0.001$) and electrical conductivity ($r = 0.632$; $p < 0.001$), suggesting a concurrent rise in suspended particles and dissolved constituents, primarily driven by runoff and erosion processes (Table 2).

Water temperature, along with the concentration and mobility of dissolved ions, determines electrical conductivity (EC). The World Health Organization recommends an upper limit of 1500 μS cm^{-1} for EC in drinking water (WHO, 2017). In the present study, EC values remained within the permissible range, varying from 691.33 ± 125.04 to 995.17 ± 84.53 μS cm^{-1} (Table 1). Similar EC values were reported by Reddy et al. (2025). A strong positive relationship was observed between EC and total dissolved solids ($r = 0.772$; $p < 0.001$) (Table 2), indicating that EC effectively reflects the overall ionic composition of the river water.

Seasonal variation in total hardness was evident, with values ranging from 156.67 ± 42.74 mg/L during the monsoon to 251.67 ± 23.17 mg/L in winter

Table 2. Intercorrelation between physicochemical parameters

	Water temp.	pH	TDS	Turbidity	EC	Hardness	chloride	Alkalinity	Nitrate	DO	BOD	Phosphorus
pH	-0.076 NS											
TDS	0.382 NS	0.281 NS										
Turbidity	0.468 *	0.008 NS	0.658 ***									
EC	0.336 NS	0.275 NS	0.772 ***	0.632 ***								
Hardness	0.049 NS	-0.096 NS	0.036 NS	0.247 NS	-0.235 NS							
chloride	-0.212 NS	0.037 NS	-0.206 NS	-0.213 NS	-0.466 *	0.774 ***						
Alkalinity	-0.187 NS	0.374 NS	-0.230 NS	-0.199 NS	-0.412 *	0.660 ***	0.817 ***					
Nitrate	0.348 NS	-0.049 NS	0.092 NS	0.300 NS	-0.003 NS	0.756 ***	0.544 **	0.590 **				
DO	-0.200 NS	-0.131 NS	-0.616 **	-0.602 **	-0.476 *	-0.196 NS	0.085 NS	-0.098 NS	-0.466 *			
BOD	-0.168 NS	0.479 *	0.576 **	0.256 NS	0.386 NS	0.110 NS	0.161 NS	0.197 NS	0.097 NS	-0.518 **		
Phosphorus	0.232 NS	0.204 NS	0.387 NS	0.159 NS	0.439 *	-0.037 NS	0.039 NS	-0.013 NS	0.202 NS	-0.220 NS	0.021 NS	
Sulphate	-0.639 ***	0.153 NS	0.060 NS	-0.248 NS	0.282 NS	-0.503 *	-0.230 NS	-0.323 NS	-0.637 ***	0.139 NS	0.244 NS	0.193 NS

Note: NS = $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

(Table 1). Total hardness exhibited significant positive correlations with chloride ($r = 0.774$; $p < 0.001$) and alkalinity ($r = 0.660$; $p < 0.001$), suggesting that these parameters together represent the mineral richness of the water (Table 2).

Chloride concentrations showed a substantial seasonal decline, decreasing from 102.80 ± 14.82 mg/L in winter to 48.43 ± 10.67 mg/L in summer. This variation was statistically significant ($F = 22.55$; $p < 0.001$) and likely reflects seasonal changes in anthropogenic inputs and natural dilution processes (Table 1).

Alkalinity exhibited significant seasonal differences ($F = 13.35$; $p < 0.001$), with the highest values observed in winter (281.02 ± 25.04 mg/L). This variation may be attributed to changes in carbonate and bicarbonate concentrations, influenced by biological activity and runoff. Alkalinity of the Gambhiri River also showed a positive correlation with hardness and chloride (Table 2).

Nitrate concentrations were significantly higher in winter (19.18 ± 6.82 mg/L) compared to monsoon and post-monsoon periods ($F = 10.46$; $p < 0.001$), suggesting enhanced inputs from agricultural runoff or reduced dilution during comparatively dry conditions. Variations in nitrogen levels are often linked to changes in dissolved oxygen, reflecting microbial activity associated with nutrient-rich inputs from domestic sewage, industrial effluents, and agricultural waste. Elsayed et al. (2019) reported similar observations. Nitrate exhibited strong positive correlations with total hardness ($r = 0.756$; $p < 0.001$), chloride ($r = 0.544$; $p < 0.01$), and alkalinity ($r = 0.590$; $p < 0.01$), indicating that nutrient enrichment may be associated with increased mineral and ionic loads (Table 2).

Among the physicochemical parameters analyzed, dissolved oxygen (DO) displayed considerable seasonal fluctuation (Table 1). DO concentrations in the Gambhiri River ranged from 4.65 ± 1.15 mg/L during summer to 7.10 ± 0.85 mg/L in the monsoon season. Statistical analysis revealed negative correlations between DO and other water parameters, such as water temperature, pH, total hardness, and alkalinity (Table 2). A similar trend was also reported by Muthukumaravel et al. (2025). Reduced dissolved oxygen levels can adversely affect aquatic organisms, as oxygen availability is critical for sustaining aquatic life. Higher DO values during cooler periods may be attributed to lower temperatures and increased vegetation growth, as cooler water holds more dissolved oxygen than warmer water (Sherif et al., 2018). Additionally, DO showed negative correlations with TDS ($r = -0.616$; $p < 0.01$), turbidity ($r = -0.602$;

$p < 0.01$), electrical conductivity ($r = -0.476$; $p < 0.05$), and nitrate ($r = -0.466$; $p < 0.05$) (Table 2), suggesting that elevated levels of dissolved solids and nutrients can reduce oxygen availability, thereby impacting aquatic ecosystem health.

Biochemical oxygen demand (BOD) represents the quantity of dissolved oxygen, which microorganisms utilize during the decomposition of organic matter in aquatic systems. In the present study, BOD values in the river water ranged from 4.12 ± 2.22 mg/L during winter to 6.28 ± 2.97 mg/L in the post-monsoon season (Table 1). Comparable trends were also reported in previos studies. The observed BOD levels indicate favorable conditions for fish breeding, as they lie close to the optimum range recommended for fish growth (Bhatnagar and Devi, 2013). BOD exhibited positive correlations with pH ($r = 0.479$; $p < 0.05$) and total dissolved solids (TDS) ($r = 0.576$; $p < 0.01$), suggesting a close relationship between organic matter decomposition and water chemistry (Table 2).

Phosphorus plays a vital role in cellular metabolism and enzyme synthesis, commonly occurring in aquatic systems in various phosphate forms derived from both natural and anthropogenic sources. In the present investigation, phosphorus concentrations ranged from 0.14 ± 0.10 mg/L during the post-monsoon season to 0.25 ± 0.06 mg/L in the monsoon period (Table 1). No statistically significant seasonal variation in phosphorus levels was observed ($p > 0.05$). Elevated concentrations at certain sites may be associated with industrial effluent discharge, whereas lower values may result from increased planktonic uptake, leading to nutrient depletion in the water column (Lawson, 2011).

Sulphate concentrations in the Gambhiri River varied from 28.19 ± 4.58 mg/L in winter to 47.64 ± 3.91 mg/L during the post-monsoon season. Similar seasonal variation reported by Singh et al. (2025) for the River Ganga, India. Statistical analysis revealed a significant increase in sulphate levels from winter to post-monsoon ($F = 32.82$, $p < 0.001$), which may be attributed to enhanced oxidation of sulphur-containing compounds and increased anthropogenic inputs during later seasons. Sulphate exhibited strong negative correlations with water temperature ($r = -0.639$, $p < 0.001$) and nitrate ($r = -0.637$, $p < 0.001$) (Table 2), indicating an inverse relationship with thermal conditions and nutrient dynamics.

The zooplankton community in the study area was classified into four major groups: Cladocera, Copepoda, Ostracoda, and Rotifera, accounting for 38.67%, 18.57%, 7.03%, and 35.72% of the total abundance, respectively (Fig. 2, 3). The seasonal variation in zooplankton density across all six sampling sites (Table 3) revealed marked fluctuations among different seasons and groups. The highest total zooplankton density was recorded during summer (3381 ± 24.71 ind./L), followed by winter (1501 ± 11.24 ind./L), monsoon (1192 ± 9.28 ind./L), while the lowest density was observed during the post-monsoon season (1109 ± 11.19 ind./L). Group-wise analysis indicated that Cladocera was the most dominant group (2778 ± 17.77 ind./L), followed by Rotifera (2566 ± 16.42 ind./L), Copepoda (1334 ± 36.28 ind./L), and Ostracoda (505 ± 15.39 ind./L), which showed the least contribution. All zooplankton groups exhibited peak densities during summer, with Cladocera (1345 ± 13.08 ind./L) and Rotifera (1111 ± 16.56 ind./L) being particularly abundant, whereas comparatively lower densities of all groups were observed during the post-monsoon season. During the monsoon season, Cladocera (38.59%) and Rotifera (37.84%) were the dominant groups, contributing almost equally to the total density, while Ostracoda showed the least contribution (5.12%). A similar trend was observed in the post-monsoon season, where Rotifera (37.87%) and Cladocera (35.62%) remained dominant, with a slight increase in Ostracoda (8.39%). In summer, all zooplankton groups showed a marked increase in density, with Cladocera (39.78%) maintaining dominance, followed by Copepoda (20.11%), Rotifera (32.86%), and Ostracoda (7.25%). The winter

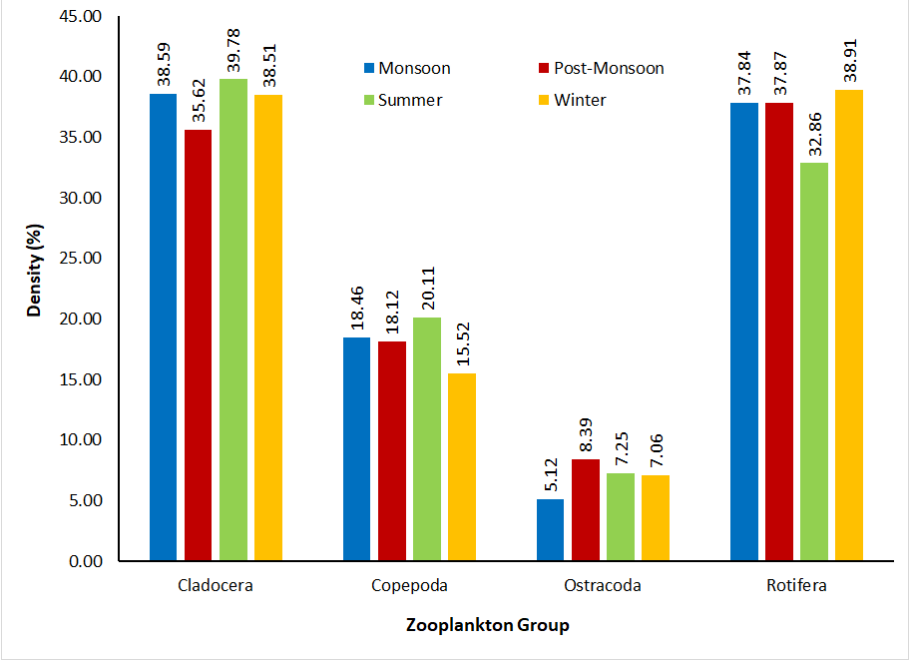

Fig.2. Seasonal and groupwise zooplankton percentage density.

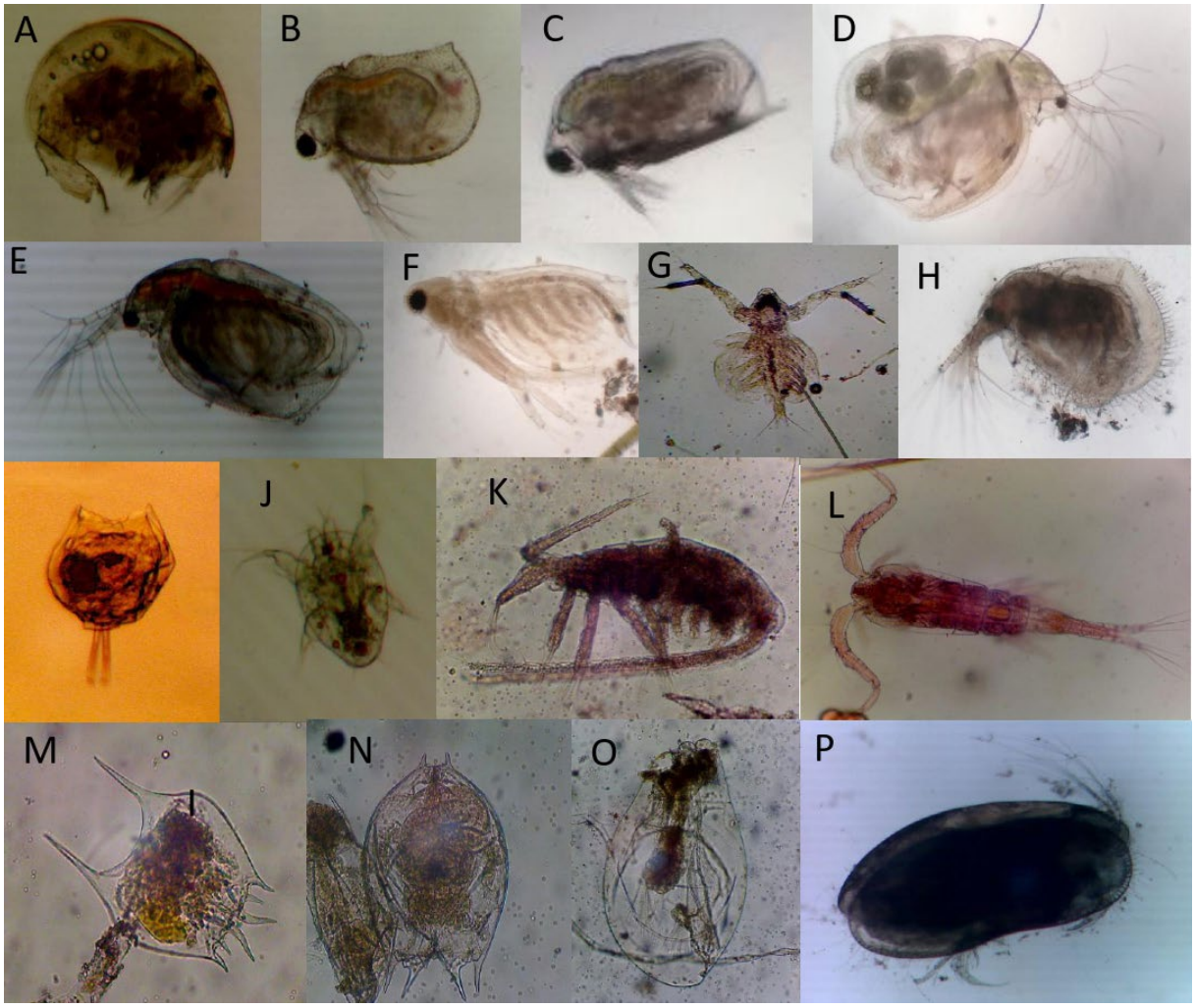

Fig.3. Examples of common zooplankton species collected during the study period: (A) *Chydorus ovalis*, (B) *Ceriodaphnia laticaudata*, (C) *Scapholeberis kingi*, (D) *Simocephalus serrulatus*, (E) *Simocephalus vetulus*, (F) *Diaphanosoma sarsi*, (G) *Diaphanosoma brachyurum*, (H) *Ilyocryptus spinifer*, (I) *Lecane leontina*, (J) *Nauplius*, (K) *Sinodiaptomus indicus*, (L) *Thermocyclops hyalinus*, (M) *Brachionus quadridentata*, (N) *Brachionus elevatus*, (O) *Asplanchna brightwelli*, and (P) *Stenocypris major*.

season exhibited a balanced distribution, with Rotifera (38.91%) slightly dominating over Cladocera (38.51%), while Copepoda (15.52%) and Ostracoda (7.06%) contributed comparatively less (Fig. 2). Elevated zooplankton species diversity during the summer season has also been documented in other freshwater ecosystems. Comparable observations were also recorded by Muthukumaravel et al. (2025) in Chellikurichi Lake, Thanjavur District, Tamil Nadu, India

To compare the mean densities of different groups and in different seasons, analysis of variance tests were conducted. An interaction test between two factors was also conducted. The test results show a highly significant difference in the mean densities of zooplankton species in different seasons ($F = 27.03$, $p < 0.001$). The mean densities differed significantly among groups, indicating a highly significant variation ($F = 20.41$, $p < 0.001$). The test results also indicated that the interaction between season and group was significant ($F = 1.97$, $p < 0.05$) (Table 4). It can be observed that the mean density of Cladocera and Rotifera were the dominant zooplankton groups throughout all seasons, whereas Copepoda and Ostracoda contributed comparatively less to the overall density. Cladocera exhibited higher densities than Rotifera during the summer and post-monsoon seasons, while Rotifera slightly dominated during the monsoon and winter periods. Copepoda consistently ranked as the third most abundant group across all seasons, whereas Ostracoda recorded the lowest density throughout the study period (Table 3).

Table 3. Season and groupwise zooplankton density at all six sites (lndividual per L)

Season	Cladocera	Copepoda	Ostracoda	Rotifera	Total
Monsoon	460 ± 6.26	220 ± 13.85	61 ± 4.92	451 ± 8.96	**1192 ± 9.28**
Post-Monsoon	395 ± 8.09	201 ± 16.77	93 ± 9.81	420 ± 11.66	**1109 ± 11.19**
Summer	1345 ± 13.08	680 ± 46.16	245 ± 16.99	1111 ± 16.56	**3381 ± 24.71**
Winter	578 ± 7.62	233 ± 18.89	106 ± 4.18	584 ± 12.05	**1501 ± 11.24**
Total	**2778 ± 17.77**	**1334 ± 36.28**	**505 ± 15.39**	**2566 ± 16.42**	**7183 ± 20.94**

Table 4. Density Comparison of different zooplankton groups

Variable	SSR	df	MSR	Sig.
Season	205.56	3	68.52	F = 27.03; p = 0.000***
Group	155.24	3	51.75	F = 20.41; p = 0.000***
Interaction	44.99	9	5.00	F = 1.97; p = 0.039*
Residual	3731.33	1472	2.53	

Note: NS = p > 0.05; * = p < 0.05; ** = p < 0.01; *** = p < 0.001

The results indicate that, among the 65 identified zooplankton species, the community is diverse and well-structured, with a few species showing higher mean densities. *Nauplii* and *Thermocyclops hyalinus* (Rehberg, 1880) were the most dominant, followed by rotifers such as *Keratella tropica* (Apstein, 1907), *Brachionus falcatus* (Zacharias, 1898), and *Lecane leontina* (Turner, 1892). Other species, including *Ceriodaphnia pulchella* (Sars, 1862), *Brachionus elevatus* (Michaloudi et al., 2018), and *Asplanchna brightwelli* (Gosse, 1850), also contributed significantly to the overall community composition. Moderate densities were observed in such species as *Daphnia magna* (Straus, 1820), *Eucyclops elegans* (Herrick, 1884), and *Ilyocryptus spinifer* (Herrick, 1882), indicating balanced distribution. In contrast, a few species, such as *Testudinella* sp., *Philodina citrina* (Ehrenberg, 1832), and *Testudinella patina* (Hermann, 1783) showed very low densities (Table 5). Overall, the findings suggest a highly diverse zooplankton assemblage characterized by the dominance of a few species and the presence of many others in moderate to low proportions.

Table 5. List of zooplankton species recorded and percentage in the Gambhiri River during the study period

Zooplankton species	Density %	Zooplankton species	Density %
Alona guttata (Sars, 1862)	1.60	*Hexarthra mira* (Hudson, 1871)	1.04
Alona quadranhgularis (O.F. Muller, 1785)	1.59	*Ilyocryptus spinifer*	1.68
Asplanchna brightwelli	1.28	*Indialona Ganpati* (Petkovski, 1966)	1.49
Asplanchna priodonta (Gosse, 1850)	1.21	*Keratella* sp.	1.99
Bosmina longirostris (O.F. Muller, 1785)	1.67	*Keratella tropica*	2.12
Bosminopsis deitersi (Richard, 1895)	1.66	*Keratella valga* (Ehrenberg, 1834)	0.78
Brachionus calyciflorus (pallas, 1766)	1.64	*Lecane leontina*	2.59
Brachionus caudatus (Barrois & Daday, 1894)	1.48	*Lecane luna* (O.F. Muller, 1776)	1.24
Brachionus diversicornis (Daday, 1883)	2.23	*Lecane papuana* (Murray, 1913)	1.02
Brachionus elevatus	2.26	*Lecane ungulata* (Gosse, 1887)	1.10
Brachionus falcatus	2.49	*Macrothrix laticornis* (Jurine, 1820)	1.46
Brachionus forficula (Wierzejski, 1891)	1.88	*Macrothrix rosea* (Jurine, 1820)	1.07
Brachionus havanaensis (Rousselet, 1911)	1.85	*Mesocyclops leuckarti* (Claus, 1857)	1.11
Brachionus quadridentatus (Hermann, 1783)	1.34	*Mesocyclops* sp.	1.80
Ceriodaphnia laticaudata (P. E. Muller, 1867)	1.80	*Moina* sp.	1.85
Ceriodaphnia pulchella	1.85	*Monostyla bulla* (Gosse, 1851)	1.32
Ceriodaphnia reticulata (Jurine, 1820)	1.68	*Nauplii*	3.83
Ceriodaphnia rigaudi (Richard, 1894)	1.52	*Paracyclops affinis* (Sars, 1873)	1.42
Chydorus ovalis (Kurz, 1875)	1.14	*Philodina citrina*	0.57
Chydorus sphaericus (O.F. Muller, 1785)	1.56	*Philodina megalotrocha* (Ehrenberg, 1832)	0.65
Cyprinotus cassidula (Smith & Chang, 2020)	0.88	*Pleuroxus aduncus* (Jurine, 1820)	1.25
Cypris sp.	0.95	*Scapholeberis kingi* (Sars, 1888)	1.38
Daphnia ambigua (Scourfield, 1947)	1.42	*Scapholeberis mucronate* (O.F. Muller, 1785)	1.77
Daphnia magna	1.24	*Simocephalus serrulatus* (Koch, 1841)	0.93
Daphnia pulex (Leydig, 1860)	1.00	*Simocephalus vetulus* (O.F. Müller, 1776)	2.80
Diaphonosoma brachyurum (Lieven, 1848)	1.98	*Sinodiaptomus indicus* (Kiefer, 1936)	1.63
Diaphonosoma sarsi (Richard, 1894)	1.28	*Stenocypris major* (Baird, 1859	1.38
Eucyclops elegans	1.88	*Strandesia* sp.	0.85
Eucypris sp.	0.97	*Testudinella patina*	0.63
Filinia longiseta (Ehrenberg, 1834)	0.88	*Testudinella* sp.	0.24
Filinia opoliensis (Zacharias, 1898)	0.93	*Thermocyclops hyalinus*	4.87
Heliodiaptomus viduus (Gurney, 1916)	2.03	*Trichocerca elongata* (Gosse, 1886)	0.97
Heterocypris sp.	2.00	**Total**	**100.00**

The predominance of Cladocera and Rotifera aligns with common patterns in freshwater ecosystems, where these groups contribute substantially to trophic dynamics. The findings of the present investigation are consistent with earlier studies, which were conducted in various freshwater bodies across India. Similar patterns were reported by Balai et al. (2014) from Jaisamand Lake, Udaipur, and by Khaire (2020) in Chandani Dam, Maharashtra. Comparable observations were also documented by Rajani (2023) in Mulukanoor Lake of Karimnagar district, Telangana, and by Muthukumaravel et al. (2025) from Chellikurichi Lake, Thanjavur District, Tamil Nadu, thereby reinforcing the results of the present study. The dominance of zooplankton species indicates environmental conditions that are conducive to their growth, reflecting their affinity for nutrient-rich waters. Seasonal variations in zooplankton density also reflect ecological responses to changes in temperature, food availability, and hydrological conditions. The summer and post-monsoon peaks in Copepoda and Cladocera densities likely reflect optimal thermal conditions and enhanced primary productivity, which promote reproductive success. Conversely, reduced densities during the monsoon season may result from dilution effects and increased turbidity, which negatively influence zooplankton populations (Banerjee et al., 2024).

4. Conclusion

The present investigation of the Gambhiri River, Chittorgarh (Rajasthan), provides a comprehensive assessment of seasonal and spatial variability in physicochemical characteristics and zooplankton community structure, thereby elucidating the ecological status of this freshwater ecosystem. Statistically significant seasonal variations were observed in key water quality parameters, including temperature, electrical conductivity, total hardness, chloride, alkalinity, nitrate, and sulphate, reflecting the integrated influence of climatic variability, hydrological processes, and anthropogenic inputs. Although most parameters remained within or proximate to the permissible limits prescribed by WHO and ICMR, signs of localized ecological stress were obvious.

The zooplankton assemblage exhibited high taxonomic diversity, comprising 65 species across four main groups. Cladocera and Rotifera dominated in terms of relative abundance, while Copepoda contributed substantially to overall density. Seasonal trends revealed peak zooplankton densities during summer and winter, likely driven by optimal temperature regimes, enhanced nutrient availability, and elevated primary productivity. In contrast, reduced densities during the monsoon season were associated with dilution effects, increased turbidity, and hydrodynamic disturbances.

A strong and statistically supported relationship between physicochemical parameters and zooplankton distribution underscores the sensitivity of these communities to environmental fluctuations. The predominance of certain taxa indicates nutrient-enriched (mesotrophic to eutrophic) conditions and reaffirms the utility of zooplankton as robust bioindicators of water quality and trophic dynamics. Furthermore, correlation and ANOVA analyses substantiated the pivotal role of water chemistry in regulating the composition and structure of zooplankton assemblages.

Collectively, the findings suggest that the Gambhiri River sustains a moderately healthy yet ecologically responsive aquatic system under increasing anthropogenic pressure. This study highlights the critical importance of integrating biological indicators with physicochemical monitoring for holistic ecosystem assessment and provides essential baseline data for long-term ecological evaluation. Implementation of continuous monitoring frameworks, along with targeted pollution control and conservation strategies, is strongly recommended to safeguard the ecological integrity of this vital river system in Rajasthan's semi-arid region.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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Functional digestive morphology and feeding intensity of the halfbeak *Zenarchopterus clarus* (Hemiramphidae) in a tropical estuarine habitats, southern Vietnam

Original Article

LIMNOLOGY FRESHWATER BIOLOGY

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ABSTRACT. This study examines the functional digestive morphology and feeding intensity of the halfbeak *Zenarchopterus clarus* (Hemiramphidae) in a tropical estuarine habitats of southern Vietnam. A total of 892 specimens were collected monthly from August 2024 to July 2025 at two estuarine sites. The species exhibited a superior mouth with an elongated lower jaw, dense conical dentition, well-developed pharyngeal tooth plates, and numerous gill rakers. The digestive tract consisted of a muscular esophagus and a short intestine, lacking a clearly differentiated stomach, indicating rapid processing of soft prey. Feeding intensity was evaluated using the gut-somatic index (GI) and analyzed with generalized linear mixed models. The model indicated significant variation in GI ($p < 0.001$). The GI differed significantly between sexes and sampling locations, with higher values in females and at Dam Doi. Although the season had no significant main effect, a significant sex × season interaction indicated contrasting seasonal feeding patterns between males and females. Morphological traits and GI collectively suggest that *Z. clarus* is adapted for surface-oriented feeding on small, mobile prey in dynamic estuarine environments. However, the feeding strategy was inferred from morphological traits and GI, as diet composition was not directly examined. These findings provide baseline insights into the digestive morphology and feeding ecology of an estuarine hemiramphid fish.

Keywords: digestive morphology, feeding intensity, gut-somatic index, Hemiramphidae, *Zenarchopterus clarus*

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1. Introduction

Digestive tract morphology is a key determinant of feeding strategy and trophic adaptation in fishes, particularly in environmentally dynamic systems such as estuaries. Estuarine ecosystems are characterized by high environmental variability, supporting diverse fish assemblages and complex trophic interactions (Dien, 2024; Nguyen et al., 2024). Within these systems, feeding strategy and digestive morphology play crucial roles in determining trophic performance and energy allocation. Structural features of the digestive tract, including mouth orientation, dentition, gill rakers, and intestinal configuration, are closely associated with dietary habits and feeding mechanisms in teleost fishes (Nikolsky, 1963; Berkovitz and Shellis, 2023). Moreover, variation in digestive morphology often reflects ecological adaptation to specific feeding niches (Amundsen et al., 2004; Day et al., 2011).

The family Hemiramphidae comprises surface-oriented fishes widely distributed in tropical and subtropical coastal and estuarine waters (Talwar and Jhingran, 1991; More et al., 2022). Many species within this family exhibit characteristic morphological adaptations, including an elongated lower jaw and specialized dentition associated with surface feeding. Previous studies have described digestive morphology and feeding traits in several hemiramphid species, including *Hyporhamphus limbatus* (Nguyen et al., 2025) and related taxa (Tibbetts and Carseldine, 2003; Buddery et al., 2009), demonstrating considerable interspecific variation linked to trophic specialization. However, detailed functional information integrating digestive morphology and feeding intensity remains limited for many regional species.

Zenarchopterus clarus (Mohr, 1926) is a common halfbeak species inhabiting brackish and estuarine waters of the Mekong Delta, Vietnam (Nguyen, 2005;

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Tran et al., 2013). Despite its frequent occurrence in coastal ecosystems, detailed descriptions of its digestive tract morphology and quantitative assessments of feeding intensity remain lacking. Feeding intensity in fishes can be estimated using somatic indices, such as the gut-somatic index (GI), which reflects the relative development of digestive organs in relation to body weight and provides insight into energy allocation and feeding activity (Desai, 1970; Egerton et al., 2018). Differences in feeding intensity between sexes and seasons have been documented in several fish species and are often associated with reproductive investment and environmental variation (Gebremedhin and Mingist, 2014; Hua et al., 2023).

To date, no study has examined simultaneously digestive tract morphology and seasonal variation in the GI in *Z. clarus* from the Mekong Delta. Therefore, this study aims to: (i) describe the functional digestive tract morphology of *Z. clarus* in relation to feeding strategy, and (ii) evaluate the effects of sex, season, and sampling location on GI using generalized linear mixed models. By integrating morphological descriptions with quantitative analysis, this study provides functional insights into trophic adaptation and feeding ecology of *Z. clarus* in estuarine environments.

2. Materials and Methods

Study area and sample collection

Specimens of *Z. clarus* were collected monthly from August 2024 to July 2025 at two estuarine locations in Ca Mau Province, southern Vietnam: Vinh Phuoc (VP; 9°26′47.8″N, 105°27′03.4″E) and Dam Doi (DD; 9°05′00.0″N, 105°09′00.0″E) (Fig. 1). These sites represent brackish-water habitats within the Mekong Delta estuarine system and differ in local hydrological conditions. Tidal processes and freshwater input influence both Dam Doi and Vinh Phuoc; however, spatial variation in water exchange, sediment characteristics, and local hydrodynamics may result in differences in turbidity, nutrient availability, and prey distribution between sites. These environmental variations are expected to influence feeding conditions and digestive traits in *Z. clarus*.

Fish were captured using hand nets (mesh size 1.0 cm) during late afternoon, when individuals were less active. Immediately after capture, specimens were euthanized following approved ethical procedures of Can Tho University (CTU–AEC25025) using tricaine methanesulfonate (10 g/L). All samples were fixed in 4% formaldehyde and transported to the laboratory for analysis. Species identification and sex determination were performed as described by Tran et al. (2013). A total of 892 individuals were examined. Specimens were collected consistently across months and sites to ensure representative sampling coverage.

Morphological examination

Total body weight (W, ±0.01 g) was recorded prior to dissection using an electronic balance (AND EK-610). Morphometric measurements included lower jaw length (LJ, ±0.01 cm), upper jaw length (UJ, ±0.01 cm), and mouth width between corners (AB, ±0.01 mm). Measurements were taken using digital calipers (MOORMAN-110-15DP) and a measuring ruler (TPS-R021). Mouth diameter (MD) was calculated following Shirota (1970): $MD = AB \times \sqrt{2}$, where AB represents the linear mouth width measured as the distance between the left and right mouth corners (mm).

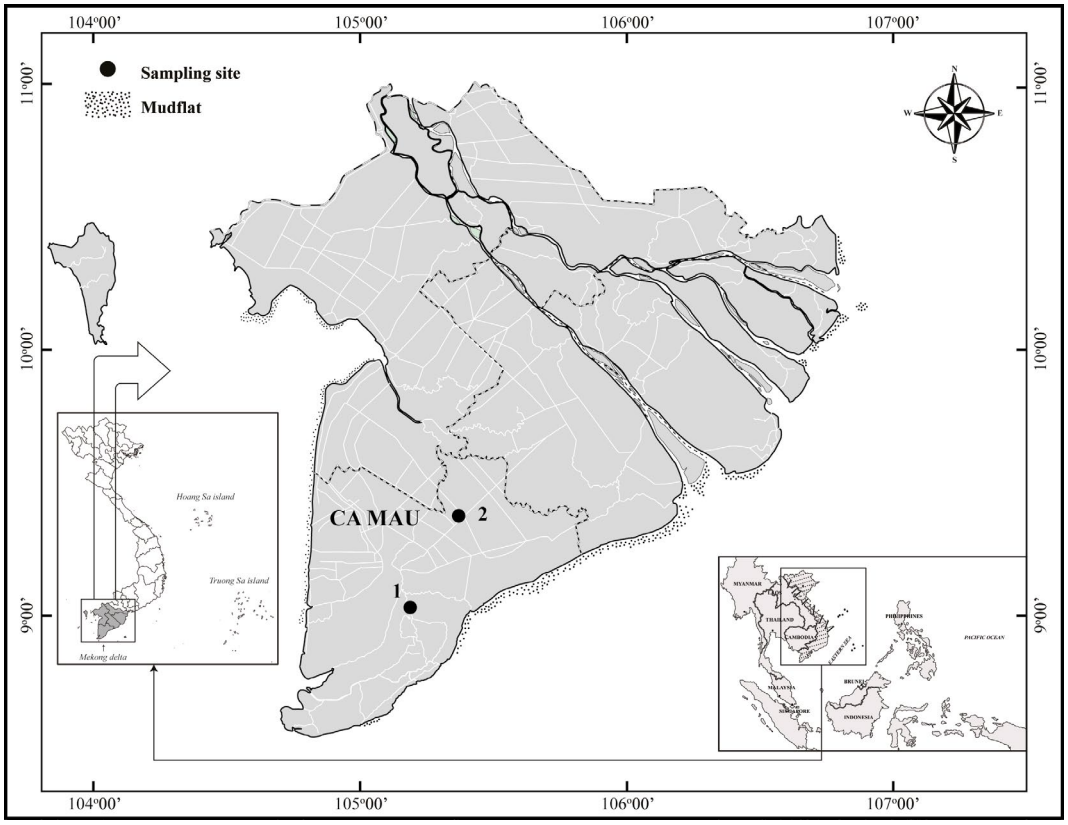

Fig.1. Map of sampling sites in Ca Mau Province, Vietnam (1: Dam Doi; 2: Vinh Phuoc; modified from Dinh (2018)).

The digestive tract was dissected and examined under a stereomicroscope (Motic DM143). Detailed images of dentition were obtained using an Olympus CX41 microscope equipped with a digital camera (Olympus U-CMAD3). The following structures were observed and described: mouth, dentition, tongue, gill arches, esophagus, and intestine. Digestive morphology was described following standard ichthyological criteria outlined by Nikolsky (1963).

Gill rakers and gill filaments were counted on each gill arch. Pharyngeal teeth were examined and quantified. Intestinal configuration was recorded to determine the presence or absence of stomach differentiation. Gill raker and pharyngeal tooth counts were recorded from a randomly selected subsample of 67 specimens. These measurements were conducted as an additional post hoc analysis; therefore, metadata on sex and sampling site were not retained for this subsample.

Gut-somatic index

Feeding intensity was assessed using the gut-somatic index (GI), calculated according to Desai (1970): $GI = (Wg / W) \times 100$, where Wg is intestinal weight (g), and W is total body weight (g). GI was used as a proxy for relative digestive development and feeding intensity.

Statistical analysis

All statistical analyses were performed using Jamovi version 2.6.44 with the GAMLj module (The jamovi project, 2024). To evaluate variation in MD, a generalized linear mixed model (GLMM) with a Gamma error distribution and log link function was applied, with sex as a fixed effect and month as a random intercept. The GI, a continuous positive variable, was analyzed using a similar GLMM framework. Fixed effects included sex (male, female), season (dry, wet), and location (VP, DD), along with their two-way and three-way interactions. The month was included as a random intercept to account for temporal variation and repeated monthly sampling. Estimated marginal means (EMMs) were calculated on the response scale, and pairwise comparisons were conducted using Tukey-adjusted tests. Statistical significance was set at $p < 0.05$. Model assumptions and goodness-of-fit were evaluated using residual diagnostics and model fit indices.

3. Results

Digestive tract morphology

The mouth of *Z. clarus* was superior, with the upper jaw approximately one-quarter the length of the elongated lower jaw (Fig. 2A–B). The upper jaw was flattened and triangular, whereas the lower jaw was pointed and projected upward. Mean lower jaw length was 3.39 ± 0.01 cm (SE). GLMM analysis revealed a significant difference in MD between sexes ($\chi^2 = 14.07$; df = 1; $p < 0.001$). Estimated marginal means indicated that males exhibited larger MD values than females (8.54 ± 0.57 mm (SE) vs. 8.12 ± 0.55 mm (SE)). MD did not vary significantly among months, seasons, or sampling locations ($p > 0.05$).

Teeth were small, conical, and densely distributed on both upper and lower jaws (Fig. 3A–D). Teeth were elongated, with pointed tips and broad bases firmly attached to the jaw margins. In the upper jaw, tooth size increased from the inner to the outer margin (Fig. 3A–B). In the lower jaw, teeth were sparser near the mouth edge and denser toward the inner region (Fig. 3C). High-magnification images revealed pointed tooth tips and dense packing along the jaw margins (Fig. 3D). Tooth density on the outer jaw surface averaged 25 ± 0.6 (17–39) N/mm^2 in the upper jaw and 22 ± 0.4 (14–32) N/mm^2 in the lower jaw. Inner tooth density averaged 24 ± 0.5 (15–33) N/mm^2 in the upper jaw and 24 ± 0.6 (16–39) N/mm^2 in the lower jaw. The lower pharyngeal tooth plate (LPT) was triangular with rounded lateral margins and a blunt anterior apex, whereas the upper pharyngeal tooth plate (UPT) exhibited a three-lobed triangular structure (Fig. 4A–B). Both plates were covered with densely packed conical teeth. Mean counts of pharyngeal teeth were 88 ± 1.7 (54–120) in the upper plate and 131 ± 2.4 (84–162) in the lower plate.

The tongue was poorly developed and firmly attached to the floor of the buccal cavity (Fig. 5). The anterior region exhibited a rough texture, gradually becoming smoother toward the posterior region. This reduced development suggests a limited role in food manipulation, consistent with a feeding strategy that relies primarily on jaw and dentition for prey capture.

Four pairs of gill arches were observed (Fig. 6A–B). Each arch bore two rows of gill filaments and one row of gill rakers. Gill rakers on the first arch were longer and larger than those on subsequent arches (Fig. 6C–D). The arrangement of filaments and rakers is further illustrated in the transverse section of the gill arch (Fig. 6E). Mean gill raker counts were 118 ± 1.0 (97–148) for the first arch, 109 ± 2.0 (88–142) for the second arch, 96 ± 2.0 (70–136) for the third arch, and

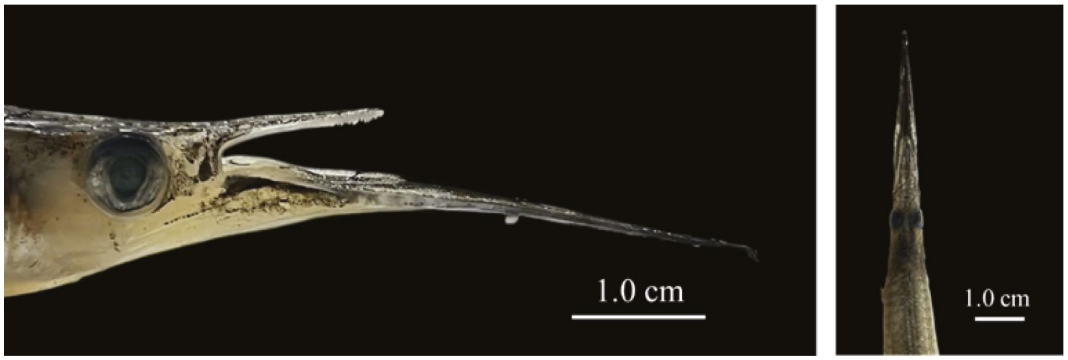

Fig.2. Mouth morphology of *Zenarchopterus clarus* (A: lateral view; B: dorsal view).

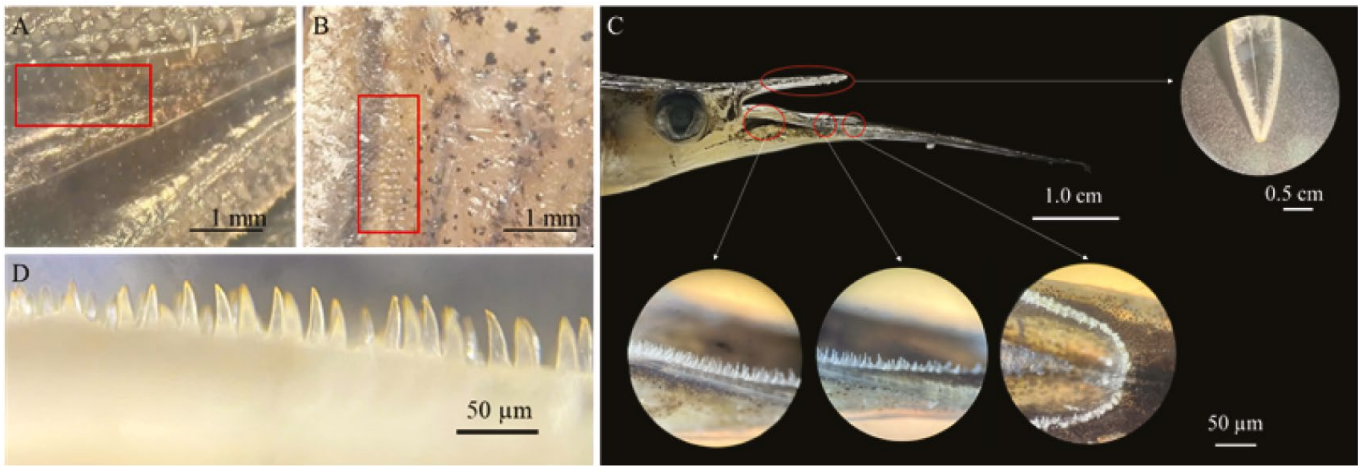

Fig.3. Dentition of *Zenarchopterus clarus* (Inner teeth: A: upper jaw, B: lower jaw; C: distribution pattern of teeth on the jaws; D: morphology of the upper jaw teeth).

79 ± 2.0 (68–114) for the fourth arch. Mean numbers of gill filaments were 14 ± 1.0 (7–22), 14 ± 1.0 (11–23), 13 ± 1.0 (9–20), and 12 ± 1.0 (8–16) for arches I–IV, respectively.

The digestive tract consisted of a tubular esophagus followed by a short intestine divided into anterior and posterior sections (Fig. 7). The esophagus had a relatively thick wall, whereas the intestinal wall was thinner. No clearly differentiated stomach structure was observed.

Gut-somatic index

The generalized linear mixed model (GLMM) explained a moderate proportion of the variation in GI and was overall significant (χ^2 = 154.97, df = 8, p < 0.001). Sex had a significant effect on GI (estimate = −0.100 ± 0.036 (SE), 95% CI: −0.171 to −0.029, p = 0.006), with males exhibiting lower GI values than females. Estimated marginal means indicated that females had higher GI values (2.52 ± 0.20 (SE)) compared to males (2.28 ± 0.18 (SE)). Sampling location also had a significant effect (estimate = 0.170 ± 0.038 (SE), 95% CI: 0.097 to 0.244, p < 0.001), with higher GI values observed at Dam Doi (2.60 ± 0.21 (SE)) compared to Vinh Phuoc (2.20 ± 0.17 (SE)). Season alone did not significantly influence GI (estimate = 0.024 ± 0.152 (SE), p = 0.876). However, a significant interaction between sex and season was detected (estimate = 0.158 ± 0.072 (SE), 95% CI: 0.015 to 0.300, p = 0.030), indicating contrasting seasonal trends between sexes. Specifically, female GI decreased during the wet season, whereas male GI increased (Fig. 8). A significant interaction between season and location was also observed (estimate = −0.265 ± 0.075 (SE), 95% CI: −0.413 to −0.118, p < 0.001), suggesting that seasonal variation differed between sampling sites. No significant interaction was found between sex and location (p = 0.776) or among sex × season × location (p = 0.912) (Table 1).

4. Discussion

This study integrates digestive morphology and GI variation to characterize the trophic adaptation of *Z. clarus* in the estuarine waters of the Mekong Delta. The combined evidence from jaw configuration, dentition, gill structures, intestinal organization, and spatiotemporal GI dynamics indicates that this species is functionally adapted to exploit surface-associated prey under environmentally fluctuating conditions. By linking structural traits with feeding intensity patterns, the present study provides a more comprehensive perspective on trophic strategy in estuarine halfbeaks.

Fig.4. Pharyngeal tooth plates of *Zenarchopterus clarus* (scale bar = 1 mm). (A: lower pharyngeal tooth plate; B: upper pharyngeal tooth plate).

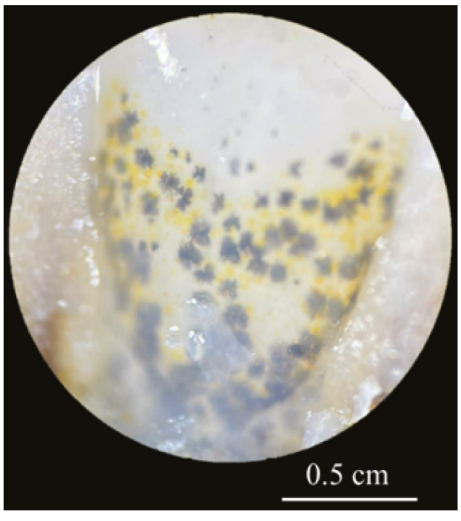

Fig.5. Tongue morphology of *Zenarchopterus clarus* showing a poorly developed structure with a rough anterior surface and smoother posterior region.

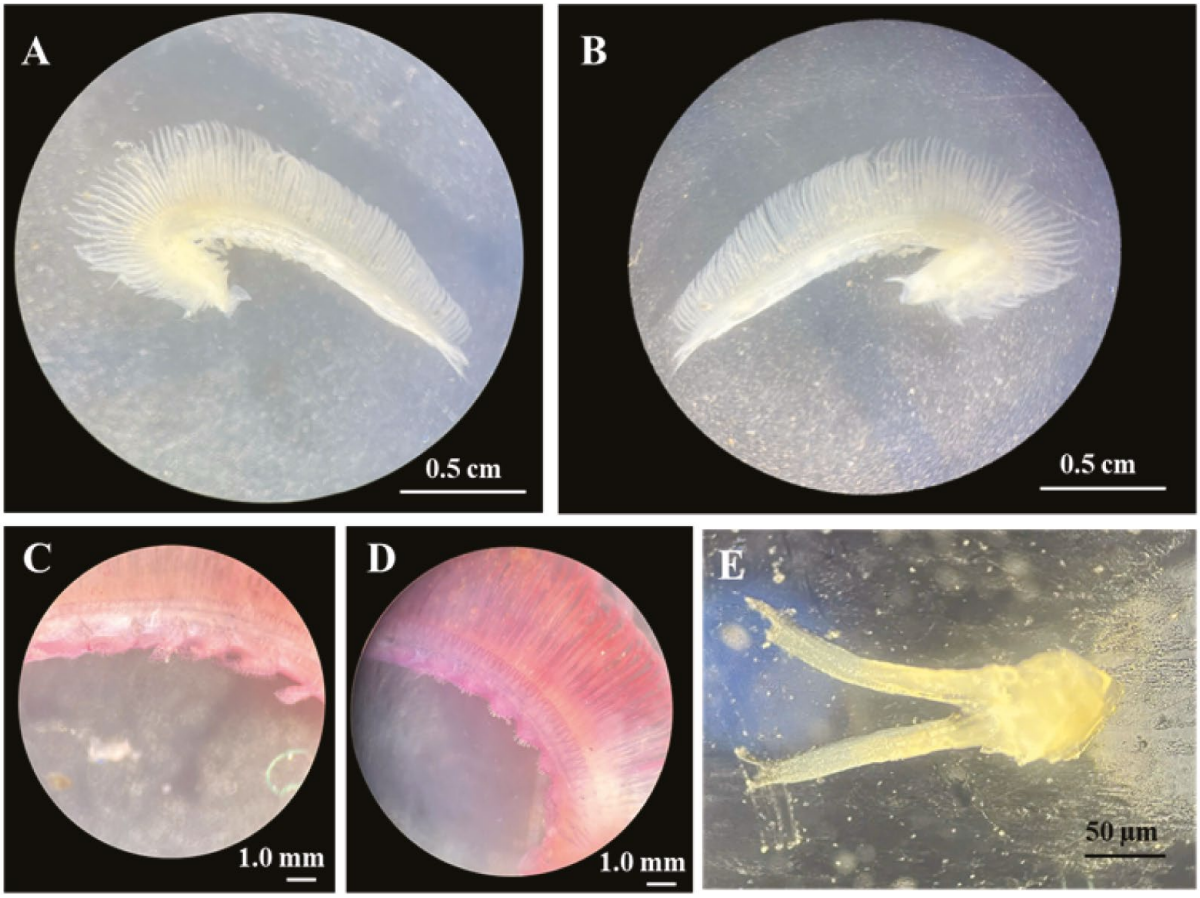

Fig.6. Gill structure of *Zenarchopterus clarus* (A: anterior view; B: posterior view; C: Gill rakers in first gill arch; D: Gill rakers in second gill arch; E: Transverse section of the gill arch).

Morphological integration and surface-oriented feeding strategy

The superior mouth orientation and elongated lower jaw observed in *Z. clarus* are consistent with the surface-feeding functional guild typical of hemiramphids (Talwar and Jhingran, 1991; More et al., 2022). In estuarine systems characterized by turbidity, tidal mixing, and surface aggregation of invertebrates, prey resources are commonly concentrated near the air–water interface. The elongation of the lower jaw likely enhances prey detection and capture efficiency within this narrow vertical feeding zone. The MD, which differed significantly between sexes, may influence prey size selection or handling efficiency rather than representing a shift in trophic niche.

Dentition further supports a carnivorous or insectivorous feeding mode. The densely distributed conical teeth on both jaws and the high counts of pharyngeal teeth suggest specialization for grasping and retaining mobile prey (Berkovitz and Shellis, 2023). Similar pharyngeal modifications have been described in other hemiramphids with functional pharyngeal mills, in which mechanical reinforcement during intraoral processing enhances prey-handling efficiency (Tibbetts and Carseldine, 2003; Buddery et al., 2009). Compared with *Hyporhamphus limbatus* from Southwest Vietnam (Nguyen et al., 2025), *Z. clarus* exhibits a comparable pattern of dense dentition and well-developed pharyngeal plates, suggesting conserved trophic traits within the family. Such morphological consistency may reflect phylogenetic constraints combined with ecological convergence toward surface-oriented carnivory.

Fig.7. Digestive tract of *Zenarchopterus clarus* (A: esophagus; B: anterior intestine; C: posterior intestine).

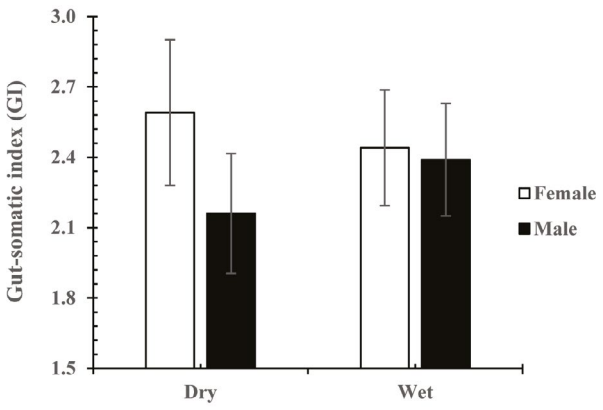

Fig.8. Seasonal variation in gut-somatic index by sex in *Zenarchopterus clarus*.

Gill raker morphology provides additional insight into prey size retention. The relatively high number of gill rakers, particularly on the first arch, is consistent with retention of small prey items (Amundsen et al., 2004). Although diet composition was not directly examined in the present study, the combination of numerous gill rakers and sharp dentition supports the interpretation that *Z. clarus* captures and retains small, mobile prey efficiently in surface microhabitats.

The absence of a clearly differentiated stomach and the presence of a short intestine indicate rapid food throughput, a condition observed in several stomachless or weakly stomach-differentiated teleosts (Day et al., 2011). In estuarine environments where prey patches may be spatially and temporally unpredictable, rapid digestion and turnover may confer an adaptive advantage by allowing individuals to exploit transient feeding opportunities. Thus, the digestive organization of *Z. clarus* appears well suited for high-frequency feeding on soft-bodied prey rather than prolonged gastric processing.

Energy allocation, reproductive investment, and spatial heterogeneity

The GI differed significantly between sexes, with females exhibiting higher values than males. In teleost fishes, somatic indices are commonly associated with feeding activity and physiological condition (Gebremedhin and Mingist, 2014). Higher GI values in females may indicate increased feeding or digestive activity, particularly during periods related to reproductive development. Similar patterns have been reported in other fish species, where females exhibit higher feeding indices under certain biological conditions (Gebremedhin and Mingist, 2014; Hua et al., 2023). Differences in GI between sampling locations suggest spatial variation in feeding conditions. Estuarine habitats are characterized by environmental heterogeneity, including variation in hydrodynamics, turbidity, and food availability (Nguyen et al., 2024). Such differences may influence feeding activity and digestive development in fish. The higher GI values observed at Dam Doi may therefore reflect more favorable feeding conditions at this site. Comparable spatial variation in feeding intensity has been reported in other estuarine fish species (Hua et al., 2023).

Seasonal interaction and adaptive plasticity

Although no significant seasonal effect on GI was detected, the significant interaction between sex and season indicates differences in feeding patterns between males and females. Female GI decreased during the wet season, whereas male GI increased. Seasonal variation in feeding intensity has been documented in many fish species and is often associated with changes in environmental conditions and biological cycles (Gebremedhin and Mingist, 2014; Hua et al., 2023). The observed differences between sexes suggest that males and females may respond differently to seasonal changes in estuarine environments. In particular, reproductive processes may influence feeding activity, leading to variation in digestive indices between sexes (Gebremedhin and Mingist, 2014). In estuarine systems, seasonal changes in rainfall and nutrient input can affect food availability (Hua et al., 2023), which may contribute to the patterns observed in the present study. However, because reproductive status and diet composition were not directly examined, the mechanisms underlying these differences remain unclear. Further studies incorporating reproductive and dietary data would help clarify the factors influencing seasonal variation in feeding intensity in this species.

Table 1. Fixed effects from the GLMM for gut-somatic index

Factor	Estimate	SE	95% CI	p
Sex (M–F)	-0.100	0.036	-0.171 – -0.029	0.006
Season (Wet–Dry)	0.024	0.152	-0.274 – 0.321	0.876
Site (DD–VP)	0.170	0.038	0.097 – 0.244	< 0.001
Sex × Season	0.158	0.072	0.015 – 0.300	0.030
Season × Site	-0.265	0.075	-0.413 – -0.118	< 0.001

Comparative context within Hemiramphidae

Within Hemiramphidae, morphological specialization for surface feeding is well documented (Talwar and Jhingran, 1991; Tibbetts and Carseldine, 2003). The morphological patterns observed in *Z. clarus* align with those described in other halfbeaks, suggesting a conserved functional design optimized for exploiting surface-associated prey. However, the integration of morphological evidence with quantitative GI analysis in the present study extends beyond descriptive anatomy by linking structure to the dynamics of feeding intensity. Compared with other estuarine fishes in the Mekong Delta, including gobiid taxa exhibiting variable gut length and somatic indices (Nguyen et al., 2020; Hua et al., 2023), *Z. clarus* demonstrates a trophic profile consistent with rapid surface-oriented carnivory rather than benthic or detritivorous feeding modes. This distinction reinforces its ecological role within the surface trophic network of estuarine systems.

Ecological implications and limitations

By integrating morphological and functional indicators, this study provides baseline evidence of trophic adaptation in *Z. clarus* in estuarine ecosystems. The coordinated expression of surface-feeding morphology, dense dentition, numerous gill rakers, and sex-specific GI dynamics suggests that this species exhibits both structural specialization and functional plasticity in response to environmental heterogeneity. Nevertheless, gill raker and pharyngeal tooth counts were derived from a subsample, and metadata were not retained for those specimens, preventing evaluation of spatial or sexual variation in these traits. In addition, diet composition and reproductive stage were not directly quantified. Therefore, the feeding strategy in this study was inferred from morphological traits and GI and should be considered a functional interpretation rather than direct evidence. Future studies incorporating stomach content analysis, reproductive staging, and stable isotope approaches would help clarify trophic niche breadth and seasonal energy allocation in this species.

5. Conclusion

The species *Z. clarus* exhibits digestive morphological traits consistent with surface feeding, including an upturned mouth, dense conical dentition, numerous gill rakers, and a short intestine without a clearly differentiated stomach. The GI varied significantly between sexes and sampling locations, and a significant sex × season interaction was detected, indicating sex-specific seasonal feeding strategies. Overall, these findings highlight the functional significance of digestive tract morphology for surface-oriented feeding and provide baseline evidence for sex-specific seasonal variation in feeding intensity in an estuarine hemiramphid fish.

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Animal Ethics statement

The study was approved by the Animal Ethics Committee of Can Tho University (CTU-AEC25025) and conducted in accordance with relevant animal welfare guidelines.

Author contributions (CRediT taxonomy)

Vinh Nguyen Quoc: Conceptualization, Methodology, Investigation, Writing - Original Draft, Writing - Review & Editing, Project administration; Anh Ngoc Tran: Conceptualization, Methodology, Investigation, Writing - Original Draft, Writing - Review & Editing; Hung Tran Gia Nguyen: Methodology, Investigation, Writing - Original Draft, Writing - Review & Editing; Thinh Quoc Nguyen: Methodology, Investigation, Writing - Original Draft, Writing - Review & Editing; Han Thi Kim Nguyen: Methodology, Investigation, Writing - Original Draft, Writing - Review & Editing; Quang Minh Dinh: Conceptualization, Supervision, Writing - Review & Editing.

Declaration of Generative AI and AI-assisted technologies

During the preparation of this work, the authors used ChatGPT to improve English language clarity and academic writing style. The prompts were related to grammar correction. After using this tool, the authors reviewed and edited the content as needed and took full responsibility for the final manuscript.

Pre-print server/online repository

This manuscript has not been deposited in any pre-print server or online repository.

Conflict of interest

The authors declare no conflict of interest.

Informed consent

Not applicable.

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Problems of biological invasions in the fish fauna of southern Vietnam: the example of the Dong Nai River basin

Original Article
LIMNOLOGY FRESHWATER BIOLOGY

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ABSTRACT. Biological invasions of fish are among the key drivers of transformation in freshwater ecosystems, particularly in regions with intensive aquaculture development and high anthropogenic pressure. The aim of this study was to assess the extent of introduction and degree of naturalization of non-native fish species in the Dong Nai River basin (southern Vietnam), as well as to identify patterns of their spatial distribution and main pathways of introduction. Ichthyological sampling was conducted in April–May 2025 at 56 stations in the upper and middle reaches of the Dong Nai River, including the Da Nhim and Da Dang rivers, their tributaries, and lentic water bodies in Dong Nai and Lam Dong provinces. A total of 17 non-native fish species were recorded across 13 of the 17 surveyed areas. The highest diversity of introduced species was observed in large water bodies subjected to significant anthropogenic impact, particularly in Tri An Lake (11 species), as well as in the middle reaches of the Da Nhim River and the Dai Ninh Reservoir (6 species each). In contrast, the number of non-native species was considerably lower in highland areas of the Central Highlands (1–3 species), while no alien species were recorded in water bodies within Cat Tien National Park. Most species exhibited low to moderate occurrence frequency; however, two species—guppy (*Poecilia reticulata* Peters, 1859) and Nile tilapia (*Oreochromis niloticus* (Linnaeus, 1758))—showed very high prevalence. The results indicate a substantial scale of biological invasions in the Dong Nai River basin. Aquaculture and the aquarium trade are identified as the primary sources of non-native fish introductions, while their spatial distribution is strongly associated with the level of anthropogenic impact and the type of water body.

Keywords: biological invasions, non-native species, fish diversity, spatial distribution, Vietnam

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1. Introduction

Biological invasions are now widely regarded as one of the key processes that influence the structure and functioning of freshwater ecosystems. In fish communities, non-native species may alter trophic interactions, compete with native taxa, promote hybridization, and facilitate the spread of parasites and pathogens. These processes are occurring with increasing frequency as a consequence of expanding urbanization, infrastructure development, and global trade. The issue is particularly acute in Southeast Asia, where exceptional biodiversity coincides with rapid economic growth and intensive aquaculture.

Large palaeotropical river systems are characterized by exceptional species richness and complex spatiotemporal organization. The Dong Nai River in southern Vietnam represents such a system, combining mountainous and lowland sections, an extensive tributary network, floodplain habitats, reservoirs, and artificial canals (Pham and Vo, 2025). Strong monsoonal seasonality drives pronounced discharge fluctuations, extensive floodplain inundation, and active fish migrations. While this environmental dynamism may enhance ecosystem resilience through habitat heterogeneity, it simultaneously creates favorable conditions for the establishment of introduced species, particularly those with broad ecological tolerance and high repro-

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ductive capacity. River fragmentation by dams and the formation of reservoirs further contribute to invasion processes by creating lentic habitats often more suitable for non-native than for rheophilic native species (Baran and Myschowoda, 2009).

The main vectors of fish bioinvasions in Vietnam are associated with human economic activity (Stolbunov and Tran, 2019; Dien et al., 2025):

1. Aquaculture, including the farming of both native and introduced species (e.g., tilapia, pangasius, various cyprinids, and catfish) (Thi Thanh Vinh, 2006; Abd Hamid et al., 2023). Escapes from pond farms and cage systems, especially during flood periods, regularly introduce cultured species into natural waters.
2. The aquarium and ornamental trade, which facilitates the import and domestic spread of exotic species; their intentional release or accidental introduction into the wild creates foci of invasion near urban agglomerations (Hewitt et al., 2024).
3. Interbasin transfers and stocking, associated with the movement of planting material between regions, as well as introductions to increase fish productivity in water bodies.
4. Hydraulic infrastructure and transport, facilitating the secondary dispersal of already naturalized species through canals, reservoirs, and irrigation systems.

Aquaculture plays a particularly significant role in shaping the invasion pool in Vietnam. According to reports from the Vietnam Association of Seafood Exporters and Producers (https://seafood.vasep.com.vn/), aquaculture production increased from 4.1 to 5.7 million tons between 2018 and 2024 (a 38% increase), reaching 5.753 million tons in 2024 (+4% year-on-year). Freshwater aquaculture accounts for approximately 380 000 ha and produces ~3.197 million tonnes, including pangasius (1.787 million tons), tilapia (300 000 tons), and other species (1.11 million tons). Although production is concentrated in the Mekong Delta, interregional transport of juveniles, feed, and equipment facilitates the spread of cultured and associated species into other basins, including the Dong Nai. Given the scale of production, even low escape rates can lead to substantial propagule pressure (Nguyen et al., 2023).

The state of knowledge regarding this issue in the Dong Nai Basin remains poor. Existing publications are primarily devoted to the general taxonomic composition of the ichthyofauna (Freyhof et al., 1998; Nguyen et al., 2019), while specific studies aimed at identifying alien species, analyzing their penetration pathways, and the degree of naturalization are few (An et al., 2009; Vu et al., 2013). There is insufficient data on the spatial distribution of introduced species across different habitat types (mainstream, tributaries, reservoirs, and urbanized channels), their contribution to commercial catches, and their potential impact on native populations. Long-term monitoring series that could allow for assessing the dynamics of invasions and the rate of expansion of individual species are virtually absent.

Therefore, the Dong Nai River basin represents a model system for analyzing biological invasions under conditions of intensive anthropogenic pressure in a large tropical river. The aims of this study were to (i) assess the extent of introduction and naturalization of non-native fish species, (ii) identify major introduction pathways and distribution patterns, and (iii) define priorities for monitoring freshwater ecosystems in southern Vietnam.

2. Material and methods

Ichthyological sampling was collected in April–May 2025 at 56 stations located in the Da Nhim and Da Dang rivers (forming the upper Dong Nai River), as well as in the main channel, tributaries, and lentic water bodies within Dong Nai and Lam Dong provinces. For further analysis, stations that were close in geographical and biotopic terms were combined into 17 districts (Fig. 1).

Fish were collected using cast nets, gill nets, and hand nets (mesh size 2–5 mm). Additional specimens were obtained from local fishermen using various fishing gears employed in small-scale fisheries. Sampling effort and material volume are summarized in Table 1.

Species identification was based on morphological and meristic characters, as well as coloration patterns, using standard taxonomic keys and reference guides (Tran et al., 2013; Taki et al., 2021).

For non-native species, occurrence frequency (F) was calculated as the percentage ratio of the number of areas where a species was recorded to the total number of surveyed areas.

3. Results

A total of 17 non-native fish species were recorded across 13 of the 17 surveyed areas (Table 2; Fig. 2). In terms of species richness, the family Cyprinidae was the most represented, comprising six species. The families Poecilidae and Cichlidae followed, each with three species. Each of the remaining families were represented by a single species (Fig. 2).

No alien species were detected within the aquatic systems of Cat Tien National Park (stations 3–6: Mada River, small streams, Dong Nai River channel, and Bau Sau Lake). Across other sites, species richness ranged from 1 to 11 non-native species. The highest number (11 species) was recorded in Tri An Reservoir. Six species were observed in both the middle reaches of the Da Nhim River and the Dai Ninh Reservoir. Relatively high diversity was also found in the upper Da Nhim River (four species), Dankia Lake (five species), Kala Lake (four species), and various watercourses in the lower Central Highlands (four species). Other sites contained between one and three species, with the lowest diversity observed in highland areas subjected to minimal anthropogenic disturbance.

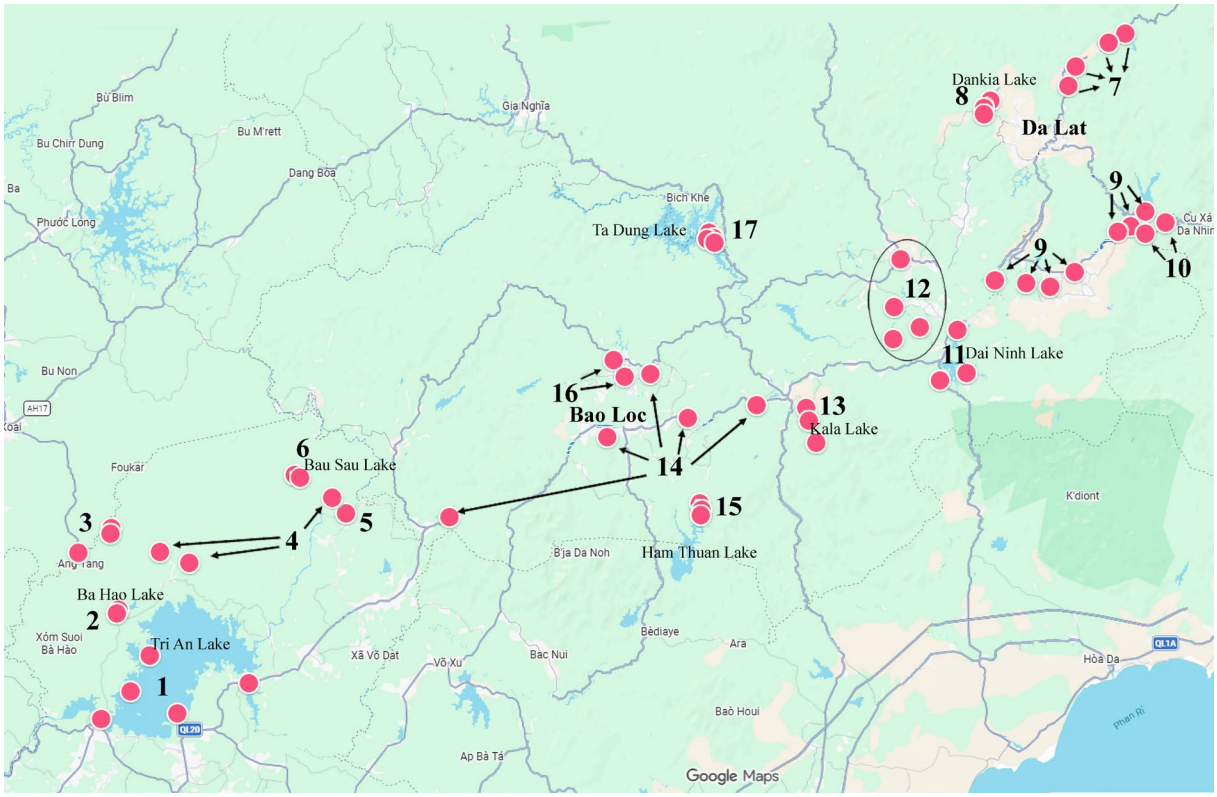

Fig.1. Scheme of stations (red markers) and study areas: 1 – Tri An Lake; 2 –Ba Hao Lake; 3 – Ma Da River; 4 – small rivers and streams of Cat Tien National Park; 5 – Dong Nai River; 6 – Bau Sau Lake; 7 - upper reaches of the Da Nhim River; 8 –Dankia and Suoi Vang lakes; 9 – Da Nhim River; 10 – high mountain streams Hoa Binh district; 11 – Dai Ninh Lake; 12 - upper reaches of the Dong Nai River; 13 –Kala Lake; 14 – rivers of the Central Highlands of Vietnam; 15 –Ham Thuan Lake; 16 –Bao Lam Lake; 17 –Ta Dung Lake.

Low occurrence frequency (5.9%) was recorded for eight species (*Acipenser sinensis*, *Labeo rohita*, *Cichla ocellaris*, *Xiphophorus hellerii*, *Osphronemus goramy*, *Hypophthalmichthys nobilis*, *H. molitrix*, and *Ctenopharyngodon idella*). Moderate frequency (11.8–29.4%) characterized seven species (*Carassius auratus*, *Cyprinus carpio*, *Piaractus brachypomus*, *Pterygoplichthys disjunctivus*, *Clarias gariepinus*, *Gambusia holbrooki*, and *Coptodon zillii*). Very high occurrence (69.2–92.3%) was observed for *Poecilia reticulata* and *Oreochromis niloticus*, the latter being nearly ubiquitous except for high-altitude streams.

Table 1. Sampling effort and material volume

№	Study areas	Number of sites	Number of species	Number of specimens
1	Tri An Lake	5	65	95
2	Ba Hao Lake	2	10	29
3	Ma Da River	3	9	52
4	Small rivers and streams of Cat Tien National Park	3	19	27
5	Dong Nai River (Cat Tien National Park)	1	12	38
6	Bau Sau Lake	2	8	28
7	Upper reaches of the Da Nhim River	4	8	71
8	Dankia and Suoi Vang lakes	3	9	72
9	Da Nhim River	7	16	374
10	High mountain streams Hoa Binh district	2	6	27
11	Dai Ninh Lake	3	25	214
12	Upper reaches of the Dong Nai River	4	18	132
13	Kala Lake	3	11	59
14	Rivers of the Central Highlands of Vietnam	5	13	68
15	Ham Thuan Lake	3	11	32
16	Bao Lam Lake	2	6	18
17	Ta Dung Lake	4	8	22
	TOTAL	56	105	1358

Table 2. Species composition, distribution and occurrence of alien fish species in the studied water bodies of Dong Nai and Lam Dong provinces

Species	Study areas													F, %
	1	2	7	8	9	10	11	12	13	14	15	16	17	
Sinosturio sinensis Gray, 1835									+					5.9
Labeo rohita Hamilton, 1822	+													5.9
Carassius auratus (Linnaeus, 1758)			+	+	+		+							23.5
Cyprinus carpio (Linnaeus,1758)	+			+	+		+			+				29.4
Ctenopharyngodon idella Valenciennes, 1844	+													5.9
Hypophthalmichthys molitrix Valenciennes, 1844	+													5.9
Hypophthalmichthys nobilis Richardson, 1845	+													5.9
Piaractus brachypomus (Cuvier, 1818)	+						+							11.8
Pterygoplichthys disjunctivus Weber, 1991	+				+		+	+					+	29.4
Clarias gariepinus Burchell, 1822							+							17.6
Osphronemus goramy Lacepède, 1801	+													5.9
Gambusia holbrooki (Girard 1859)		+	+											11.8
Poecilia reticulata Peters, 1859	+		+	+	+	+		+	+	+		+		52.9
Xiphophorus hellerii Heckel, 1848				+										5.9
Cichla ocellaris Bloch & Schneider, 1801	+													5.9
Oreochromis niloticus Linnaeus, 175815,4-	+	+	+	+	+		+	+	+	+	+	+	+	70.6
Coptodon zillii (Gervais, 1848)					+				+	+				17.6
Total	11	2	4	5	6	1	6	3	4	4	1	2	2	

Note: 1 – Tri An Lake; 2 –Ba Hao Lake; 7 - upper reaches of the Da Nhim River; 8 –Dankia and Suoi Vang lakes; 9 – Da Nhim River; 10 – high mountain streams Hoa Binh district; 11 – Dai Ninh Lake; 12 - upper reaches of the Dong Nai River; 13 –Kala Lake; 14 – rivers of the Central Highlands of Vietnam; 15 –Ham Thuan Lake; 16 –Bao Lam Lake; 17 –Ta Dung Lake

4. Discussion

Current knowledge of non-native fish introductions in Vietnam remains incomplete. Approximately 50 freshwater and euryhaline species have been reported from inland waters (GBIF, 2026), with a clear increasing trend compared to earlier estimates of 15–20 species (Zvorikin et al., 2014; An et al., 2013). Our data indicate that the problem of biological invasions in the Dong Nai River basin has already reached significant proportions. Its severity varies significantly depending on the type of water body, its ecological status, and altitudinal zonation.

The 17 non-native species recorded represent ~16% of the total ichthyofaunal richness identified in this study. Although this proportion appears moderate and is comparable to other regions of Vietnam (Ruykys et al., 2021), the ecological impact of these species may be substantial (Stolbunov and Tran, 2019).

One of the most characteristic findings of the study is the pronounced spatial heterogeneity in the distribution of alien species. The complete absence of introduced species in the water bodies of Cat Tien National Park demonstrates the important role of relatively undisturbed ecosystems as natural barriers to biological invasions. This situation is consistent with the general notion that high natural ecosystem integrity and low anthropogenic impact significantly limit the successful naturalization of alien organisms. (Bănăduc et al., 2024).

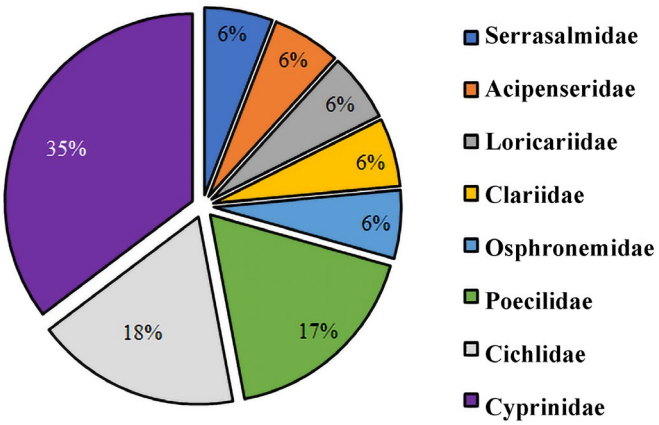

Fig.2. Family level species diversity.

In contrast, the greatest diversity of introduced species was observed in water bodies experiencing significant economic impact, particularly large reservoirs and aquaculture-related water bodies. For example, the highest number of alien species was recorded in Lake Tri An (11 species), as well as in the middle reaches of the Da Nhim River (6 species), which is associated with a large number of artificial reservoirs, including the Dai Ninh Reservoir (6 species). This pattern is consistent with research findings in other regions of the world. (Bănăduc et al., 2024).

The reduced number of non-native species in highland areas (1–3 species) likely reflects both lower anthropogenic pressure and more restrictive environmental conditions (e.g. temperature regimes and hydrology).

Most species exhibited low or moderate occurrence frequencies, whereas *P. reticulata* and *O. niloticus* were highly widespread. Additionally, *Pterygoplichthys disjunctivus* was notable for its high abundance, particularly juveniles in lotic habitats. Such patterns are typical of invasion dynamics, where only a limited number of species become dominant colonizers (Stolbunov and Tran, 2019).

Nile tilapia (*O. niloticus*) appears to be the most ecologically significant invasive species in the region. Its near-ubiquitous distribution reflects high ecological plasticity, broad diet, rapid growth, and competitive ability (Shuai and Li, 2022; Feng et al., 2025). Similar trends were documented elsewhere in Vietnam (Dien et al., 2025). Increasing abundance of tilapias may lead to competitive displacement of native species and restructuring of fish communities. The widespread occurrence of *P. reticulata*, historically introduced for mosquito control (El-Sabaawi et al., 2016), reflects its high reproductive rate and tolerance to degraded conditions.

Pathway analysis indicates that aquaculture is the dominant source of introductions. Many recorded species (e.g. *Cyprinus carpio*, *Hypophthalmichthys spp.*, *Ctenopharyngodon idella*, *Labeo rohita*, *Piaractus brachypomus*, and *Clarias gariepinus*) are widely cultured (Vu et al., 2013). The rapid expansion of aquaculture in Vietnam (Wei et al., 2025) increases propagule pressure and the likelihood of escape events, leading to the establishment of self-sustaining populations.

The ornamental fish trade represents a secondary pathway, particularly for *Pterygoplichthys* spp. and livebearers (Stolbunov and Tran, 2019), as documented globally.

Ecological impacts vary among species. Tilapias are known to exert strong competitive pressure, whereas others (e.g. *Gambusia*) may occupy relatively vacant niches. Loricariid catfishes (*Pterygoplichthys*) may cause substrate disturbance, bank erosion, and trophic alterations (Stolbunov and Tran, 2019; Dien et al., 2025).

Hybridisation also poses a potential risk (Zvorikin et al., 2014), particularly given the widespread use of hybrid tilapias and clariid catfishes in aquaculture. Their ecological roles and invasion potential remain poorly understood.

Overall, the role of non-native species in shaping fish assemblages in the Dong Nai basin remains insufficiently quantified. There is a critical need for long-term monitoring, quantitative assessments of ecological impacts, and evaluation of invasion dynamics, particularly for dominant species such as tilapias.

5. Conclusion

The Dong Nai River basin is experiencing significant biological invasions driven primarily by aquaculture and, to a lesser extent, the ornamental fish trade. The distribution of non-native species is strongly influenced by anthropogenic pressure and habitat type, with reservoirs and modified systems acting as invasion hotspots, while protected and highland areas remain relatively resistant.

Only an integrated approach will enable the timely identification of new invasions and the minimization of their potential impacts on the biodiversity and sustainability of freshwater ecosystems in the Dong Nai River basin.

Conflict of interest

The authors declare that they have no conflicts of interest.

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Ethics statement

This study was approved by the Bioethics Committee of the IBSS, at a meeting of which the authors’ compliance with all international, national and/or institutional principles for the use of animals was confirmed (protocol No. 1(10) dated 10 March 2025).

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Проблемы биологических инвазий в рыбной фауне южного Вьетнама: пример бассейна реки Донгнай

Оригинальная статья

LIMNOLOGY FRESHWATER BIOLOGY

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АННОТАЦИЯ. Биологические инвазии рыб являются одними из ключевых факторов трансформации пресноводных экосистем, особенно в регионах с интенсивным развитием аквакультуры и высоким антропогенным давлением. Целью данного исследования было оценить масштабы интродукции и степень натурализации чужеродных видов рыб в бассейне реки Донгнай (южный Вьетнам), а также выявить закономерности их пространственного распределения и основные пути интродукции. Отбор ихтиологических проб проводился в апреле-мае 2025 года на 56 станциях, расположенных в верхнем и среднем течении реки Донгнай, включая реки Даньим и Даданг, их притоки и стоячие водоемы в провинциях Донгнай и Ламдонг. В общей сложности на 13 из 17 обследованных участков было зарегистрировано 17 чужеродных видов рыб. Наибольшее разнообразие интродуцентов наблюдалось в крупных водоемах, подверженных значительному антропогенному воздействию, особенно в озере Чиан (11 видов), а также в среднем течении реки Даньим и водохранилище Дайнинь (по 6 видов в каждом). Количество видов-вселенцев было значительно ниже в высокогорных районах Центрального нагорья (1–3 вида), а в водоемах национального парка Каттьен они не были зарегистрированы. Большинство видов демонстрировали низкую или умеренную частоту встречаемости; однако два из них — гуппи (*Poecilia reticulata* Peters, 1859) и нильская тилапия (*Oreochromis niloticus* (Linnaeus, 1758)) — были очень широко распространены. Полученные результаты указывают на существенный масштаб биологических инвазий в бассейне реки Донгнай. Аквакультура и аквариумная торговля являлись основными источниками интродукции чужеродных видов рыб, а их пространственное распределение было тесно связано с уровнем антропогенного воздействия и типом водоема.

Ключевые слова: биологические инвазии, чужеродные виды, разнообразие рыб, пространственное распределение, Вьетнам

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1. Введение

Биологические инвазии в пресноводных экосистемах рассматриваются в настоящее время как один из ключевых факторов трансформации структуры и функционирования сообществ. В ихтиофауне чужеродные виды способны вызывать каскадные изменения трофических сетей, усиливать конкурентное давление на аборигенные таксоны, провоцировать гибридизацию и генетическую эрозию локальных популяций, а также служить переносчиками паразитов и заболеваний. В условиях нарастающей урбанизации, гидротехнического строительства и глобализации торговли темпы интродукций и вторичного расселения рыб существенно возросли. Для стран Юго-Восточной Азии, обладающих высоким уровнем эндемизма и одновременно интенсивным развитием рыбного хозяйства, проблема биоинвазий приобретает особую актуальность.

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Крупные реки палеотропиков характеризуются исключительно высокой видовой насыщенностью и сложной пространственно-временной организацией экосистем. В таких системах, как река Донгнай в южном Вьетнам, сочетаются горные и равнинные участки, разветвлённая сеть притоков, пойменные водоёмы, водохранилища и каналы (Pham and Vo, 2025). Выраженная сезонность муссонного климата формирует резкие колебания стока, затопление обширных пойм и активные миграции рыб. С одной стороны, такая динамичность повышает устойчивость сообществ за счёт пространственной мозаичности местообитаний; с другой — создаёт благоприятные условия для закрепления интродуцентов, особенно видов с широкой экологической валентностью и высокой плодовитостью. Дополнительным фактором риска является фрагментация русла плотинами и создание водохранилищ, формирующих новые лимнофильные биотопы, часто более подходящие для чужеродных видов, чем для реофильных аборигенных форм (Baran and Myschowoda, 2009).

Основные векторы биоинвазий рыб во Вьетнаме связаны с хозяйственной деятельностью человека (Stolbunov and Tran, 2019; Dien et al., 2025). К числу ключевых относятся:

1. Аквакультура, включающая разведение как автохтонных, так и интродуцированных видов (например, тилапий, пангасиуса, различных карповых и сомовых) (Thi Thanh Vinh, 2006; Abd Hamid et al., 2023). Побеги из прудовых хозяйств и садковых установок, особенно в период паводков, приводят к регулярному поступлению культивируемых форм в естественные водоёмы.

2. Аквариумистика и декоративная торговля, обеспечивающие импорт и внутреннее распространение экзотических видов; их преднамеренный выпуск или случайное попадание в природу формируют очаги инвазий вблизи городских агломераций (Hewitt et al., 2024).

3. Межбассейновые переносы и зарыбления, связанные с перемещением посадочного материала между регионами, а также с интродукциями для повышения рыбопродуктивности водоёмов.

4. Гидротехническая инфраструктура и транспорт, способствующие вторичному расселению уже натурализованных видов по каналам, водохранилищам и ирригационным системам.

Особую роль в формировании инвазионного пула играет масштаб аквакультуры во Вьетнаме. Согласно отчетов вьетнамской ассоциации экспортеров и производителей морепродуктов (https://seafood.vasep.com.vn/) в 2018–2024 гг. объём её производства увеличился с 4,1 до 5,7 млн т (рост 38%), а в 2024 г. достиг 5,753 млн т (+4% к предыдущему году). Общая площадь аквакультуры составила 1,3 млн га во внутренних водоёмах и 9,7 млн м^3 морских садков. Пресноводный сектор охватывает около 380 тыс. га с объёмом продукции порядка 3,197 млн т, включая пангасиуса (5,7 тыс. га; 1,787 млн т), тиляпию (30 тыс. га; 300 тыс. т) и другие виды (344 тыс. га; 1,11 млн т). Экспортно-ориентированное производство сосредоточено преимущественно в дельте реки Меконг (до 95% пангасиуса и 80% креветок), однако транспортировка молоди, кормов и оборудования, а также межрегиональные хозяйственные связи создают предпосылки для заноса культивируемых и сопутствующих видов в другие бассейны, включая р. Донгнай. Учитывая объёмы производства и плотность хозяйств, даже низкая доля побегов может приводить к значительному абсолютному числу особей, поступающих в природные экосистемы (Nguyen et al., 2023).

Состояние изученности проблемы в бассейне Донгнай остаётся недостаточным. Имеющиеся публикации преимущественно посвящены общему таксономическому составу ихтиофауны (Freyhof et al., 1998; Nguyen et al., 2019), тогда как специальные исследования, направленные на выявление чужеродных видов, анализ путей их проникновения и степени натурализации, немногочисленны (An et al., 2009; Vu et al., 2013). Недостаточно данных о пространственном распределении интродуцентов по различным типам местообитаний (главное русло, притоки, водохранилища, урбанизированные каналы), об их участии в промысловых уловах и о потенциальном воздействии на аборигенные популяции. Практически отсутствуют долгосрочные мониторинговые ряды, позволяющие оценить динамику инвазий и скорость экспансии отдельных видов.

Таким образом, бассейн реки Донгнай представляет собой модельную систему для анализа процессов биоинвазий в условиях интенсивного антропогенного воздействия на крупную тропическую реку. Целью настоящей работы являлись: (1) оценка масштабов интродукции и степени натурализации чужеродных видов рыб, (2) выявление основных путей их поступления и закономерностей распространения и (3) определение приоритетных направлений мониторинга пресноводных экосистем юга Вьетнама.

2. Материал и методы

Сбор проб ихтиофауны осуществляли в апреле-мае 2025 г. на 56 станциях в реках Даньим и Даданг, образующих верхнее течение реки Донгнай, ее русле, притоках и лентических водоемах бассейна в провинциях Донгнай и Ламдонг. Для дальнейшего анализа станции, близкие в географическом и биотопическом отношении, объединили в 17 районов. Схема станций и районов приведена на Рисунке 1.

Сбор проб на станциях осуществляли с применением кастинговой сети, жаберных сетей, ручных сачков с ячеей от 2 до 5 мм, помимо этого приобретали образцы у местных рыбаков из различных орудий лова, используемых в местном промысле. Объем исследованного материала приведен в Таблице 1.

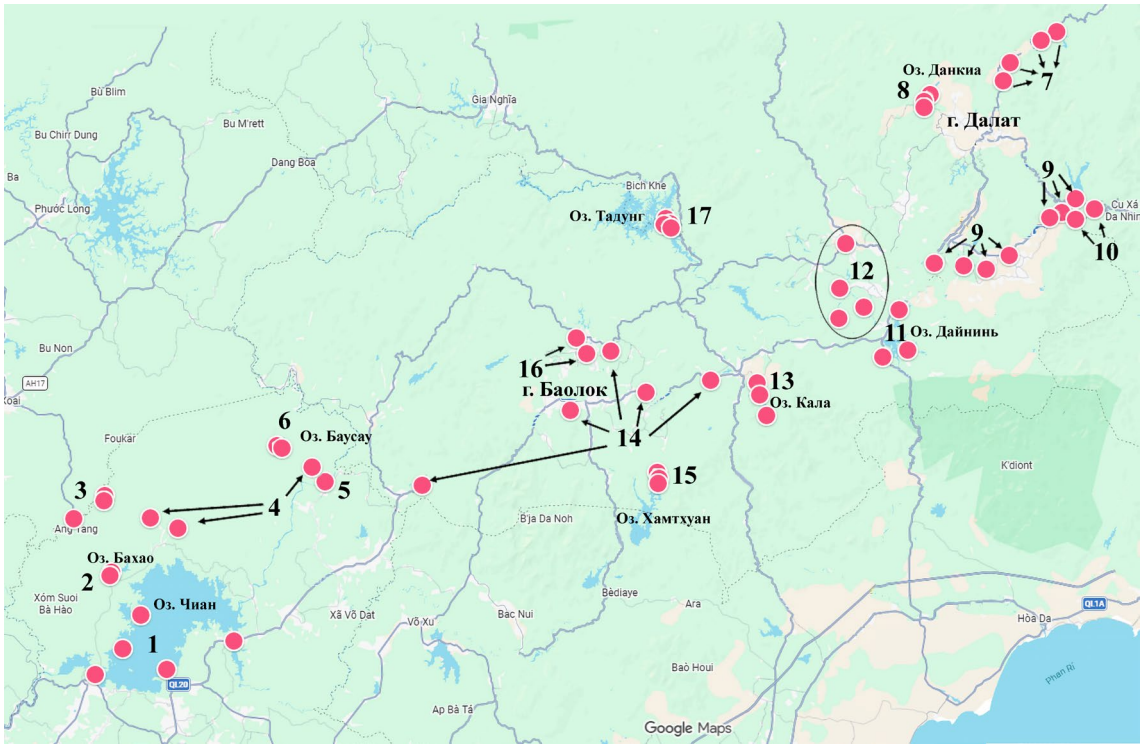

Рис.1. Схема станций (красные маркеры) и районов исследований: 1 – оз. Чиан; 2 – оз. Бахао; 3 – р. Мада; 4 – малые реки и ручьи национального парка Каттьен; 5 русло р. Донгнай; 6 – оз. Баусау; 7 - верховья р. Даньим; 8 – оз. Данкиа и Суойванг; 9 – р. Даньим; 10 – высокогорные ручьи р-н Хоабинь; 11 – оз. Дайнинь; 12 - верховья р. Донгнай; 13 – оз. Кала; 14 – водотоки Центрального нагорья Вьетнама; 15 – оз. Хамтхуан; 16 – оз. Баолам; 17 – оз. Тадунг.

При определении вида использовали комплекс морфологических, меристических признаков, особенностей окраски. Идентификацию проводили с использованием определителей и справочников (Tran et al., 2013; Taki et al., 2021).

Для чужеродных видов определяли их встречаемость (F) как отношение числа районов, где регистрировался вид к их общему количеству, выраженное в процентах.

3. Результаты

При обследовании 17 районов в провинциях Донгнай и Ламдонг в различных водоёмах и водотоках было отмечено 17 чужеродных видов рыб, зарегистрированных в 13 из 17 обследованных районов (Таблица 2; Рис. 2). По числу видов наиболее представительным оказалось семейство Cyprinidae, включавшее 6 видов. Семейства Poecilidae и

Таблица 1. Объем исследованного ихтиологического материала

№	Район исследований	Количество станций	Количество видов	Количество экземпляров
1	Оз. Чиан	5	65	95
2	Оз. Бахао	2	10	29
3	Р. Мада	3	9	52
4	Водотоки национального парка Каттьен	3	19	27
5	Р. Донгнай (Каттьен)	1	12	38
6	Оз. Баусау	2	8	28
7	Верховья р. Даньим	4	8	71
8	Оз. Данкиа и Суойванг	3	9	72
9	Р. Даньим	7	16	374
10	Высокогорные ручьи, Хоабинь	2	6	27
11	Оз. Дайнинь	3	25	214
12	Верховья р. Донгнай	4	18	132
13	Оз. Кала	3	11	59
14	Водотоки Центрального нагорья	5	13	68
15	Оз. Хамтхуан	3	11	32
16	Оз. Баолам	2	6	18
17	Оз. Тадунг	4	8	22
	Всего	56	105	1358

Таблица 2. Видовой состав, распространение и встречаемость чужеродных рыб в исследованных водных объектах провинций Донгнай и Ламдонг

Виды	Районы исследований													F, %
	1	2	7	8	9	10	11	12	13	14	15	16	17	
Sinosturio sinensis Gray, 1835									+					5,9
Labeo rohita Hamilton, 1822	+													5,9
Carassius auratus (Linnaeus, 1758)			+	+	+		+							23,5
Cyprinus carpio (Linnaeus,1758)	+			+	+		+			+				29,4
Ctenopharyngodon idella Valenciennes, 1844	+													5,9
Hypophthalmichthys molitrix Valenciennes, 1844	+													5,9
Hypophthalmichthys nobilis Richardson, 1845	+													5,9
Piaractus brachypomus (Cuvier, 1818)	+						+							11,8
Pterygoplichthys disjunctivus Weber, 1991	+				+		+	+					+	29,4
Clarias gariepinus Burchell, 1822							+							17,6
Osphronemus goramy Lacepède, 1801	+													5,9
Gambusia holbrooki (Girard 1859)		+	+											11,8
Poecilia reticulata Peters, 1859	+		+	+	+	+		+	+	+		+		52,9
Xiphophorus hellerii Heckel, 1848				+										5,9
Cichla ocellaris Bloch & Schneider, 1801	+													5,9
Oreochromis niloticus Linnaeus, 175815,4-	+	+	+	+	+		+	+	+	+	+	+	+	70,6
Coptodon zillii (Gervais, 1848)					+				+	+				17,6
Всего	11	2	4	5	6	1	6	3	4	4	1	2	2	

Примечание: 1 – оз. Чиан; 2 – оз. Бахао; 7 - верховья р. Даньим; 8 – оз. Данкиа и Суойванг; 9 – р. Даньим; 10 – высокогорные ручьи р-н Хоабинь; 11 – оз. Дайнинь; 12 - верховья р. Донгнай; 13 – оз. Кала; 14 – водотоки Центрального нагорья Вьетнама; 15 – оз. Хамтхуан; 16 – оз. Баолам; 17 – оз. Тадунг

Cichlidae были представлены тремя видами каждое. Остальные семейства включали по одному виду (Рис. 2).

Ни одного чужеродного вида не было обнаружено в водных объектах национального парка Каттьен (станции 3-6 - р. Мада, малые водотоки, русло р. Донгнай, оз. Баусау). Во всех прочих водоемах и водотоках отмечалось от 1 до 11 видов-вселенцев. Наибольшее количество (11 видов) зарегистрировано в оз. Чиан, по 6 видов отмечено в среднем течении р. Даньим и расположенном на ней водохранилище Дайнинь, высокое видовое разнообразие вселенцев также наблюдалось в верховьях р. Даньим (4) и оз. Данкиа (5) и Кала (4), разнообразных водотоках нижней части Центрального нагорья Вьетнама (4). Прочие водоемы и водотоки насчитывали от 1 до 3 видов, причем наименьшее их количество наблюдалось в высокогорных районах с незначительной антропогенной нагрузкой/

Невысокая встречаемость (5,9%) отмечена для 8 видов (*Acipenser sinensis, Labeo rohita, Cichla ocellaris, Xiphophorus hellerii, Osphronemus goramy, Hypophthalmichthys nobilis, Hypophthalmichthys molitrix, Ctenopharyngodon idella*). Средняя (11,8-29,4%) – для 7 видов (*Carassius auratus, Cyprinus carpio, Piaractus brachypomus, Pterygoplichthys disjunctivus, Clarias gariepinus, Gambusia holbrooki, Coptodon zillii*). Очень высокая (69,2-92,3) была характерна для двух – гуппи *Poecilia reticulata* и нильской тиляпии *Oreochromis niloticus*. Последний вид встречался практически повсеместно, за исключением высокогорных ручьев.

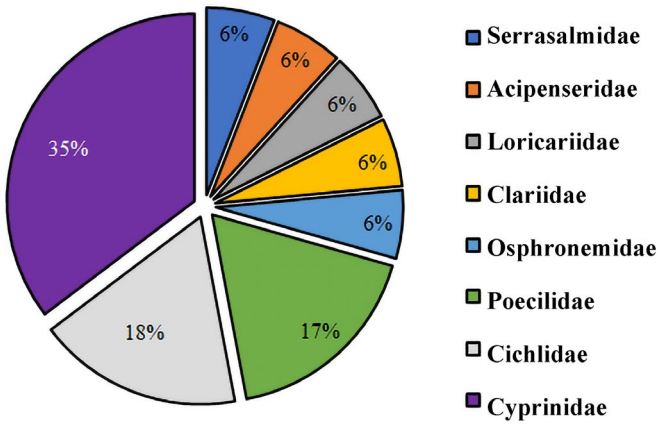

Рис.2. Таксономическое разнообразие чужеродных видов рыб на уровне семейств.

4. Обсуждение

Сведения по вселению чужеродных видов рыб во внутренних водоемах Вьетнама нельзя считать полными и исчерпывающими. В настоящее время указывается на присутствие около 50 видов пресноводных и эвригалинных морских видов, встреченных в пресных и солоноватых водах рек (GBIF, 2026). При этом явно выражен тренд на увеличение числа инвазивных видов - сравнительно недавно их список насчитывал около 15-20 представителей (Зворыкин и др., 2014; An et al., 2013). Полученные нами данные свидетельствуют о том, что проблема биологических инвазий в бассейне р. Донгнай уже

приобрела заметные масштабы. Степень её выраженности существенно варьирует в зависимости от типа водоёма, его экологического состояния и высотной зональности.

Нами было зарегистрировано 17 чужеродных видов рыб, что составляет около 16 % всего видового богатства ихтиофауны исследованного региона. С одной стороны, их доля может показаться сравнительно невысокой по отношению к общему числу видов (при этом она сопоставима с оценками для других регионов Вьетнама, где также отмечается относительно ограниченное число натурализовавшихся интродуцентов (Ruykys et al., 2021)), но при этом экологическое значение вселенцев может быть весьма велико (Stolbunov and Tran, 2019).

Одним из наиболее характерных результатов исследования является выраженная пространственная неоднородность распространения чужеродных видов. Полное отсутствие интродуцентов в водных объектах национального парка Каттьен свидетельствует о важной роли относительно слабо нарушенных экосистем как естественных барьеров для биологических инвазий. Подобная ситуация хорошо согласуется с общими представлениями о том, что высокая природная целостность экосистем и низкая степень антропогенного воздействия существенно ограничивают успешную натурализацию чужеродных организмов (Bănăduc et al., 2024).

Напротив, наибольшее разнообразие интродуцентов отмечено в водоёмах, испытывающих значительное хозяйственное воздействие, прежде всего в крупных водохранилищах и водоёмах, связанных с аквакультурой. Так, максимальное число чужеродных видов зарегистрировано в оз. Чиан (11 видов), а также в среднем течении р. Даньим (6 видов), связанном с большим количеством искусственно созданных водоемов, в том числе водохранилищем Дайнинь (6 видов). Подобная картина хорошо согласуется с результатами исследований в других регионах мира (Bănăduc et al., 2024).

Снижение числа интродуцентов в высокогорных районах Центрального нагорья, где было отмечено лишь 1–3 чужеродных вида, вероятно, это связано как с меньшей интенсивностью хозяйственной деятельности, так и с более экстремальными экологическими условиями (температурный режим, гидрологические особенности), которые могут ограничивать успешную натурализацию многих интродуцированных рыб.

Большинство видов характеризуется относительно низкой или средней частотой обнаружения, но два вида — гуппи P. reticulata и нильская тиляпия O. niloticus — демонстрируют чрезвычайно высокую распространённость. По своей численности выделались кольчужные сомы *Pterygoplichthys disjunctivus*, молодь которых хотя и присутствовала преимущественно в лотических водоемах, была чрезвычайно многочисленной. Подобная картина типична для многих инвазионных сообществ, где лишь ограниченное число видов становится по-настоящему успешными колонизаторами (Stolbunov and Tran, 2019).

Нильская тиляпия является, по-видимому, наиболее значимым инвазивным видом в исследованном регионе. Её практически повсеместное распространение, за исключением высокогорных ручьёв, подтверждает данные о высокой экологической пластичности и конкурентоспособности представителей рода *Oreochromis* (Shuai and Li, 2022; Feng et al., 2025). Ранее аналогичные тенденции были отмечены и в других районах Вьетнама, где тиляпии встречаются даже чаще многих аборигенных видов (Dien et al., 2025). Нарастающая численность этих видов в естественных водоёмах Вьетнама может приводить к усилению конкуренции с аборигенными видами и постепенному изменению структуры ихтиоценозов. Сходным образом высокая встречаемость отмечена и у гуппи, широко используемой ранее в программах биологического контроля комаров (El-Sabaawi et al., 2016). Этот вид отличается высокой скоростью размножения и устойчивостью к загрязнению воды, что способствует его успешной натурализации в самых различных водоёмах.

Анализ путей распространения показывает, что ведущую роль здесь играет аквакультура. Большинство обнаруженных чужеродных видов — такие как *Cyprinus carpio*, *Hypophthalmichthys molitrix*, *H. nobilis*, *Ctenopharyngodon idella*, *Labeo rohita*, *Piaractus brachypomus* и *Clarias gariepinus* — широко используются в рыбоводстве и регулярно культивируются на фермах (Vu et al., 2013). Во Вьетнаме эта проблема особенно актуальна в связи с быстрым ростом рыбоводческой отрасли и расширением площади аквaферм (Wei et al., 2025). В таких условиях практически неизбежно регулярное проникновение выращиваемых рыб в природные водоёмы. В результате формируются устойчивые популяции интродуцентов.

Вторым важным каналом интродукций является аквариумная торговля. В частности, представители рода Pterygoplichthys, а также некоторые живородящие карпозубые попали в природные водоёмы именно таким путём (Stolbunov and Tran, 2019). Аналогичные случаи известны во многих регионах мира, где аквариумные рыбы нередко становятся источником новых инвазий.

Экологические последствия подобных инвазий могут быть весьма разнообразными и не всегда легко поддаются однозначной оценке. Некоторые виды, такие как тиляпии, обладают значительным потенциалом негативного воздействия на аборигенные сообщества, конкурируя с местными рыбами за пищевые ресурсы и местообитания. Другие интродуценты (такие как гамбузия) могут занимать относительно свободные экологические ниши и не вызывать заметных изменений в структуре сообществ. Отдельную группу потенциально проблемных видов составляют представители семейства Loricariidae, в частности Pterygoplichthys. Хотя их влияние на экосистемы Вьетнама пока слабо исследовано, данные свидетельствуют о возможности серьёзных экологических последствий, включая разрушение донных субстратов, эрозию берегов и изменение трофиче-

ских связей (Stolbunov and Tran, 2019; Dien et al., 2025).

Следует также учитывать потенциальную роль гибридизации (Зворыкин и др., 2014). В аквакультуре широко используются гибридные формы тиляпий и клариевых сомов, способные проникать в естественные водоёмы. Их экологические свойства и способность к формированию устойчивых популяций остаются практически неизученными, что представляет дополнительный риск для природных экосистем.

В целом, роль чужеродных видов в формировании рыбных сообществ в бассейне реки Донгнай остается недостаточно количественно оцененной. Существует острая необходимость в долгосрочном мониторинге, количественной оценке экологического воздействия и оценке динамики инвазии, особенно для доминирующих видов, таких как тиляпии.

5. Заключение

В бассейне реки Донгнай наблюдается высокая интенсивность биологических инвазий, вызванных в основном аквакультурой и, в меньшей степени, торговлей декоративными рыбами. Распространение чужеродных видов сильно зависит от антропогенного воздействия на водоем и типа местообитания: водохранилища и измененные экосистемы выступают в качестве очагов инвазии, в то время как охраняемые и высокогорные районы остаются относительно устойчивыми.

Только комплексный подход позволит своевременно выявлять новые инвазии и минимизировать их потенциальное воздействие на биоразнообразие и устойчивость пресноводных экосистем в бассейне реки Донгнай.

Конфликт интересов

Авторы заявляют об отсутствии конфликта интересов.

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Заявление об этике

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Paleohydrology of the Manych Strait in the Khvalynian basin of the Caspian Sea during the Late Pleistocene

Original Article

LIMNOLOGY FRESHWATER BIOLOGY

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ABSTRACT. The paper discusses controversial issues of the paleohydrology of the Manych Strait—a key element in the water exchange system between the Khvalynian basin of the Caspian Sea and the Neoeuxinian basin of the Black Sea during the Late Pleistocene. Special attention is paid to two parameters: the maximum level of the Khvalynian transgression and the height of the spillway threshold through the Manych depression. Geological-geomorphological analysis, digital terrain modelling, and hydraulic modelling in the HEC-RAS system allowed reconstructing scenarios of Caspian water discharge through the Manych valley. The modelling results indicate that the most probable maximum level of the Caspian Sea during the Early Khvalynian transgression was approximately 40 m a.s.l. with a spillway threshold at 31 m a.s.l. Hypothetical limits of the discharge capacity of the Manych Strait channel of the Khvalynian Caspian basin were also calculated. The results can be used in further research.

Keywords: Caspian Sea, Late Pleistocene, Khvalynian transgression, Manych valley, paleohydrology, hydraulic modelling, spillway threshold, digital elevation model, sea level, paleoenvironmental reconstruction

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1. Introduction

The Manych depression is a tectonic trough-like lowland that separates the Ciscaucasia from the steppe part of the southern East European Plain and connects the Kuban-Azov and Caspian lowlands. The Manych River flows along the bottom of the depression.

N.Ya. Danilevsky (1869) first substantiated in the possibility of water exchange between the Black Sea and Caspian basins through the Manych valley. Quaternary geological studies of the region have been conducted for over 150 years, during which deposits (including molluscan fauna) have been studied in detail, and the chronology of water exchange episodes between the Black and Caspian seas has been reconstructed (Bogachev, 1903; Lisitsyn, 1932; Goretsky, 1953; Popov, 1983; Chepalyga and Pirogov, 2005; Svitoch et al., 2010; Semikolennykh et al., 2022).

Contemporary understanding of the history of the Manych valley formation during the Pleistocene is largely based on the fundamental studies of G.I. Popov (1983), who used numerous sections and drilling data to reconstruct in detail the geological structure and formation history of the Manych valley.

The last time the Manych valley was filled with marine waters was at the end of the Late Pleistocene, during the Khvalynian transgression of the Caspian Sea. According to the latest data on OSL dating, the Manych Strait functioned between approximately 17.7 and 14.9 ka (Semikolennykh et al., 2022), corresponding to the period of degradation of the Late Valdai (Ostashkov) glaciation (MIS 2).

Despite the long history of paleogeographic research in the Manych valley, the hydrological parameters of the Manych Strait during the Khvalynian transgression remain the subject of active scientific debate. The two most controversial parameters are as follows:

1. **Maximum level of the Khvalynian transgression.** According to the prevailing viewpoint, the maximum level of the Khvalynian transgression reached 48 m a.s.l. (Fedorov, 1957; Rychagov, 1997; Svitoch et al., 2010; Chepalyga et al., 2007, and others). Terraces at this elevation were described on the coast of Dagestan (Rychagov, 1997) and on the Krasnovodsk Peninsula on the eastern Caspian coast (Fedorov, 1957). Additionally, terraces at an elevation of 48 m

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above sea level were identified based on data from the SRTM3 digital elevation model (Lavrentyev, 2013). However, these terraces lacked molluscan fauna and radiocarbon dates. The highest terrace with Khvalynian molluscan fauna was recorded in the Yergeni at 40 m a.s.l. (Lavrentyev et al., 2024; Svitoch et al., 2017). Similar elevations (up to 40 m a.s.l.) were observed near the Samara Bend, the valley of the Maly Karaman River (Makshaev et al., 2025). Thus, dates or Khvalynian molluscan fauna do not support the Khvalynian transgression terraces above 40 m a.s.l., making the maximum transgression level a matter of debate.

2. **Height of the Manych Strait spillway threshold.** According to geological profile No. 16 (Popov, 1983), the spillway threshold near Zunda-Tolga was located at ~18–20 m a.s.l. Some studies demonstrate that at such a threshold height, the Caspian level could not have reached 48 m a.s.l. (Kvasov, 1975; Popov, 1983; Varushenko et al., 1987; Svitoch et al., 2010; Rychagov, 1997; Chepalyga and Pirogov, 2005). Hydraulic calculations indicate a high discharge capacity of the channel at 45 m a.s.l.—from 200,000 to 300,000 m^3/s (Sidorchuk and Panin, 2022), comparable to the discharge of the Amazon River. More conservative estimates of maximum discharge through the Manych valley are ~50,000 m^3/s (Chepalyga and Pirogov, 2005), based on the character of deposits near Zunda-Tolga, or up to 65,000 m^3/s (Sidorchuk et al., 2011), based on the cross-sectional area of a large meander near Sukhoy Khutor. These values significantly exceed the reconstructed river inflow to the Caspian during the Early Khvalynian transgression—520–570 km^3/year (~16,500–18,000 m^3/s) (Sidorchuk et al., 2021), of which up to 80% was provided by the Volga (~423 km^3/year). Alternative estimates of river inflow yield 320–375 km^3/year (Gelfan et al., 2024). The present-day long-term Volga discharge is 228–274 km^3/year (Georgiadi et al., 2017). This discrepancy makes a high level of the Khvalynian basin impossible with a spillway threshold of 18–20 m a.s.l. Consequently, researchers hypothesized on a higher spillway threshold at the beginning of the Khvalynian transgression (Kvasov, 1975; Popov, 1983; Chepalyga and Pirogov, 2005; Svitoch et al., 2010; Sidorchuk et al., 2011), primarily formed by deposits of the Kalaus River delta. A higher Manych valley spillway threshold explains the presence of Khvalynian terraces above 30 m a.s.l. However, there is no geological evidence for the existence of a higher spillway threshold. Therefore, the height of the Manych Strait spillway threshold at the beginning of the Khvalynian transgression remains a subject of scientific debate.

Thus, the maximum level of the Khvalynian transgression and the height of the spillway threshold require additional analysis. It is necessary to model scenarios of Caspian water discharge through the Manych valley using digital elevation models and hydraulic calculations. This will allow refinement of the key paleohydrological parameters of the Manych Strait in the Khvalynian Caspian basin.

2. Materials and methods

2.1. Reconstruction of the Manych Strait channel relief

2.1.1. Preparation of elevation data

Elevation data were obtained from the SRTM3 digital elevation model (DEM). However, SRTM3 contains minor noise and distortions, requiring preliminary processing. Therefore, data processing was performed using SAGA GIS software.

The SRTM3 DEM was reprojected into the Universal Transverse Mercator (UTM) projection using the UTM Projection module. To obtain a smoothed relief necessary for subsequent reconstruction, the Simple Filter module was applied. After filtering, contour lines with a 1 m interval were vectorized from the smoothed relief.

The question arises regarding the accuracy assessment of SRTM elevation data. L.A. Muravyev (2007) presented a comparative characterization of SRTM with more accurate topographic survey data at a scale of 1:5,000. According to L.A. Muravyev (2007), the inaccuracy in displaying SRTM elevation data compared to 1:5,000 topographic survey was due to “wandering” planimetric coordinates (X, Y) with an amplitude of 30 meters; elevation distortions were particularly evident on steep slopes of river valleys and gullies, where correct planimetric referencing of elevation data is especially important.

Using SRTM 3 for paleoreconstructions at scales starting from 1:100,000 seems to be correct (Lavrentyev et al., 2008), since the deviation of planimetric coordinates by an average of 30 m is displayed at a scale of 1:100,000 as 0.03 mm.

It is also necessary to consider the specifics of applying SRTM 3 in forested areas. Since radar surveying may record tree height rather than the actual Earth’s surface. In our case, the study object—the Manych valley—is located in the steppe zone, and no elevation correction of the DEM is required.

2.1.2. Creation of the digital paleochannel model

The digital paleochannel model is a digital elevation model of the ancient water body’s channel. To create it, the spatial coordinates (X, Y, and Z) of Pleistocene deposits in the Manych Strait were required. For this purpose, geological profiles presented in the monograph by G.I. Popov (1983) and on sheet L-38-XIII of the State Geological Map GGC-200_1 (Geological Map L-38-XIII, 1965) were used.

The scanned maps with geological profiles were georeferenced in QGIS 3.14. Given the small scale of the original schemes in Popov’s monograph (1983), elevation profiles based on SRTM3 data were constructed to refine the georeferencing.

The obtained profiles were then aligned with geological cross-sections in the Inkscape graphics editor (Fig. 1). Since the coordinates of the elevation profiles were known in advance, their alignment with the geological profiles enabled the determination of the spatial coordinates of the Pleistocene deposits.

The obtained elevation marks of Pleistocene deposits were transferred to LibreOffice Calc and used to create a set of XYZ coordinates, based on which the digital paleochannel model was built. Interpolation of elevation values with a 1 m step was performed manually.

The obtained paleochannel contour lines were combined with the contour lines of the modern SRTM3 DEM. Natural Neighbours interpolation in SAGA GIS was used to construct the digital elevation model of the paleochannel. If it was necessary to change the height of the spillway threshold, the channel height and its gradient were modified by manual interpolation. Based on the selected scenario for modelling, contour lines of the required height were drawn. The Fill Sinks (Wang & Liu) module in SAGA GIS was used to simulate the filling of the Manych valley with deposits.

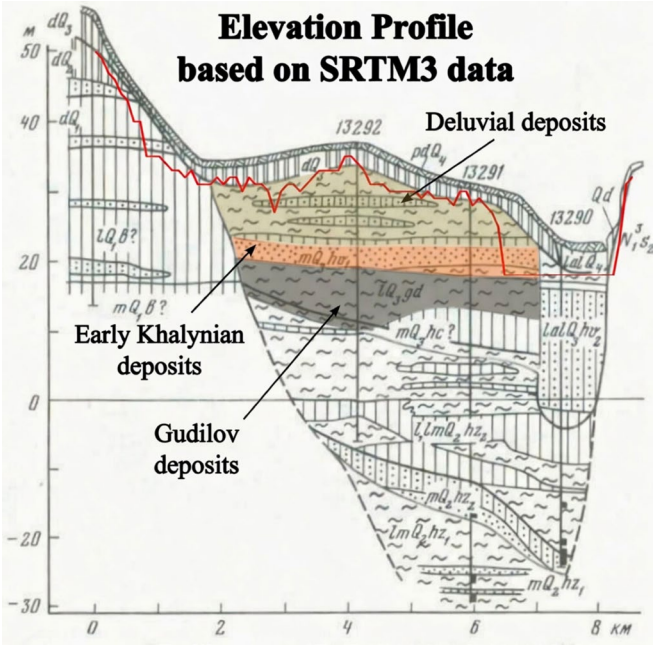

Fig.1. Geological cross-section No. 16 by Popov (1983) aligned with an elevation profile constructed from SRTM3 data.

2.2. Geological-geomorphological characteristics of the Manych Strait of the Khvalynian Caspian basin

Paleohydrological reconstruction requires the restoration of the relief of the Manych Strait channel that functioned during the existence of the Khvalynian Caspian basin. Published geological profiles from the monograph by G.I. Popov (1983), geological maps, descriptions of sections, and the author's own field observations provided the basis for such a reconstruction (Fig. 2).

Based on the above sources, the geological-geomorphological structure of the Manych Strait paleochannel was reviewed. The relief of this channel is composed of Gudilov lacustrine, Surozh, and Khvalynian marine deposits (Table 1).

According to G.I. Popov (1983), five structural elements are distinguished within the Manych depression: the Zunda-Tolga uplift, the Eastern Manych depression, the Manych-Gudilov depression, the Salsk uplift, and the Western Manych depression (Fig. 2).

The spillway threshold of the Manych Strait was located near the Zunda-Tolga uplift—the narrowest section of the entire depression. The reconstruction of the paleorelief of the channel was based on transverse geological profiles (Popov, 1983), on which Khvalynian deposits are located at elevations of 18–20 m a.s.l. (Fig. 1). These deposits crop out at the surface and contain characteristic Khvalynian molluscan fauna. The age of the deposits, determined from molluscs, is 14.2–14.9 ka (Semikolennykh et al., 2025).

In the absence of precise data on the height of the original spillway threshold, terraces traceable along the valley are of particular importance (Fig. 3, Fig. 4). Thus, near Zunda-Tolga, according to SRTM3 data, a terrace approximately 44–45 m a.s.l. is observed on the right bank of the valley. Similar terraces (40–45 m a.s.l.) are recorded downstream from the Kalaus River delta (Fig. 3). The floodplain width here reaches 2 km at an elevation of about 20 m a.s.l.

Further, the waters flowed into the Eastern Manych and Manych-Gudilov depressions, where longitudinal ridges and closed depressions, first described by

Table 1. Stratigraphy and correlation of horizons and layers of the Manych valley in the Upper Pleistocene according to G.I. Popov (1983) with modifications.

Main subdivisions	Western Manych depression	Salsk uplift	Manych-Gudilov depression	Eastern Manych depression	Zunda-Tolga uplift
Holocene	Subaerial deposits				
Upper Pleistocene	Subaerial deposits				Upper Khvalynian deposits
	Surozh deposits	Lower Khvalynian deposits			
	Gudilov deposits				
	Girkan deposits				Girkan deposits
	Karangat deposits				

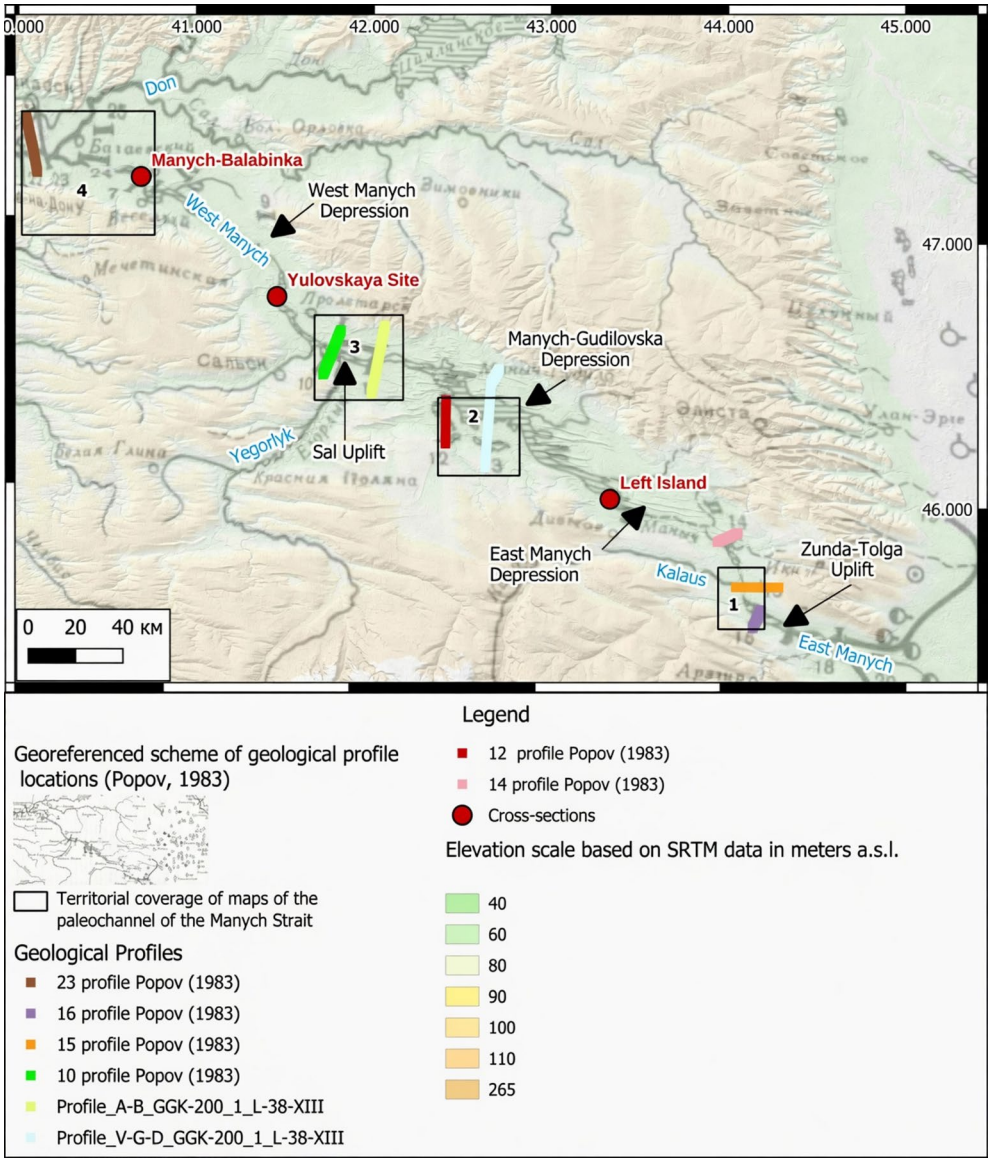

Fig.2. Map showing the location of reference geological cross-sections and sections.

N.Ya. Danilevsky (1864), are widespread. Khvalynian molluscan fauna was recorded in outcrops of the longitudinal ridges (Chepalyga and Pirogov, 2005; 2007; Svitoch et al., 2010). Khvalynian deposits were most likely abutted against Gudilov deposits, which probably form the base of the longitudinal ridges. These longitudinal ridges were formed as a result of erosional processes during the discharge of Caspian waters through the Manych valley (Popov, 1983; Svitoch et al., 2010). There is also a view that the longitudinal ridges began to form during the regressive stage of Gudilov Lake (Svitoch et al., 2010 and others).

The regressive stage of Gudilov Lake began ~20–17 ka (Lavrentyev, 2025). The lowering of the lake level was probably associated with the maximum of the Late Valdai (Ostashkov) glaciation, leading to significant cooling and aridification of the climate, which was the main cause of the Gudilov Lake regression.

The structure of the longitudinal ridges was studied in greatest detail on Levyy Island. According to OSL dating, the age of Khvalynian deposits is 17–15 ka (Semikolennykh et al., 2022). The elevation of the boundary between Gudilov and Khvalynian deposits is ~17.4 m a.s.l.

A significant part of the Manych-Gudilov depression was occupied by Lake Manych-Gudilo since the Late Pleistocene. Judging by profile V-G-D of geological map sheet GGC-200_1_L-38-XIII (Geological Map L-38-XIII, 1965), the depth of the lake bottom before the discharge of Caspian waters was probably at elevations of 6 m a.s.l. (Fig. 5).

The valley of the Western Manych River, after widening in the area of Lake Manych-Gudilo (up to 40 km), narrows to 15 km near the mouths of the Sredny and Bolshoy Egorlyk rivers. Here, the Salsk uplift is located (Fig. 6). In this area, Khvalynian fauna was identified mainly from drilling data on the first floodplain terrace (height ~20 m a.s.l.) above the mouth of the Bolshoy Egorlyk River (Popov, 1983). The second terrace is represented by lacustrine clays, sandy loams, and loams with molluscan fauna characteristic of flowing water bodies (*Dreissena polymorpha*, *Lithoglyphus*, and *Valvata*) (Popov, 1983), at an elevation of ~25 m a.s.l. It is assumed that a second spillway threshold of the Manych Strait, 20 m a.s.l. high, formed by deposits of the tributaries Bolshoy and Sredny Egorlyk, which existed in this area (Kvasov, 1975; Popov, 1983; Lavrentyev and Chepalyga, 2011).

After the Caspian waters overcame the first spillway threshold near Zunda-Tolga, the basin of Lake Manych-Gudilo was filled, resulting in the formation, for a relatively short time, of a bay of the Early Khvalynian basin in the central part of the Manych valley. Upon reaching a water level of +20 m a.s.l., overflow of Caspian waters began across the second spillway threshold—the Salsk uplift. This is indirectly evidenced by changes in the character of deposits in the Khvalynian section on Levyy Island (Semikolennykh et al., 2022). The structure of the section reflects a gradual change in sedimentation environments—from calm lagoonal conditions associated with the ingression of Caspian waters to dynamic flowing conditions caused by the development and activation of the strait.

Below the confluence of the Sredny Egorlyk River, the valley widens again to 20 km. The valley bottom becomes flat.

The first Khvalynian terrace of the lower reaches of the Western Manych River was studied by many authors (Danilevsky, 1869; Bogachev, 1903; Lisitsyn, 1932, and others). These are typically sections with mixed Black Sea-Caspian and freshwater fauna (*Cardium edule*, *Bittium reticulatum*, *Didacna trigonoides*, *Dreissena caspia*, *Dr. polymorpha*, and *Viviparus viviparus*). Such sections with mixed fauna are traceable throughout the Western Manych depression. At present, the study of these sections is complicated because they are flooded by the Veselovskoye Reservoir. An exception is the section in front of the dam of the Veselovskoye Reservoir near the Manych-Balabinka village. It has been known since 1932 (Lisitsyn, 1932). The fauna is mixed and redeposited, including Caspian and Black Sea molluscs. Khvalynian molluscs are represented by *Didacna protracta* and *Didacna ebersini*, for which a date exists— calibrated age (OxCal v4.4) 17.138 ka, MGU-1491 (Svitoch and Yanina, 2001).

The steep banks of the Veselovskoye Reservoir are mainly represented by Gudilov deposits with freshwater molluscan fauna of standing water bodies (second floodplain terrace). As an example, we can cite the deposits underlying the cultural layers of the Yulovskaya site (Lavrentyev et al., 2012). This lower unit is represented by coarsely bedded lacustrine loams with freshwater fauna, *Planorbis* sp. and *Valvata* sp.; visible thickness—3 m. A bone found in these deposits yielded a date (Chepalyga et al., 2008). Calibrated date (OxCal v4.4)—25,546 years ago (LU-5852). According to palynological data, this horizon belongs to the Bryansk age. According to the latest studies (Sycheva et al., 2015), the age of the Bryansk paleosol is estimated at 33–26 ka (MIS 3). Then, a change in sedimentation conditions occurs. Lacustrine sediments are replaced by subaquatic deposits containing the cultural layers of the Late Paleolithic Yulovskaya site, with an age of deposits of ~17–20 ka. Thus, we can conclude that the regressive stage of Gudilov Lake began during the period of the Late Valdai (Ostashkov) glaciation (Lavrentyev, 2022).

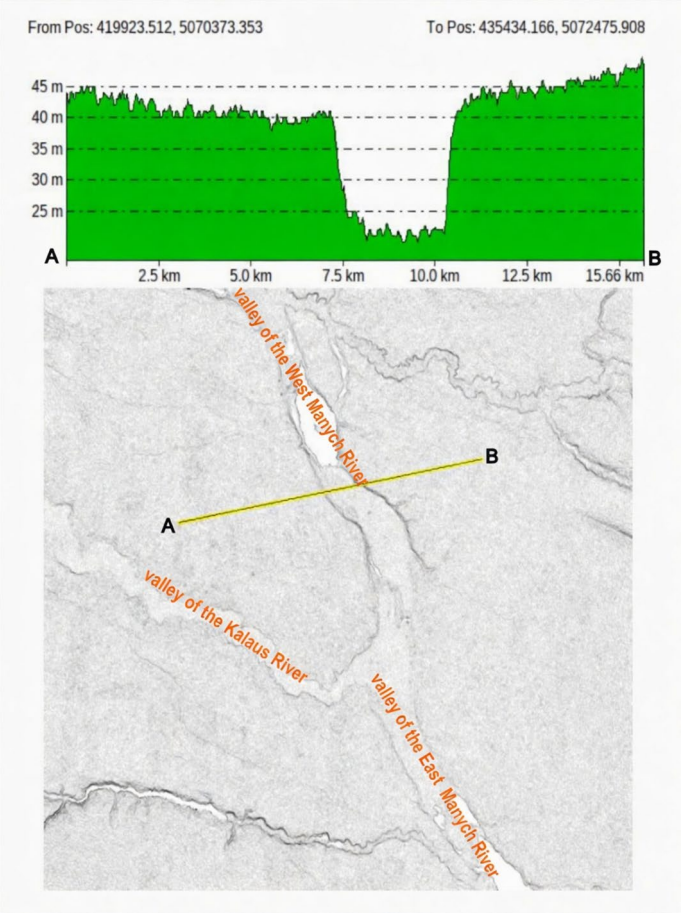

Fig.3. Profile of the Western Manych River valley, downstream from the Kalaus River delta, based on SRTM3 data.

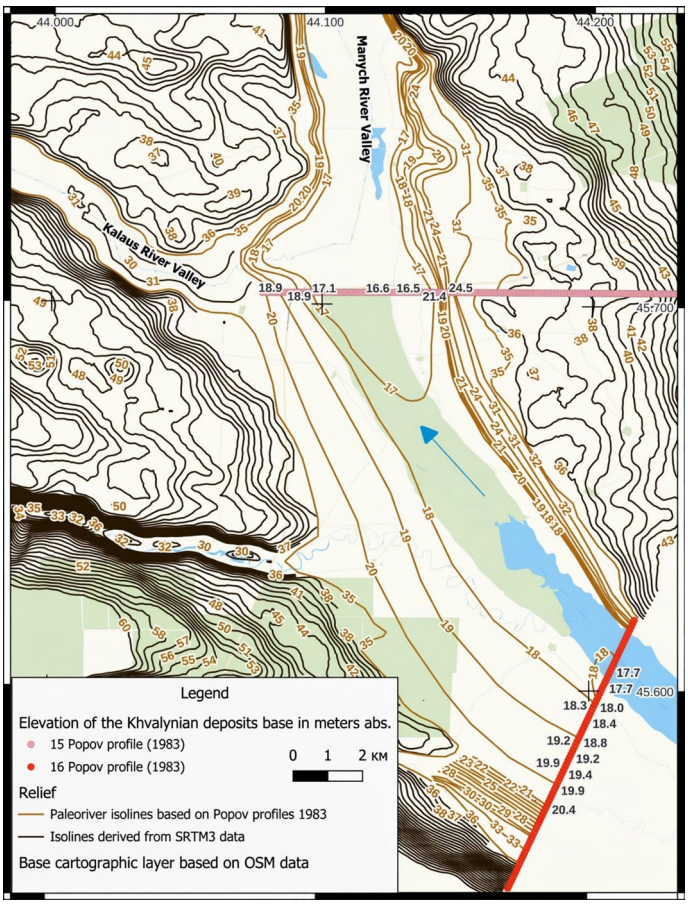

Fig.4. Map No. 1 of the paleorelief of the Manych Strait near Zunda-Tolga.

In addition to Gudilov deposits, deposits composed of Black Sea-Mediterranean species *Cardium edule*, *Bittium reticulatum*, *Chlamys* sp., as well as the freshwater mollusc *Viviparus viviparus*, can be found on the steep banks of the Western Manych River. Such a ratio of fauna gave G.I. Popov (1983) grounds to distinguish a separate Surozh horizon in the valley of the Western Manych River. According to G.I. Popov (1983), Surozh deposits pass into Khvalynian deposits near Proletarsk. However, the coexistence of freshwater and Mediterranean molluscan fauna in one water body is impossible. Most likely, the Mediterranean fauna was washed out from Karangat deposits during the discharge of Khvalynian waters through the Manych valley (Yanina, 2012; Yanina et al., 2025). Surozh deposits are also found at the Yulovskaya site, where they are abutted against Gudilov deposits (Lavrentyev, 2025). Consequently, Surozh deposits are younger than Gudilov deposits, which confirms the hypothesis that Surozh deposits were formed during the functioning of the Manych Strait.

Downstream, near the Sukhoy village, the valley widens in the form of a meander to 30 km and then ends with a narrowing to 5 km near the Manych-Balabinka village, where the section of the same name is located (Lisitsyn, 1932) at an elevation of 4 m a.s.l.

Further, Caspian waters entered the overdeepened channel of the Paleo-Don River, which, according to profile 23 by G.I. Popov (1983), reaches a depth of –20 m a.s.l. At present, the overdeepened channel of the Paleo-Don River is overlain by Holocene alluvium (Fig. 7).

It was precisely –20 m a.s.l. that served as the base level of erosion for the Manych Strait. Further, the waters of the Khvalynian basin discharged into the Neoeuxinian basin (–50, –100 m a.s.l.).

2.3. Hydraulic modelling

Based on the constructed digital paleorelief model, hydraulic modelling of Caspian water discharge through the Manych valley was performed.

Calculations were carried out in the HEC-RAS software package version 6.6, designed for one-dimensional steady flow modelling in open channels. HEC-RAS was developed by the Hydrologic Engineering Center (USA) and has acquired wide distribution in hydraulic and hydrological research due to the high quality of its algorithms and free distribution (English, 2023).

At present, HEC-RAS has effectively become the de facto global standard for solving flood risk management tasks, designing hydraulic structures, and hydraulic modelling of water bodies in many countries.

In Russia, the HEC-RAS software package has also successfully passed approbation and is actively used in scientific and design works. A vivid example is the candidate dissertation by D.A. Nikiforov, “Modelling of the Level Regime of the Yenisei River Reservoirs” (2016), in which HEC-RAS was used for detailed modelling of the hydraulic regime of the Yenisei River reservoirs.

Hydraulic calculations are based on the Saint-Venant equations and the Chezy formula describing steady uniform flow (Nikiforov, 2016, p. 6). Manning’s roughness coefficients (n) of the channel were determined from the tables of M.F. Sribny (Baryshnikov, 2003, p. 134), taking into account paleobotanical data.

According to palynological studies of the section of the Late Paleolithic Yulovskaya site (Western Manych River valley), at the beginning of the degradation of the Late Valdai glaciation (~17 ka), alder forests grew along watercourses in the floodplain of the Manych valley (Lavrentyev et al., 2012; Lavrentyev, 2022). Approximately simultaneously, the overflow of Caspian waters through the Manych depression began (Semikolennykh et al., 2022). Therefore, at the initial stage of the transgression, the model adopted a roughness coefficient (n = 0.08), characteristic of a vegetated channel.

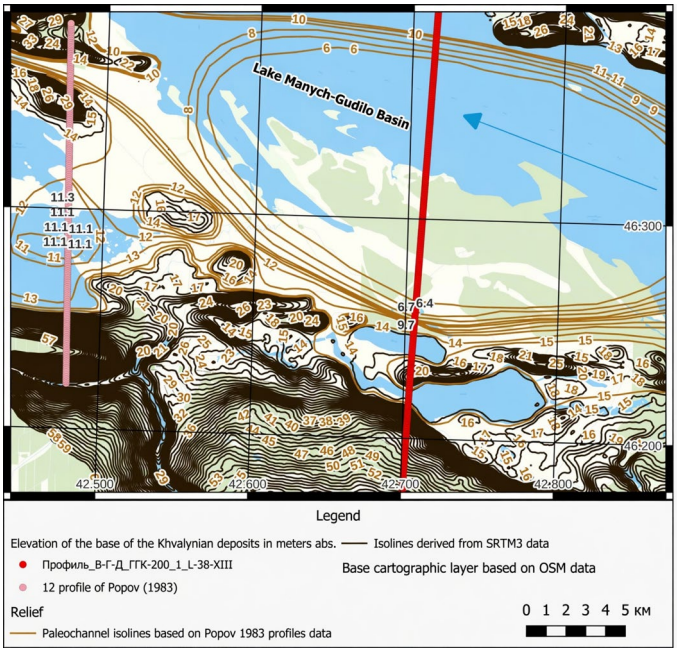

Fig.5. Map No. 2 of the paleorelief in the Manych Strait near Lake Manych-Gudilo.

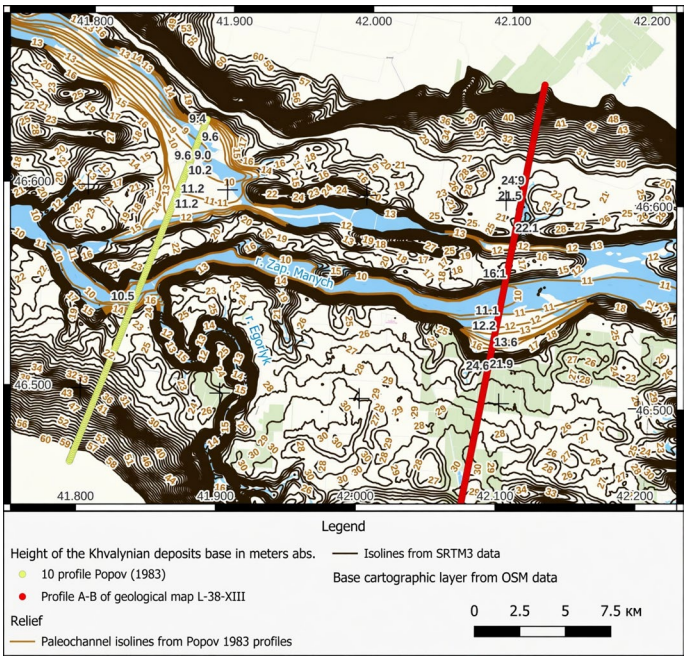

Fig.6. Map No. 3 of the paleorelief in the Manych Strait near the Salsk uplift.

As a permanent flow formed and the channel was incised, the roughness coefficient decreased to values typical of large lowland rivers (n = 0.035). Such a decrease in the roughness coefficient n naturally leads to an increase in mean flow velocity and, as a rule, to a decrease in water depth (level) at a fixed discharge.

The calculations also took into account the following parameters:

- effective evaporation during the Early Khvalynian transgression — 650 mm/year (Sidorchuk et al., 2021);
- maximum total river inflow to the Khvalynian Caspian basin (including glacial runoff) — 18,000 m^3/s (Sidorchuk et al., 2021).

When accounting for effective evaporation, the inflow to the Manych valley was adjusted by reducing the input water discharge by an amount equivalent to evaporation from the water surface (~650 mm). This approach is empirical in nature and represents a simplification. To obtain more accurate and substantiated estimates, detailed studies of the water balance of the Khvalynian Caspian basin are required, which may become the subject of further research.

Thus, hydraulic modelling enabled the assessment of flow characteristics during different periods of existence of the Manych Strait.

3. Results and discussion

During the performed research, four digital models of the Manych valley paleochannel were constructed with spillway threshold heights of 18, 31, 45, and 46 m a.s.l. The variant with a 46 m a.s.l. threshold includes filling of the Manych valley with deposits, from which the ridge relief could have formed (Fig. 8). For the digital paleochannel models with 31 and 45 m a.s.l. thresholds, a second Salsk spillway threshold 18–19 m a.s.l. high was constructed.

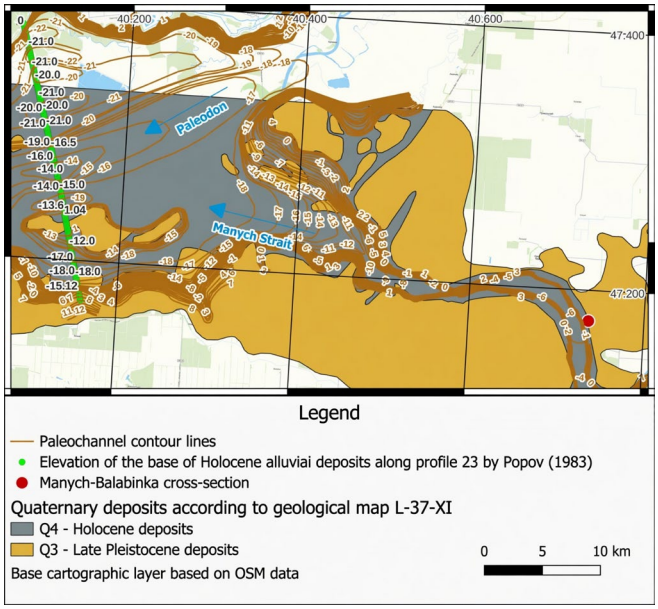

Fig.7. Map No. 4 of the paleorelief in the Manych Strait near the confluence of the Western Manych River with the Don River.

3.1. Hydraulic modelling of the Caspian water discharge through the Manych valley

Based on the digital paleochannel models, hydraulic modelling of Caspian water discharge was performed with water discharges in the following ranges:

- possible river inflow to the Caspian in the Late Glacial — 10,000–18,000 m^3/s (Sidorchuk et al., 2021; Gelfan et al., 2024);
- maximum possible discharge of Caspian waters through the Manych valley — 50,000–65,000 m^3/s (Chepalyga, 2005; Sidorchuk et al., 2011).

Additionally, the discharge capacity of the Manych Strait channel was investigated at a spillway threshold of 18 m a.s.l. and a water level of 48 m a.s.l.

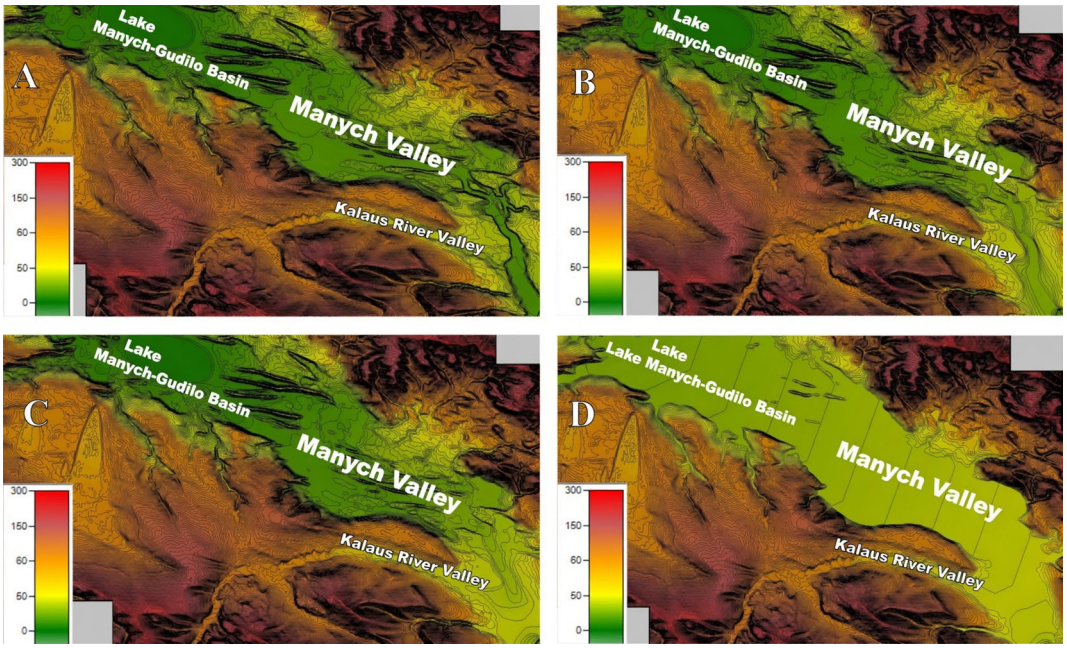

Fig.8. Paleorelief of the Manych valley channel with spillway thresholds: A – 18 m a.s.l.; B – 31 m a.s.l.; C – 45 m a.s.l.; D – 46 m a.s.l. with filling by Manych valley sediments.

Moreover, based on the elevations of the main terraces of the Khvalynian Caspian basin at 20–22, 28–30, 34–36, 46–48 m a.s.l. (Rychagov, 1997), calculations of the Manych Strait discharge, corresponding to the height of Khvalynian Caspian terraces, were presented.

3.1.1. Hydraulic calculations of the Caspian water discharge at a spillway threshold of 18 m a.s.l.

According to geological profile No. 16 (Popov, 1983), the height of the spillway threshold near Zunda-Tolga was 18 m a.s.l. (Fig. 9). The spillway threshold of 18–20 m a.s.l. formed at the end of the existence of the Manych Strait. This is evidenced by the deep erosional incision and dates of Khvalynian deposits belonging to the end of the strait's existence, 14.2–14.9 ka (Semikolennykh et al., 2025). Consequently, the roughness coefficient was approximately 0.035. Based on the presented data, the following calculation results were obtained.

When the Khvalynian basin was at 22 m a.s.l., corresponding to Khvalynian terraces at 20–22 m a.s.l. (Rychagov, 1997), the discharge was ~1,000 m^3/s (Table 2). This was the final stage of the Manych Strait's existence.

At a Khvalynian basin level of 28.1 m a.s.l., the discharge into the Manych valley was ~15,000 m^3/s. This discharge value corresponds to the maximum river inflow to the Caspian of 18,000 m^3/s minus effective evaporation of 650 mm (Sidorchuk et al., 2021). This level corresponds to Khvalynian terraces at 28–30 m a.s.l. (Rychagov, 1997).

To achieve a water level corresponding to Khvalynian terraces at 34–36 m a.s.l. (Rychagov, 1997) with a spillway threshold of 18 m a.s.l., a discharge of ~65,000 m^3/s would be required. This value corresponds to the upper limit of the maximum discharge through the Manych Strait, which was reconstructed based on the cross-sectional area of a large paleomeander in the lower reaches of the Western Manych River (Sidorchuk et al., 2011).

Table 2. Results of hydraulic modelling of the Caspian water discharge through the Manych valley at a spillway threshold of 18 m a.s.l. in the area of Popov's profile No. 16 (1983), Zunda-Tolga village.

Water level, m a.s.l.	Roughness coefficient 0.035	Discharge, m^3/s	Wetted cross-sectional area, m^2	Flow velocity, m/s
22	0.035	1,000	20,599	0.05
28.1	0.035	15,000	57,858	0.26
28.72	0.035	18,000	59,358	0.27
33	0.035	50,000	97,349	0.51
35	0.035	65,000	108,550	0.60
40	0.035	130,000	176,500	0.91
48	0.035	350,000	255,861	1.36

The discharge capacity of the Manych valley at water levels of 40–48 m a.s.l. ranges from 130,000 to 350,000 m^3/s. This value is comparable to the estimates of A.Yu. Sidorchuk, according to whose data the discharge could reach 200,000–300,000 m^3/s at a water level of 45 m a.s.l. (Sidorchuk and Panin, 2022). At such a large discharge, the Caspian level could not have risen to 40–48 m a.s.l.

The water levels of 22 m, 28.1 m, 34–36 m, and 40–48 m a.s.l. presented in this subsection do not reflect successive stages of Khvalynian basin rise at a spillway threshold of 18 m a.s.l. These elevations were used exclusively as hypothetical scenarios to assess the discharge capacity of the Manych Strait at a fixed thresh-

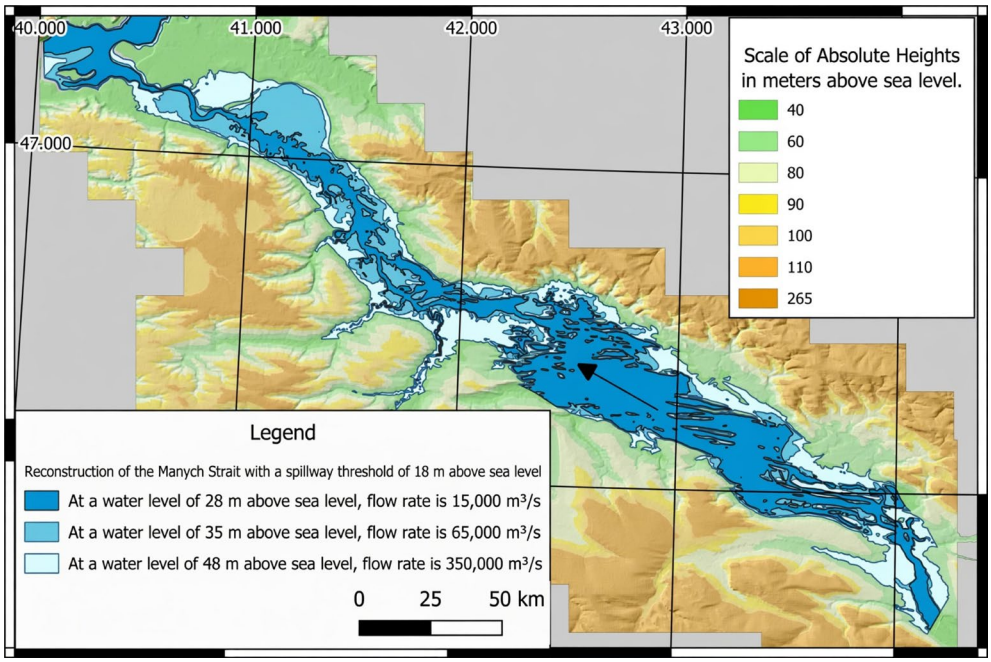

Fig.9. Reconstruction map of the Manych Strait with a spillway threshold of 18 m a.s.l. and a roughness coefficient of 0.035.

old height. The main purpose of the calculations is to demonstrate that with a geologically confirmed spillway threshold height (~18 m a.s.l., profile No. 16 by G.I. Popov, 1983) and realistic total river inflow to the Khvalynian basin (10–18 thousand m^3/s), maintaining the Caspian Sea level at the traditionally accepted maximum transgression elevations (40–48 m a.s.l.) requires a water discharge of the order of 130–350 thousand m^3/s, which appears to be an unrealistic scenario. Thus, these calculations are intended to reveal the contradiction between a low spillway threshold and ideas about a high maximum of the Early Khvalynian transgression and to justify the need to analyze alternative scenarios with a higher initial spillway threshold height.

3.1.2. Hydraulic calculations of the Caspian water discharge at a spillway threshold of 31 m a.s.l.

Since the Khvalynian basin level could not rise to 40–48 m a.s.l. with a spillway threshold of 18 m a.s.l., it was necessary to raise the Manych Strait spillway threshold to 31 m a.s.l. It was most likely from this higher spillway threshold that the discharge of the Caspian waters into the Manych valley began, where alder forests grew along watercourses (Lavrentyev et al., 2012; Lavrentyev, 2022). Therefore, a roughness coefficient (n = 0.08), characteristic of a vegetated channel, was adopted in the hydrological model.

At a threshold of 31 m a.s.l. and a discharge of 18,000 m^3/s, the water level reached 40.55 m a.s.l., taking into account effective evaporation of ~40.0 m a.s.l. (Fig. 10). The corresponding discharge was 15,500 m^3/s. This level also corresponds to the Khvalynian terrace in the Yergeni (Lavrentyev and Chepalyga, 2024). Subsequently, the water level could drop to 37 m a.s.l. due to a change in the roughness coefficient in the strait at the same water discharge (Table 3).

Table 3. Results of hydraulic modelling of the Caspian water discharge through the Manych valley at a spillway threshold of 31 m a.s.l. in the area of Popov's profile No. 16 (1983), Zunda-Tolga village.

Roughness coefficient 0.035

Water level, m a.s.l.	Discharge, m^3/s	Wetted cross-sectional area, m^2	Flow velocity, m/s
35	6,000	19,518	0.31
37.2	14,800	35,630	0.42
37.82	18,000	41,068	0.44
41	50,000	76,828	0.65
42	65,000	91,164	0.71
48	160,000	161,572	0.99

Roughness coefficient 0.08

Water level, m a.s.l.	Discharge, m^3/s	Wetted cross-sectional area, m^2	Flow velocity, m/s
35	3,000	21,217	0.14
40	15,500	62,152	0.25
40.55	18,000	67,872	0.27
46	50,000	133,918	0.37
47	65,000	154,190	0.42

At a discharge of 65,000 m^3/s, the water level reached 47.3 m a.s.l. This value is close to the maximum level of the Early Khvalynian transgression—48 m a.s.l. (Fedorov, 1957; Rychagov, 1997; Svitoch et al., 2010; Chepalyga et al., 2007 and others). Subsequently, with a decrease in the roughness coefficient, the water level could drop to 42 m a.s.l.

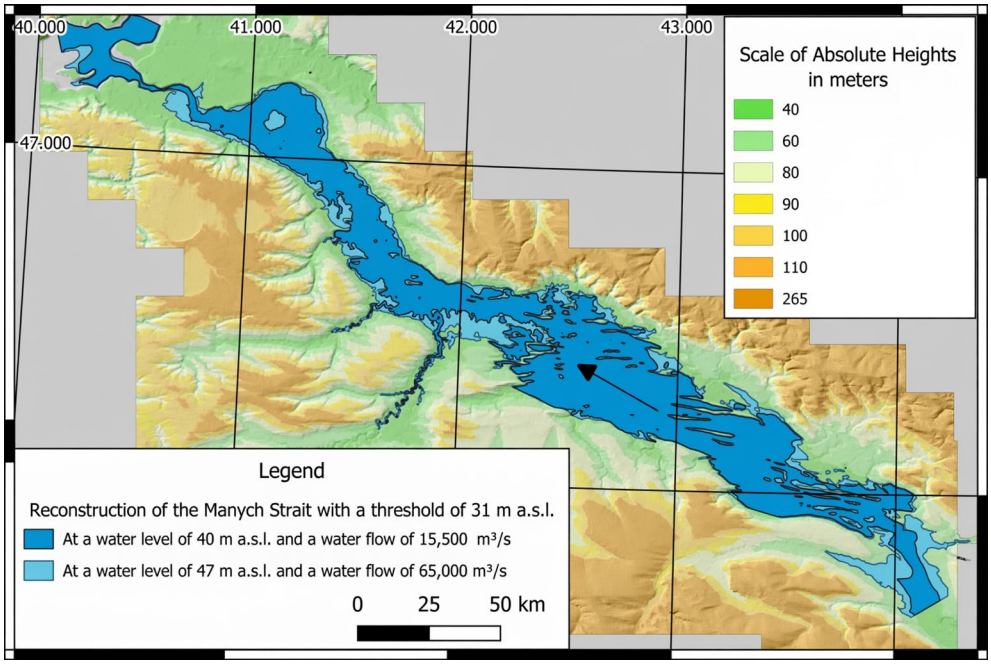

Fig.10. Reconstruction map of the Manych Strait with a spillway threshold of 31 m a.s.l. and a roughness coefficient of 0.08.

3.1.3. Hydraulic calculations of the Caspian water discharge at a spillway threshold of 45 m a.s.l.

In the area of the Kalaus River delta, terraces of 40–45 m a.s.l. high are recorded, which suggests that the initial spillway threshold could have reached 45 m a.s.l. (Kvasov, 1975; Popov, 1983; Rychagov, 1997; Svitoch et al., 2010).

At the beginning of the strait's existence, the roughness coefficient was n = 0.08. At a discharge of 18,000 m^3/s, the water level reached 47.2 m a.s.l., taking into account effective evaporation of 46.65 m a.s.l. (Table 4). The corresponding discharge was 12,400 m^3/s. This value is close to the maximum level of the Khvalynian transgression (Fig. 11).

3.1.4. Hydraulic calculations of the Caspian water discharge with sediment filling

The scenario with a 46 m a.s.l. threshold assumes partial filling of the Manych valley with sediments, which changes the morphometric parameters of the channel. The roughness coefficient was n = 0.08 (Fig. 12).

At a discharge of 18,000 m^3/s, the water level in Zunda-Tolga was 49.7 m a.s.l., taking into account effective evaporation of 49.15 m a.s.l. The corresponding discharge was 12,600 m^3/s. This value is close to the maximum level of the Khvalynian transgression (Table 5).

Reconstructions with spillway thresholds of 31, 45, and 46 m a.s.l. are hypothetical. The existence of these Manych Strait spillway thresholds is not confirmed by geological evidence. However, a higher spillway threshold of 31–45 m a.s.l. allows justifying the Khvalynian basin level in the range of 40–48 m a.s.l. from the point of view of the Caspian water balance (Fig. 13).

Table 4. Results of hydraulic modelling of the Caspian water discharge through the Manych valley at a spillway threshold of 45 m a.s.l. in the area of Popov's profile No. 16 (1983), Zunda-Tolga village.

Roughness coefficient 0.035

Water level, m a.s.l.	Discharge, m^3/s	Wetted cross-sectional area, m^2	Flow velocity, m/s
45.61	6,000	6,642	0.90
46.19	18,000	14,662	1.23
47.66	50,000	38,471	1.30
48.37	65,000	50,467	1.29

Roughness coefficient 0.08

Water level, m a.s.l.	Discharge, m^3/s	Wetted cross-sectional area, m^2	Flow velocity, m/s
45.69	3,000	7,551	0.40
46.65	12,400	21,955	0.56
47.21	18,000	31,050	0.58
49.99	50,000	78,471	0.64
50.81	65,000	93,099	0.70

The reconstruction of the Manych Strait paleochannel with a spillway threshold of 18–20 m a.s.l. is justified according to geological profiles by G.I. Popov (1983). If we look at the longitudinal profile of the Manych Strait with a spillway threshold of 18 m a.s.l., the following patterns are observed (Fig. 13). In the area of the Zunda-Tolga uplift, a channel gradient is observed. Flow velocity increases (Fig. 14), which is quite natural, since this is the narrowest section of the Manych valley, where deep erosion predominantly occurred. Then, in the area of Lake Manych-Gudilo, the

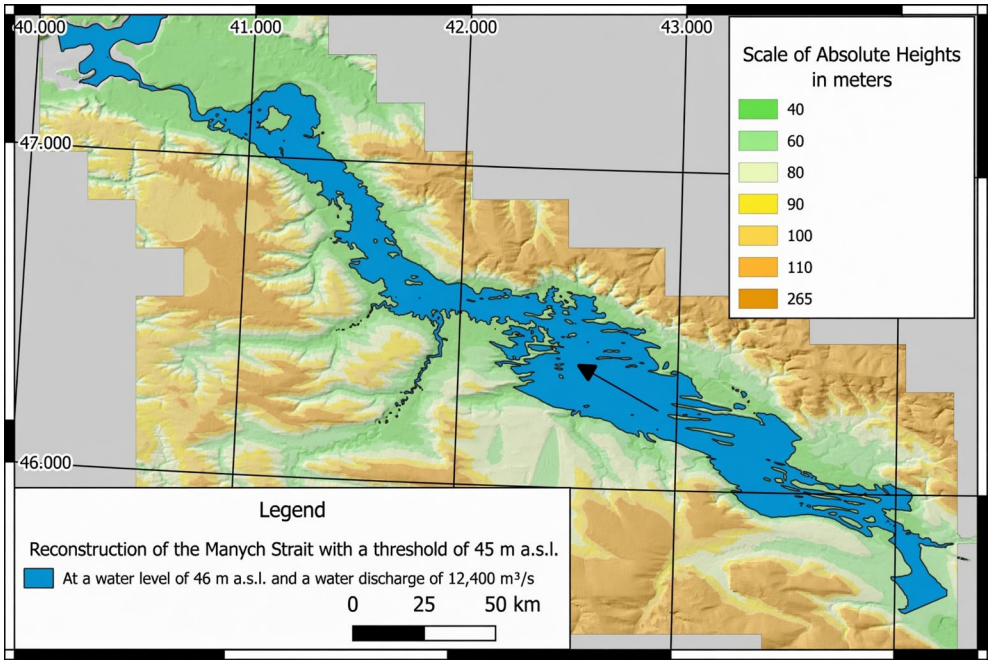

Fig.11. Reconstruction map of the Manych Strait with a spillway threshold of 45 m a.s.l. and a roughness coefficient of 0.08.

longitudinal profile of the strait levels out. Flow velocity becomes calmer (Fig. 14).

Here, Khvalynian sediments abutted against Gudilov deposits can be seen; consequently, sediment accumulation occurred. Erosion itself was not so intense. After the Salsk uplift, the channel of the strait drops again. The Western Manych depression is characterized by a large elevation difference and high flow velocities. The modelling data confirm the geological structure of the Western Manych depression. In deposits on the first and second floodplain terraces, redeposited fauna from underlying horizons is recorded, indicating active channel erosion.

However, despite intense erosion, the longitudinal profile of the Manych Strait is not sufficiently incised, which suggests the short duration of its existence.

Table 5. Results of hydraulic modelling of Caspian water discharge through the Manych valley at a spillway threshold of 46 m a.s.l. with sediment filling in the area of Popov's profile No. 16 (1983), Zunda-Tolga village.

Roughness coefficient 0.035

Water level, m a.s.l.	Discharge, m^3/s	Wetted cross-sectional area, m^2	Flow velocity, m/s
47.93	10,000	36,491	0.27
48.53	18,000	48,283	0.37

Roughness coefficient 0.08

Water level, m a.s.l.	Discharge, m^3/s	Wetted cross-sectional area, m^2	Flow velocity, m/s
49.15	12,600	61,179	0.21
49.73	18,000	73,802	0.24

4. Conclusion

Hydraulic modelling within the framework of the present study provided reconstruction of the most probable scenarios of the Caspian water discharge through the Manych valley during the Khvalynian transgression of the Caspian Sea. We identified the following main scenarios:

1. With a spillway threshold of 18 m a.s.l., to reach the maximum level of the Early Khvalynian transgression (40–48 m a.s.l.), a water discharge of the order of 130,000–350,000 m^3/s would have been required. However, in the Late Pleistocene, the rivers of the Caspian basin never provided such a high discharge. Consequently, the rise of the Caspian Sea level to 40–48 m a.s.l. with a spillway threshold of 18 m a.s.l. should be considered unlikely.
2. Most likely, the initial spillway threshold was located at a higher elevation, formed by deltaic deposits of the Kalaus River. Some researchers (Sidorchuk et al., 2011; Popov, 1983; Kvasov, 1975) estimate the height of the spillway threshold at ~45 m a.s.l., which is consistent with the elevation position of terraces in the Kalaus delta area. The results of hydraulic modelling show that river inflow during the Late Glacial was sufficient to maintain the Caspian level above 46 m a.s.l. At the same time, terraces above 40 m a.s.l. lack molluscan fauna and have not yielded radiocarbon dates; therefore, the maximum level of the Khvalynian transgression (48 m a.s.l.) remains controversial.
3. The most probable scenario is when the spillway threshold was located at 31 m a.s.l. River inflow to the Khvalynian Caspian basin would have been quite sufficient to maintain the water level in the Caspian at 40 m a.s.l. This level corresponds to the Khvalynian terrace in the Yergeni and is confirmed by findings of molluscan fauna (Lavrentyev et al., 2024; Svitoch et al., 2017).

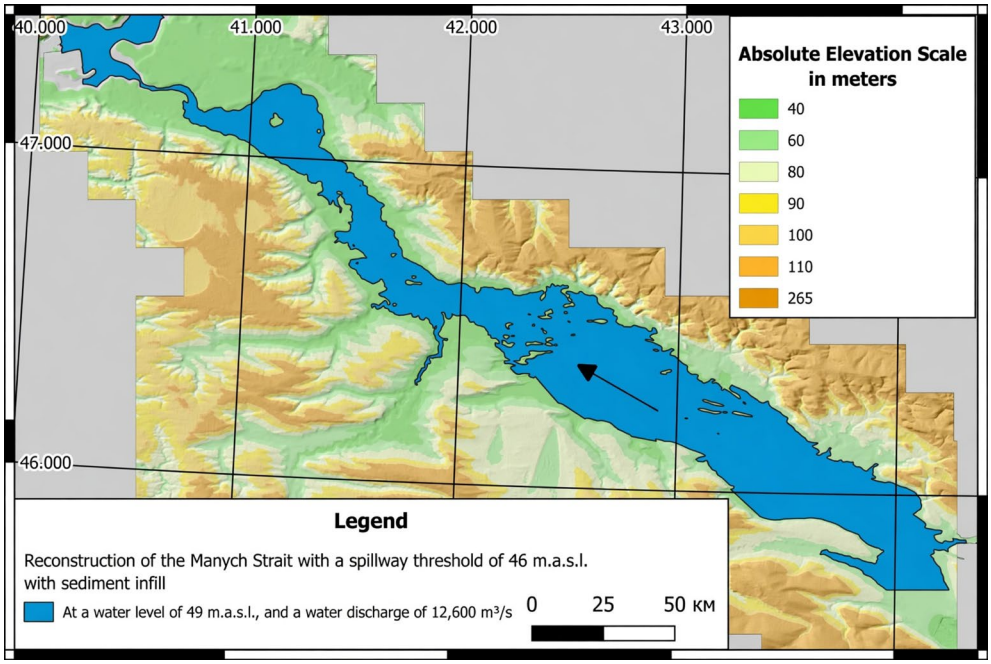

Fig.12. Reconstruction map of the Manych Strait with a spillway threshold of 46 m a.s.l., with sediment filling and a roughness coefficient of 0.08.

4. Deltaic deposits of the Kalaus River were apparently subjected to intense erosion by the waters of the Manych Strait, which caused a gradual lowering of the threshold height to 18 m a.s.l. (Sidorchuk and Panin, 2022). During the phase of active erosion, water discharge increased from 18,000 to 65,000 m^3/s. In particular, at a discharge of 65,000 m^3/s and a spillway threshold of 18 m a.s.l., the water level near Zunda-Tolga reached 35 m a.s.l., which corresponds to the elevation position of Khvalynian terraces of the Caspian (Rychagov, 1997).
5. Throughout most of the existence of the Manych Strait, the Caspian Sea level was maintained in the range of 22–35 m a.s.l., as evidenced by numerous findings of Khvalynian deposits with characteristic fauna and radiocarbon dates in this elevation interval (Arslanov et al., 2016).

Thus, the results of the conducted study indicate that the discharge of the Caspian waters through the Manych valley in the Late Pleistocene was stepwise in nature and was accompanied by a sequential lowering of the spillway threshold height. The most probable scenarios are those with spillway thresholds at 31–45 m a.s.l., corresponding to the levels of the Early Khvalynian transgressive maximum.

The results of hydraulic modeling using the HEC-RAS software package are generally in good agreement with water discharge estimates obtained from classical hydraulic calculations using the Chezy formula (Sidorchuk et al., 2011; Sidorchuk and Panin, 2022). Nevertheless, issues regarding the height of spillway thresholds, the dynamics of their erosion, and the duration of individual flow phases remain open and require further interdisciplinary study.

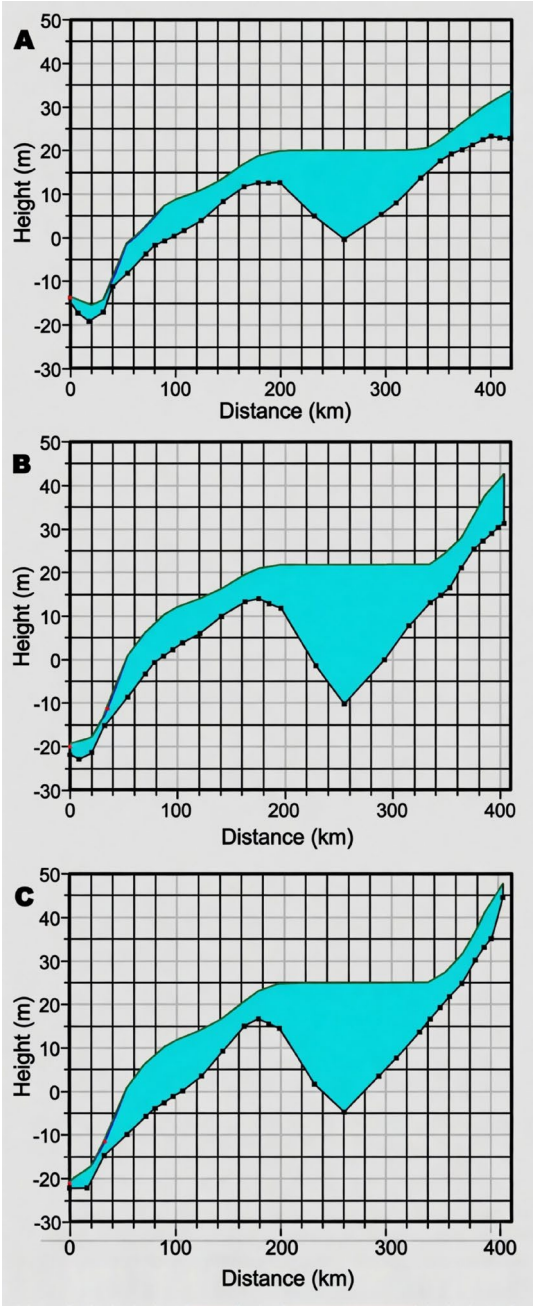

Fig.13. Longitudinal profile of the Manych Strait with a water discharge of 18,000 m^3/s: A—at a spillway threshold of 18 m a.s.l.; B—at a spillway threshold of 31 m a.s.l.; C—at a spillway threshold of 45 m a.s.l.

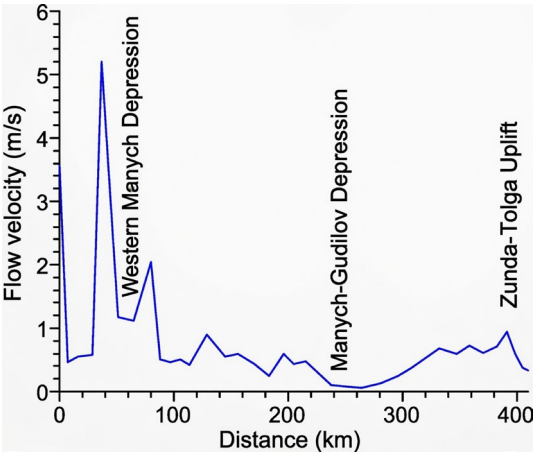

Fig.14. Longitudinal profile of the Manych Strait with flow velocities in m/s at a water discharge of 18,000 m^3/s and a spillway threshold of 18 m a.s.l.

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Conflict of interest

The author declares no conflict of interest.

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Палеогидролия Манычского пролива хвалынского бассейна Каспия в позднем плейстоцене

Оригинальная статья

LIMNOLOGY FRESHWATER BIOLOGY

Лаврентьев Н.В.

Независимый исследователь

АННОТАЦИЯ. В статье рассматриваются дискуссионные вопросы палеогидрологии Манычского пролива — ключевого звена в системе водообмена между хвалынским бассейном Каспия и новоэвксинским бассейном Чёрного моря в позднем плейстоцене. Основное внимание уделено двум параметрам: максимальному уровню хвалынской трансгрессии и высоте порога стока через Манычскую впадину. На основе геолого-геоморфологического анализа, цифрового моделирования рельефа и гидравлического моделирования в системе HEC-RAS автором реконструированы сценарии сброса каспийских вод через Манычскую долину. Результаты моделирования позволили установить, что наиболее вероятный максимальный уровень Каспия во время раннехвалынской трансгрессии составлял около 40 м н.у.м. при пороге стока в 31 м н.у.м. Также рассчитаны гипотетические пределы пропускной способности русла Манычского пролива Хвалынского бассейна Каспия. Результаты могут быть использованы в дальнейших исследованиях.

Ключевые слова: Каспийское море, поздний плейстоцен, хвалынская трансгрессия, Манычская долина, палеогидрология, гидравлическое моделирование, порог стока, цифровая модель рельефа, уровень моря, реконструкция палеосреды

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1. Введение

Манычская впадина представляет собой тектоническое желобовидное понижение, отделяющее Предкавказье от степной части юга Восточно-Европейской равнины и соединяющее Кубано-Приазовскую и Прикаспийскую низменности. По днищу впадины протекает река Маныч.

Возможность водообмена между Черноморским и Каспийским бассейнами через Манычскую долину была впервые обоснована Н. Я. Данилевским в 1869 г. (Данилевский, 1869). Исследования четвертичной геологии региона ведутся более 150 лет, в ходе которых были детально изучены отложения (включая малакофауну) и реконструирована хронология эпизодов водообмена между Чёрным и Каспийским морями (Богачев, 1903; Лисицын, 1932; Горецкий, 1953; Попов, 1983; Чепалыга и Пирогов, 2005; Свиточ и др., 2010; Семиколенных и др., 2022).

Современные представления об истории формирования Манычской долины в плейстоцене в значительной степени опираются на фундаментальные исследования Г. И. Попова (1983), который на основе анализа многочисленных разрезов и данных бурения детально реконструировал геологическое строение и историю формирования Манычской долины.

Последний раз Манычская долина заполнялась морскими водами в конце позднего плейстоцена, во время хвалынской трансгрессии Каспия. Согласно последним данным абсолютного OSL-датирования, функционирование Манычского пролива происходило в интервале примерно 17,7–14,9 тыс. лет назад (Семиколенных и др., 2022), что соответствует эпохе деградации поздневалдайского (осташковского) оледенения (MIS 2).

Несмотря на длительную историю исследований палеогеографии Манычской долины, гидрологические параметры Манычского пролива в период хвалынской трансгрессии продолжают оставаться предметом активной научной дискуссии. К числу наиболее дискуссионных относятся два ключевых параметра:

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1. Максимальный уровень хвалынской трансгрессии. Согласно преобладающей точке зрения, максимальный уровень хвалынской трансгрессии достигал 48 м н.у.м. (Федоров, 1957; Рычагов, 1997; Свиточ и др., 2010; Чепалыга, 2007 и др.). Террасы на этой отметке описаны на побережье Дагестана (Рычагов, 1997) и на Красноводском полуострове, который находится на восточном побережье Каспия (Федоров, 1957). Кроме того, террасы на высоте 48 м н.у.м. фиксируются по данным цифровой модели местности SRTM3 (Лаврентьев, 2013). Однако на этих террасах отсутствует малакофауна и радиоуглеродные датировки. Наиболее высокая терраса с хвалынской малакофауной зафиксирована в Ергенях на уровне 40 м н.у.м. (Лаврентьев и др., 2024; Свиточ и др., 2017). Аналогичные отметки (до 40 м н.у.м.) наблюдаются в районе Самарской Луки в долине р. Малый Караман (Макшаев и др., 2025). Таким образом, террасы хвалынской трансгрессии выше 40 м н.у.м. не подтверждены датировками и хвалынской малакофауной, что делает максимальный уровень трансгрессии предметом дискуссии.
2. Высота порога стока Манычского пролива. Согласно геологическому профилю № 16 (Попов, 1983), порог стока в районе с. Зунда-Толга располагался на уровне около 18–20 м н.у.м. Ряд исследований показывает, что при такой высоте порога стока уровень Каспия не мог достигать 48 м н.у.м. (Квасов, 1975; Попов, 1983; Варущенко и др., 1987; Свиточ и др., 2010; Рычагов, 1997; Чепалыга и Пирогов, 2005). Гидравлические расчёты указывают на высокую пропускную способность русла при уровне 45 м н.у.м. — от 200 000 до 300 000 м^3/с (Сидорчук и Панин, 2022), что сопоставимо со стоком р. Амазонка. Более консервативные оценки максимального стока через Манычскую долину составляют ~50 000 м^3/с (Чепалыга и Пирогов, 2005), на основе характера отложений у с. Зунда-Толга, или до 65 000 м^3/с (Sidorchuk et al., 2011), исходя из площади живого сечения крупной меандры в районе хутора Сухой. Эти значения существенно превышают реконструированный речной сток в Каспий во время раннехвалынской трансгрессии — 520–570 км^3/год (~16 500–18 000 м^3/с) (Сидорчук и др., 2021), из которых до 80 % обеспечивалось стоком Волги (~423 км^3/год). Альтернативные оценки речного стока дают 320–375 км^3/год (Gelfan et al., 2024). Современный многолетний сток Волги составляет 228–274 км^3/год (Георгиади и др., 2017). Указанное несоответствие делает невозможным высокий уровень хвалынского бассейна при пороге стока 18–20 м н.у.м. В связи с этим авторами исследований выдвигается гипотеза о существовании в начале хвалынской трансгрессии более высокого порога стока (Квасов, 1975; Попов, 1983; Чепалыга и Пирогов, 2005; Свиточ и др., 2010; Sidorchuk et al., 2011), преимущественно сформированного отложениями дельты р. Калаус. Более высокий порог стока Манычской долины позволяет объяснить наличие хвалынских террас выше 30 м н.у.м. Однако нет геологических доказательств существования более высокого порога стока. Следовательно, высота порога стока Манычского пролива в начале хвалынской трансгрессии является предметом научной дискуссии.

Таким образом, вопрос о максимальном уровне хвалынской трансгрессии и высоте порога стока требует дополнительного анализа. Необходимо провести моделирование сценариев сброса каспийских вод через Манычскую долину с использованием цифровой модели рельефа и гидравлических расчётов. Это позволит уточнить ключевые параметры палеогидрологии Манычского пролива хвалынского бассейна Каспия.

2. Материалы и методы

2.1. Реконструкция рельефа русла Манычского пролива

2.1.1. Подготовка высотных данных

Высотные данные были получены из цифровой модели местности (ЦММ) SRTM3. Однако SRTM3 содержит мелкие шумы и искажения, что потребовало предварительной обработки. Обработка данных производилась с использованием программного обеспечения SAGA GIS.

ЦММ SRTM3 была перепроецирована в универсальную поперечную проекцию Меркатора (UTM) с помощью модуля UTM Projection. Для получения сглаженного рельефа, необходимого для последующей реконструкции, применялся модуль Simple Filter. После фильтрации из сглаженного рельефа были векторизованы изолинии с шагом 1 м.

Возникает вопрос об оценке точности высотных данных SRTM. В статье Л. А. Муравьёва (2007) представлена сравнительная характеристика SRTM с более точными данными топографической съёмки местности масштаба 1:5000. По мнению Л. А. Муравьёва (2007), неточность отображения высотных данных SRTM по сравнению с топографической съёмкой масштаба 1:5000 является следствием «гуляющих» плановых координат (X, Y) с амплитудой 30 метров, особенно хорошо высотные искажения видны на крутых склонах речных долин и оврагов, где корректная плановая привязка высотных данных особенно актуальна.

Использование SRTM 3 для палеореконструкций начиная с масштабов 1:100 000 можно считать корректным (Лаврентьев и др., 2008), так как отклонение плановых координат в среднем на 30 м отображается в масштабе 1:100 000 как 0,03 мм.

Также необходимо учитывать особенности применения SRTM 3 на территории лесной зоны. Поскольку радарная съёмка может отображать высоту деревьев, а не реальной поверхности Земли. В нашем случае объект исследования — Манычская долина, которая находится в степной зоне, и высотная коррекция ЦММ не требуется.

2.1.2. Создание цифровой модели палеорусла

Цифровая модель палеорусла представляет собой цифровую модель рельефа русла древнего водоёма. Для её создания необходимо было получить пространственные координаты (X, Y, Z) плейстоценовых отложений Манычского пролива. Для этого были использованы геологические профили, представленные в монографии Г. И. Попова (1983) и на листе геологической карты ГГК-200_1_L-38-XIII (Геологическая карта L-38-XIII, 1965).

Была выполнена привязка отсканированных карт с геологическими профилями к географическим координатам в программе QGIS 3.14. Учитывая мелкомасштабность исходных схем в монографии Попова (1983), для уточнения географической привязки были построены высотные профили по данным SRTM3.

Затем полученные профили были совмещены с геологическими поперечниками в графическом редакторе Inkscape (Рис. 1). Поскольку координаты высотных профилей были известны заранее, их совмещение с геологическими профилями позволило определить пространственные координаты плейстоценовых отложений.

Полученные высотные отметки плейстоценовых отложений были перенесены в табличный редактор LibreOffice Calc и использованы для создания набора XYZ-координат, на основе которых была построена цифровая модель палеорусла. Интерполяция высотных значений с шагом 1 м производилась вручную.

Полученные изолинии палеорусла были совмещены с изолиниями современной ЦММ SRTM3. Для построения цифровой модели рельефа палеорусла использовалась интерполяция Natural Neighbours в SAGA GIS. Если была необходимость изменить высоту порога стока, то высота русла и его уклон менялись методом ручной интерполяции. Исходя из выбранного сценария для моделирования, прорисовывались изолинии нужной высоты. Для имитации заполнения Манычской долины отложениями использовался модуль Fill Sinks (Wang & Liu), входящий в состав SAGA GIS.

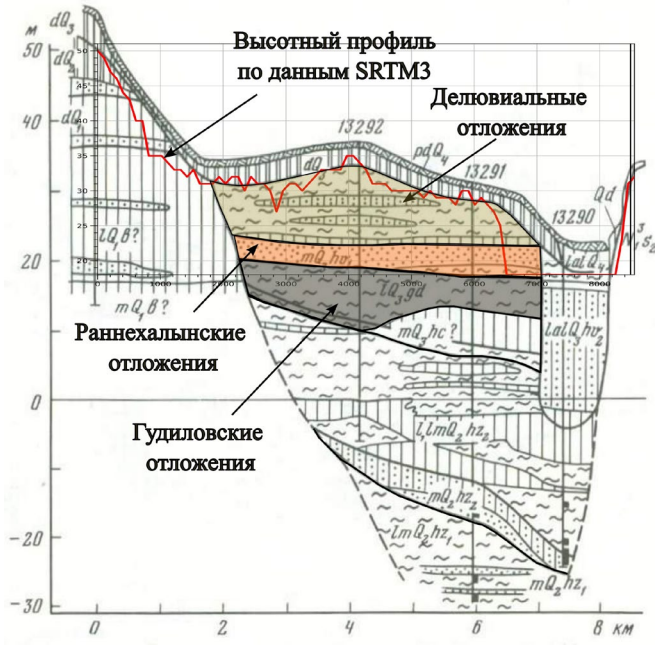

Рис.1. Геологический поперечник Попова (1983) № 16, совмещенный с высотным профилем, построенный по данным SRTM3.

2.2. Геолого-геоморфологическая характеристика Манычского пролива Хвалынского бассейна Каспия

Для проведения палеогидрологической реконструкции необходимо восстановить рельеф русла Манычского пролива, функционировавшего в период существования хвалынского бассейна Каспийского моря. Основой для такой реконструкции послужили: опубликованные геологические профили из монографии Г. И. Попова (1983), геологические карты, описание разрезов, а также собственные полевые наблюдения автора (Рис. 2).

На основе указанных источников проведём обзор геолого-геоморфологического строения палеорусла Манычского пролива. Основу рельефа данного русла составляют гудиловские озерные, сурожские и хвалынские морские отложения (Таблица 1).

Таблица 1. Стратиграфия и корреляция горизонтов и слоев Манычской долины в верхнем плейстоцене по Г.И. Попову (1983) с изменениями.

<table>
<tr><th>Основные подразделения</th><th>Западно-Манычская впадина</th><th>Сальское поднятие</th><th>Маныч-Гудиловская впадина</th><th>Восточно - Манычская впадина</th><th>Зунда-Толгинское поднятие</th></tr>
<tr><td>Голоцен</td><td colspan="5">Субаэральные отложения</td></tr>
<tr><td rowspan="6">Верхний плейстоцен</td><td colspan="4">Субаэральные отложения</td><td>Верхнехвалынские отложения</td></tr>
<tr><td>Сурожские отложения</td><td colspan="4">Нижнехвалынские отложения</td></tr>
<tr><td colspan="5">Гудиловские отложения</td></tr>
<tr><td colspan="4">Гирканские отложения</td><td rowspan="2">Гирканские отложения</td></tr>
<tr><td colspan="4">Карангатские отложения</td></tr>
</table>

Согласно Г. И. Попову (1983), в пределах Манычской впадины выделяются пять структурных элементов: Зунда-Толгинское поднятие, Восточно-Манычская впадина, Маныч-Гудиловская впадина, Сальское поднятие и Западно-Манычская впадина (Рис. 2).

Порог стока Манычского пролива находился в районе Зунда-Толгинского поднятия — наиболее узкого участка всей впадины. Основу реконструкции палеорельефа русла составили поперечные геологические профили (Попов, 1983), на которых хвалынские отложения располагаются на высотных отметках 18–20 м н.у.м. (Рис. 1). Эти отложения выходят на дневную поверхность и содержат характерную хвалынскую малакофауну. Возраст отложений, определённый по моллюскам, составляет 14,2–14,9 тыс. лет (Semikolennykh et al., 2025).

Ввиду отсутствия точных данных о высоте исходного порога стока особое значение приобретают террасы, прослеживающиеся вдоль долины (Рис. 3, Рис. 4). Так, в районе с. Зунда-Толга по данным SRTM3 на правом борту долины наблюдается терраса высотой около 44–45 м н.у.м. Подобные террасы (высотой 40–45 м н.у.м.) фиксируются ниже по течению от дельты р. Калаус (Рис. 3). Ширина поймы здесь достигает 2 км при уровне около 20 м н.у.м.

Далее воды направлялись в Восточно-Манычскую и Маныч-Гудиловскую впадины, где распространены продольные валы и замкнутые понижения, впервые описанные Н. Я. Данилевским (1864). В обнажениях продольных валов фиксируется хвалынская малакофауна (Чепалыга, 2005; 2007; Свиточ и др., 2010). Хвалынские отложения скорее всего были прислонены к гудиловским отложениям, которые вероятно составляют основу продольных валов. Эти продольные валы образовались в результате эрозионных процессов во время сброса каспийских вод через Манычскую долину (Попов, 1983; Свиточ и др., 2010). Также существует точка зрения, что продольные валы начали образовываться во время регрессивной стадии Гудиловского озера (Свиточ и др., 2010 и др.).

Регрессивная стадия Гудиловского озера началась примерно 20–17 тыс. лет назад (Лаврентьев, 2025). Понижение уровня озера, вероятно, было связано с максимумом поздневалдайского (осташковского) оледенения, которое привело к значительному похолоданию и аридизации климата, что и послужило основной причиной регрессии Гудиловского озера.

Наиболее подробно строение продольных валов изучено на о. Левый. По данным OSL-датирования, возраст хвалынских отложений составляет 17–15 тыс. лет (Семиколенных и др., 2022). Высотная отметка границы между гудиловскими и хвалынскими отложениями составляет примерно 17,4 м н.у.м.

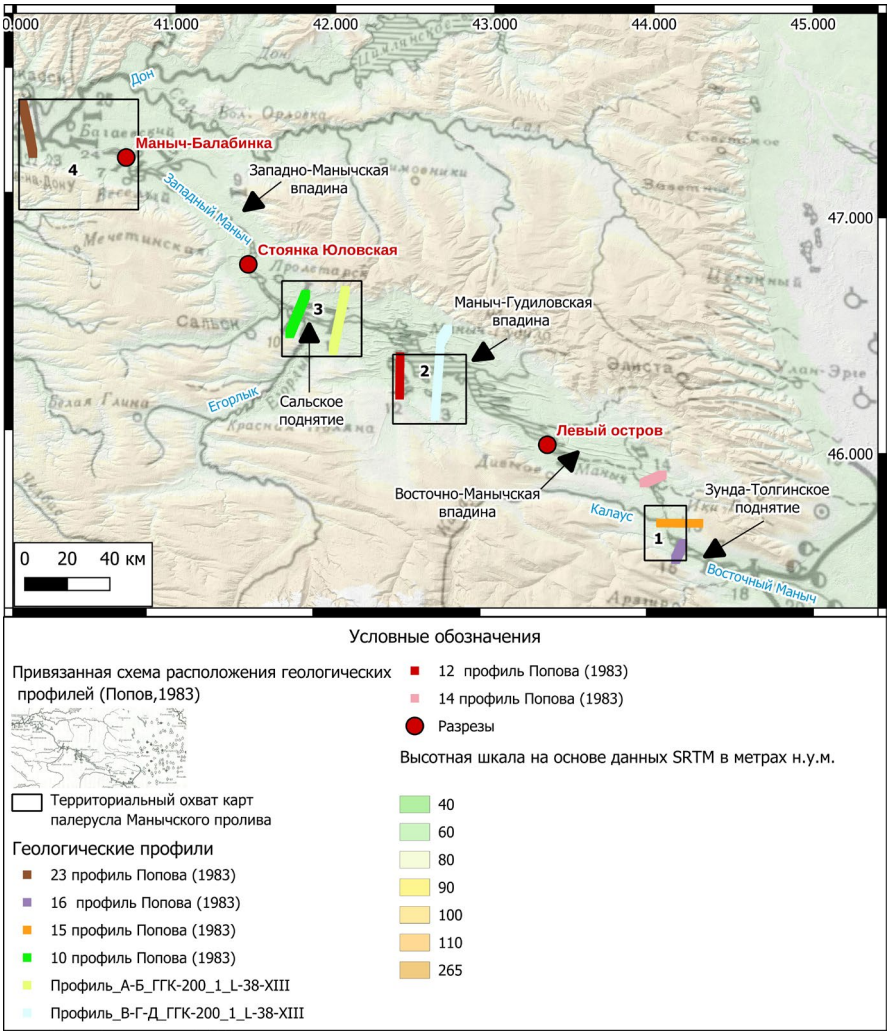

Рис.2. Карта расположения опорных геологических поперечников и разрезов.

Значительную часть Маныч-Гудиловской впадины начиная с позднего плейстоцена занимает оз. Маныч-Гудило. Судя по профилю В-Г-Д геологической карты ГГК-200_1_L-38-XIII (Геологическая карта L-38-XIII, 1965), глубина дна озера, перед сбросом каспийских вод, вероятно была на отметках 6 м н.у.м. (Рис. 5).

Долина р. Западный Маныч после расширения в районе оз. Маныч-Гудило (до 40 км) сужается до 15 км вблизи устьев р. Средний и Большой Егорлык. Здесь расположено Сальское поднятие (Рис. 6). В этом районе хвалынская фауна выявлена в основном по данным бурения на первой надпойменной террасе (высота ~20 м н.у.м.) выше устья р. Большой Егорлык (Попов, 1983). Вторая терраса представлена озёрными глинами, супесями и суглинками с малакофауной, характерной для проточных водоёмов (ассоциация *Dreissena polymorpha, Lithoglyphus, Valvata*) (Попов, 1983), на высоте около 25 м н.у.м. Предположительно в этом районе существовал второй порог стока Манычского пролива высотой 20 м н.у.м., образованный отложениями притоков Большого и Среднего Егорлыка (Квасов, 1975; Попов, 1983; Лаврентьев и Чепалыга, 2011).

Вероятно, после преодоления каспийскими водами первого порога стока в районе с. Зунда-Толга произошло заполнение котловины озера Маныч-Гудило, в результате чего на относительно короткое время в центральной части Манычской долины образовался залив раннехвалынского бассейна. При достижении уровня воды абсолютной отметки +20 м начался перелив каспийских вод через второй порог стока — Сальское поднятие. Об этом косвенно свидетельствуют изменения характера отложений в хвалынском разрезе на острове Левый (Семиколенных и др., 2022). Строение разреза отражает постепенную смену обстановок осадконакопления — от спокойных лиманных условий, связанных с ингрессией каспийских вод, к динамичным проточным условиям, обусловленным развитием и активизацией пролива.

Ниже по течению, начиная от р. Средний Егорлык, долина вновь расширяется до 20 км. Днище долины становится плоским.

Первая хвалынская терраса нижнего течения реки Западный Маныч была исследована многими авторами (Данилевский, 1869; Богачев, 1903; Лисицын, 1932 и др.). Это как правило разрезы с смешанной черноморско-каспийской и пресноводной фауной (*Cardium edule, Bittium reticulatum, Didacna trigonoides, Dreissena caspia, Dr. polymorpha, Viviparus viviparus*). Данные разрезы со смешанной фауной прослеживаются по всей Западно-Манычской впадине. В настоящее время исследование этих разрезов затруднено, так как они затоплены Веселовским водохранилищем. Исключение составляет разрез, расположенный перед плотиной Веселовского водохранилища в районе хутора Маныч-Балабинка. Он известен с 1932 года (Лисицын, 1932). Фауна смешанная, переотложенная включает каспийские и черно-

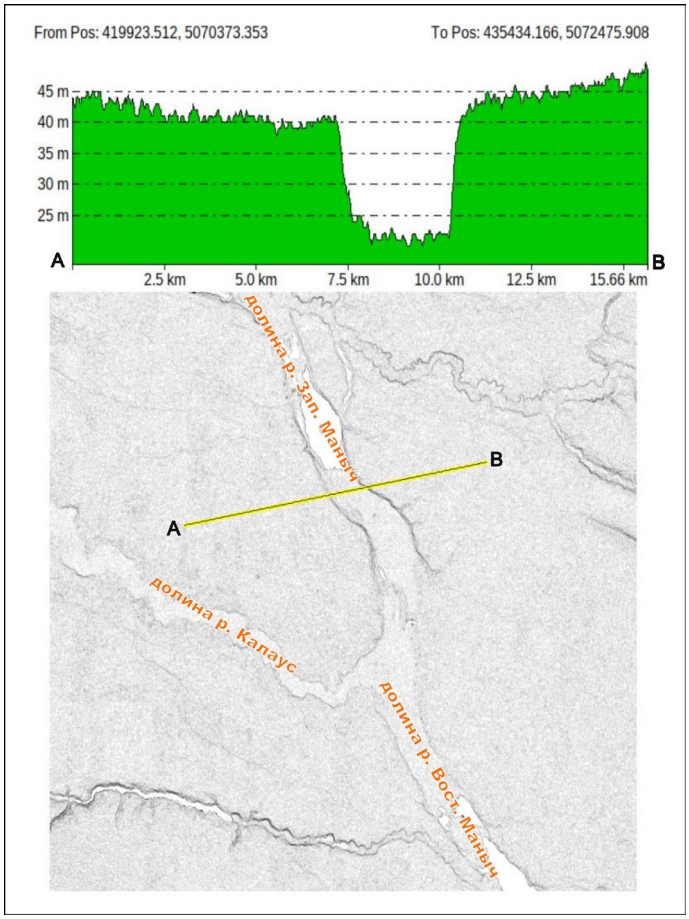

Рис.3. Профиль долины реки Западный Маныч, ниже по течению, от дельты р. Калаус, по данным SRTM3.

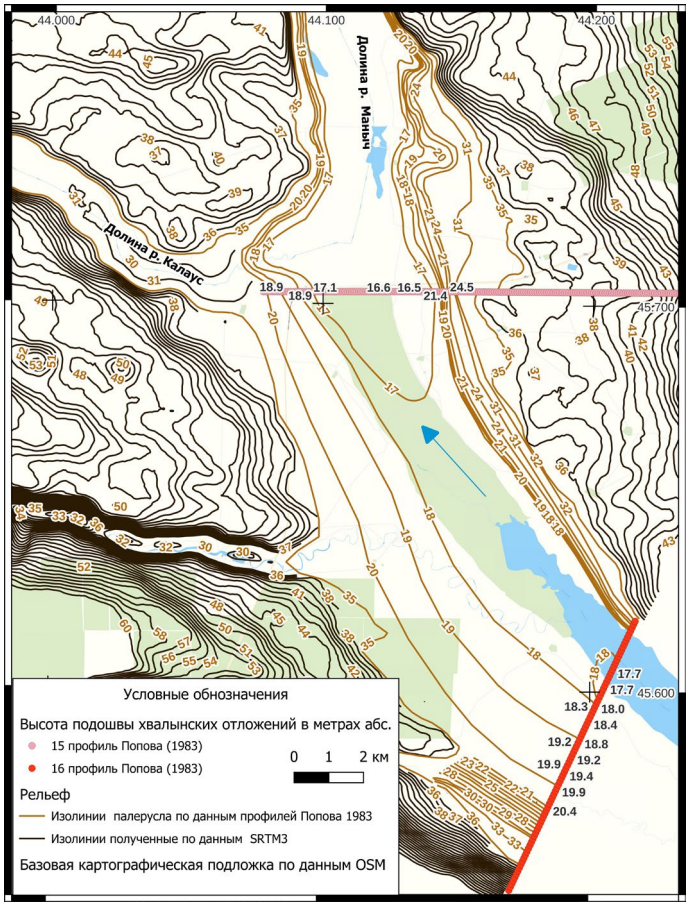

Рис.4. Карта №1 палеорельефа Манычского пролива в районе с. Зунда-Толга.

морские моллюски. Хвалынские моллюски представлены *Didacna protracta*, *Didacna ebersini*, по которым есть датировка, калиброванный при помощи OxCal 4.4, возраст 17,138 тыс. лет МГУ-1491 (Свиточ и Янина, 2001).

В основном береговые обрывы Веселовского водохранилища представлены гудиловскими отложениями с пресноводной малакофауной стоячих водоёмов (вторая надпойменная терраса). В качестве примера можно привести отложения, которые подстилают горизонты находок стоянки Юловская (Lavrentyev et al., 2012). Эта нижняя толща представлена крупнослоистыми озёрными суглинками с пресноводной фауной *Planorbis* sp., *Valvata* sp., видимая мощность — 3 м. По найденной в этих отложениях кости была получена датировка (Chepalyga et al., 2008). Калиброванная при помощи OxCal 4.4. дата — 25 546 лет назад (ЛУ-5852). По палинологическим данным этот горизонт относится к брянскому возрасту. По данным последних исследований (Сычева и др., 2015) возраст брянской палеопочвы оценивается в 33–26 тыс. лет (MIS 3). Затем происходит смена условий осадконакопления. Озёрные осадки сменяются субаквальными отложениями, в которых расположены культурные слои позднепалеолитической стоянки Юловская, возраст отложений около 17–20 тысяч лет назад. В итоге мы можем сделать вывод, что регрессивная стадия Гудиловского озера началась в период поздневалдайского (осташковского) оледенения (Lavrentyev, 2022).

Кроме гудиловских отложений на обрывистых берегах реки Западный Маныч можно встретить отложения, которые состоят из черноморско-средиземноморских видов *Cardium edule*, *Bittium reticulatum*, *Chlamys* sp., а также пресноводного моллюска *Viviparus viviparus*. Подобное соотношение фауны дало основание Г. И. Попову (1983) выделить отдельный сурожский горизонт в долине реки Западный Маныч. По мнению Г. И. Попова (1983), сурожские отложения переходят в хвалынские отложения в районе г. Пролетарск. Однако жизнь пресноводной и средиземноморской малакофауны в одном водоёме несовместима. Скорее всего средиземноморская фауна была вымыта из карангатских отложений во время сброса хвалынских вод через Манычскую долину (Янина, 2012, Янина и др., 2025). Сурожские отложения встречаются также на стоянке Юловская, где эти отложения к прислонены к гудиловским отложениям (Лаврентьев, 2025). Следовательно, сурожские отложения являются более молодыми, чем гудиловские, что подтверждает гипотезу о том, что сурожские отложения образовались во время функционирования Манычского пролива

Вниз по течению у х. Сухой долина расширяется в виде меандры до 30 км, а затем заканчивается сужением до 5 км у с. Маныч-Балабинка, где расположен одноимённый разрез (Лисицын, 1932) на высоте 4 м н.у.м.

Далее воды Каспия поступали в переуглублённое русло реки ПалеоДон, которое, судя по 23

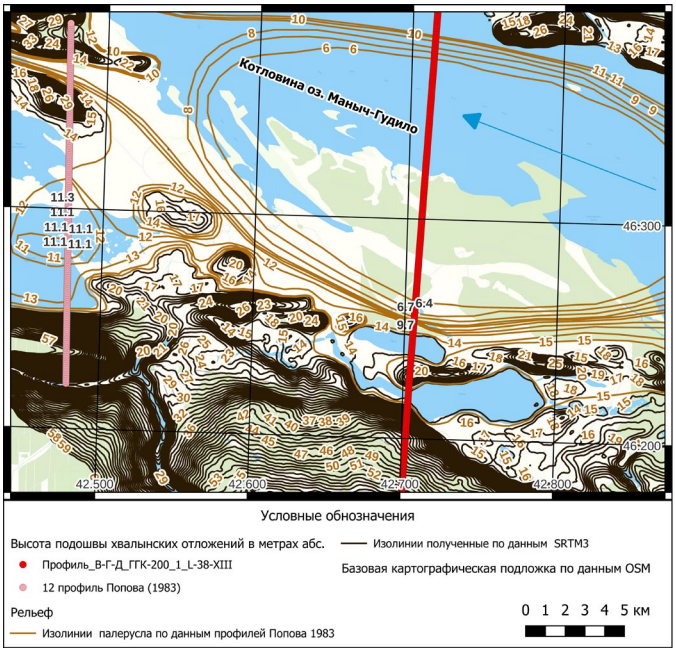

Рис.5. Карта №2 палеорельефа Манычского пролива в районе озера Маныч-Гудило.

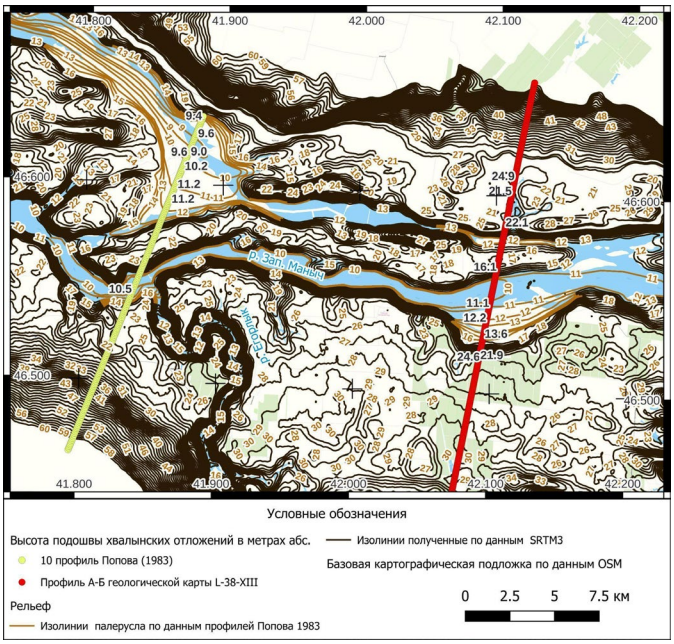

Рис.6. Карта №3 палеорельефа Манычского пролива в районе Сальского поднятия.

профилю Г. И. Попова (1983), достигает глубины −20 м н.у.м. В настоящий момент переуглублённое русло реки ПалеоДон перекрыто голоценовым аллювием (Рис. 7).

Именно −20 м н.у.м. являлся базисом эрозии Манычского пролива. Далее воды Хвалынского бассейна впадали в Новоэвксинский бассейн (−50, −100 м н.у.м.).

2.3. Гидравлическое моделирование

На основе построенной цифровой модели палеорельефа выполнено гидравлическое моделирование стока каспийских вод через Манычскую долину.

Расчёты проведены в программном комплексе HEC-RAS версии 6.6, предназначенном для одномерного стационарного моделирования течения в открытых руслах. HEC-RAS разработан Hydrologic Engineering Center (США) и получил широкое распространение в гидравлических и гидрологических исследованиях благодаря высокому качеству алгоритмов и бесплатному распространению (English, 2023).

В настоящее время HEC-RAS фактически стал де-факто мировым стандартом при решении задач управления рисками наводнений, проектирования гидротехнических сооружений и гидравлического моделирования водных объектов во многих странах.

В России программный комплекс HEC-RAS также успешно прошёл апробацию и активно применяется в научных и проектных работах. Ярким примером может служить кандидатская диссертация Д. А. Никифорова «Моделирование уровенного режима водохранилищ реки Енисей» (2016), в которой HEC-RAS использовался для детального моделирования гидравлического режима водохранилищ реки Енисей.

Гидравлические расчёты базируются на системе уравнений Сен-Венана и формуле Шези, описывающих установившееся равномерное течение (Никифоров, 2016). Коэффициенты шероховатости русла (n по Маннингу) определены по таблицам М. Ф. Срибного (Барышников, 2003) с учётом палеоботанических данных.

Согласно палинологическим исследованиям разреза позднепалеолитической стоянки Юловская (долина реки Западного Маныча), в начале деградации поздневалдайского оледенения (~17 тыс. лет назад) в пойме Манычской долины вдоль водотоков произрастали ольшаники (Lavrentyev et al., 2012; Lavrentyev, 2022). Примерно в это же время начался перелив каспийских вод через Манычскую впадину (Семиколенных и др., 2022). Поэтому на начальном этапе трансгрессии в модели принято значение коэффициента шероховатости n = 0,08, характерное для заросшего русла.

По мере формирования постоянного стока и выработки русла коэффициент шероховатости снижался до значений, типичных для крупных равнинных рек (n = 0,035). Такое уменьшение коэффициента шероховатости n закономерно приводит к росту средней скорости потока и, как правило, к снижению глубины (уровня) воды при фиксированном расходе.

В расчётах также учтены следующие параметры:

- эффективное испарение в период раннехвалынской трансгрессии — 650 мм/год (Сидорчук и др., 2021);
- максимальный суммарный речной сток в хвалынский бассейн Каспия (с учётом ледникового стока) — 18 000 м³/с (Сидорчук и др., 2021).

При необходимости учёта эффективного испарения, сток в Манычскую долину корректировался путём уменьшения входного расхода воды

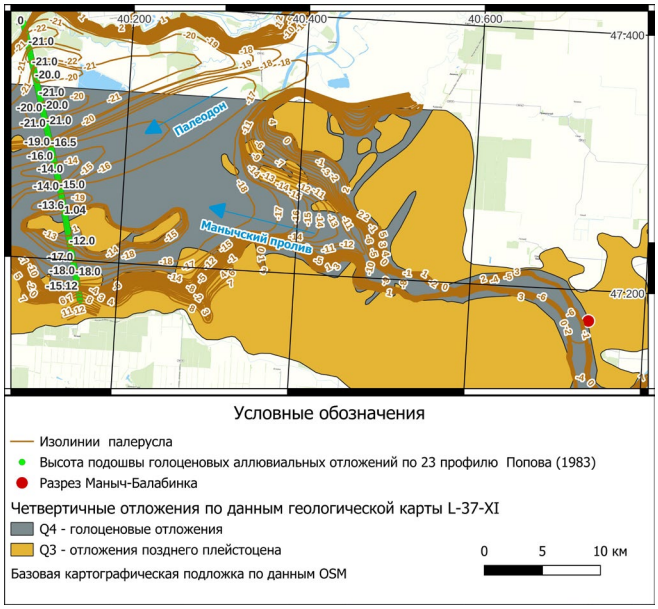

Рис.7. Карта №4 палеорельефа Манычского пролива в районе впадения р. Зап. Маныч в р. Дон.

на величину, эквивалентную испарению с зеркала водоёма (примерно на 650 мм). Данный подход носит эмпирический характер и является упрощением. Для получения более точных и обоснованных оценок требуются детальные исследования водного баланса хвалынского бассейна Каспия, что может стать предметом дальнейших исследований.

Таким образом, гидравлическое моделирование позволило оценить характеристики стока в различные периоды существования Манычского пролива.

3. Результаты и обсуждение

В ходе выполненных исследований были построены четыре цифровые модели палеорусла Манычской долины с высотой порога стока: 18, 31, 45 и 46 м н.у.м. Вариант с порогом 46 м н.у.м. включает заполнение отложениями Манычской долины, из которых возможно образовался грядовый рельеф (Рис. 8). Для цифровых моделей палеорусла 31 и 45 м н.у.м. построен второй Сальский порог стока высотой 18–19 м н.у.м.

3.1. Гидравлическое моделирование сброса каспийских вод через Маныскую долину

На основе цифровых моделей палеорусла было проведено гидравлическое моделирование сброса каспийских вод с расходом воды в следующих диапазонах:

- возможного стока рек в Каспий в позднеледниковье 10 000–18 000 м³/с (Сидорчук и др., 2021; Gelfan et al., 2024);
- максимального возможного стока каспийских вод через Манычскую долину 50 000–65 000 м³/с (Чепалыга, 2005; Sidorchuk et al., 2011).

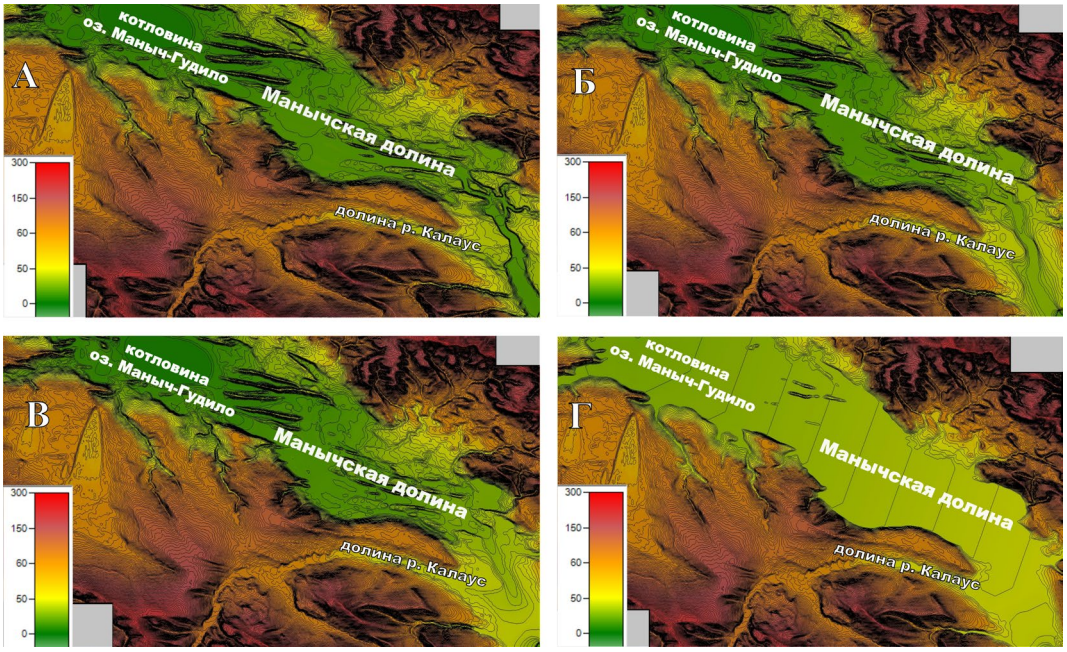

Рис.8. Палеорельеф русла Манычской долины с порогами стока: А – 18 м.н.у.м.; Б – 31 м.н.у.м.; В – 45 м.н.у.м; Г – 46 м.н.у.м с заполнением осадков Манычской долины.

Кроме того, была исследована пропускная способность русла Манычского пролива при пороге стока 18 м н.у.м. и уровне воды 48 м н.у.м.

Также исходя из уровня основных террас хвалынского бассейна Каспия 20–22, 28–30, 34–36, 46–48 м н.у.м. (Рычагов, 1997) были представлены расчёты стока Манычского пролива, которые соответствуют высоте террас хвалынского бассейна Каспия.

3.1.1. Гидравлические расчёты сброса каспийских вод при пороге стока 18 м н.у.м.

Согласно геологическому профилю № 16 (Попов, 1983), высота порога стока в районе с. Зунда-Толга составляла 18 м н.у.м. (Рис. 9). Порог стока в 18–20 м н.у.м. образовался в конце существования Манычского пролива. О чём свидетельствует глубокий эрозионный врез и датировки хвалынских отложений, которые относятся к концу существования пролива 14,2–14,9 тыс. лет (Semikolennykh et al., 2025). Следовательно, коэффициент шероховатости составлял примерно 0,035. Исходя из представленных данных были получены следующие результаты расчётов.

Когда хвалынский бассейн был на уровне 22 м н.у.м., что соответствует хвалынским террасам в 20–22 м н.у.м. (Рычагов, 1997), величина стока была ок. 1000 м^3/с (Таблица 2). Это была завершающая стадия существования Манычского пролива.

При уровне Хвалынского бассейна в 28,1 м н.у.м. сток в Манычскую долину был около 15 000 м^3/с. Эта величина стока соответствует максимальному стоку рек в Каспий 18 000 м^3/с минус эффективное испарение в 650 мм (Сидорчук и др., 2021). Данный уровень соответствует хвалынским террасам в 28–30 м н.у.м. (Рычагов, 1997).

Для достижения уровня воды, соответствующего хвалынским террасам на отметках 34–36 м н.у.м. (Рычагов, 1997), при пороге стока 18 м н.у.м. потребовался бы расход порядка 65 000 м^3/с. Эта величина соответствует верхнему пределу максимального стока через Манычский пролив, реконструированного на основании площади живого сечения крупной палеомендры в нижнем течении р. Западный Маныч (Sidorchuk et al., 2011).

Пропускная способность Манычской долины при уровне воды 40–48 м н.у.м. находится в диапазоне 130 000–350 000 м^3/с. Эта величина соизмерима с оценками А. Ю. Сидорчука, по его данным сток мог достигать 200 000–300 000 м^3/с при уровне воды 45 м н.у.м. (Сидорчук и Панин, 2022). При таком большом стоке уровень Каспия не мог подняться до 40–48 м н.у.м.

Уровни воды 22 м, 28,1 м, 34–36 м и 40–48 м н.у.м., рассматриваемые в данном подразделе, не отражают последовательные стадии подъёма хвалынского бассейна при пороге стока 18 м н.у.м. Эти отметки использованы исключительно в качестве гипотетических сценариев для оценки пропускной способности Манычского пролива при фиксированной высоте порога. Основная цель расчётов — продемонстрировать, что при геологически подтверждённой высоте порога стока (~18 м н.у.м., профиль № 16 по Г. И. Попову, 1983) и реалистичном суммарном речном стоке в хвалынский бассейн (10–18 тыс. м^3/с) поддержание уровня Каспийского моря на традиционно принимаемых отметках максимума трансгрессии (40–48 м н.у.м.) требует расхода воды порядка 130–350 тыс. м^3/с, что представляется нереалистичным сценарием. Таким образом, данные расчёты призваны выявить противоречие между низким порогом стока и представлениями о высоком максимуме раннехвалынской трансгрессии и обосновать необходимость анализа альтернативных сценариев с более высокой исходной высотой порога стока.

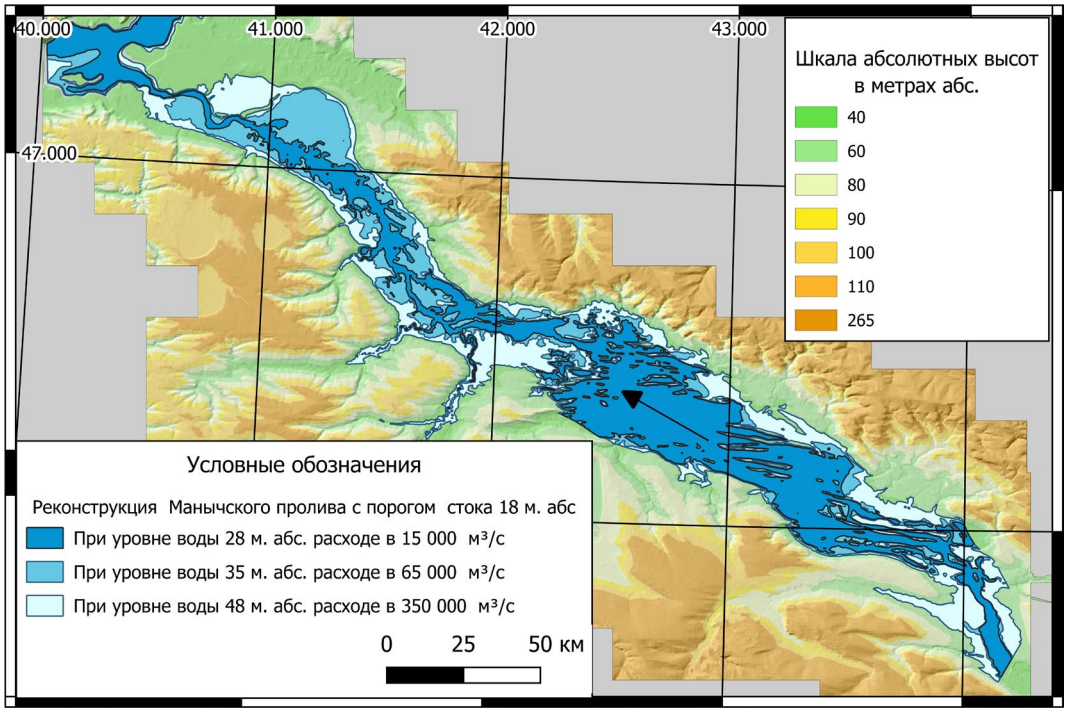

Рис.9. Карта реконструкции Манычского пролива с порогом стока 18 м.н.у.м., и коэффициентом шероховатости 0.35.

3.1.2. Гидравлические расчёты сброса каспийских вод при пороге стока 31 м.н.у.м.

Так как уровень хвалынского бассейна не мог подняться до уровня 40–48 м н.у.м. при пороге стока в 18 м н.у.м., необходимо поднять порог стока Манычского пролива до уровня 31 м н.у.м. Именно с более высокого порога стока скорее всего начался сброс каспийских вод в Манычскую долину, где вдоль водотоков произрастали ольшаники (Lavrentyev et al., 2012; Lavrentyev, 2022). Поэтому в гидрологической модели принято значение коэффициента шероховатости n = 0,08, характерное для заросшего русла.

При пороге 31 м н.у.м. и расходе 18 000 м³/с уровень воды достигал 40,55 м н.у.м., а с учётом эффективного испарения — примерно 40,0 м н.у.м. (Рис. 10). Соответствующий расход составлял 15 500 м³/с. Данный уровень также соответствует хвалынской террасе в Ергенях (Лаврентьев и Чепалыга, 2024). Затем уровень воды мог упасть до 37 м н.у.м. из-за изменения коэффициента шероховатости в проливе при том же расходе воды (Таблица 3).

При расходе 65 000 м³/с уровень воды достигал 47,3 м н.у.м. Это значение близко к максимальному уровню раннехвалынской трансгрессии — 48 м н.у.м. (Федоров, 1957; Рычагов, 1997; Свиточ и др., 2010; Чепалыга, 2007 и др.). В дальнейшем, при уменьшении коэффициента шероховатости, уровень воды мог снизиться до 42 м н.у.м.

3.1.3. Гидравлические расчёты сброса каспийских вод при пороге стока 45 м.н.у.м.

В районе дельты р. Калаус фиксируются террасы высотой 40–45 м н.у.м., что позволяет предположить, что изначальный порог стока мог достигать 45 м н.у.м. (Квасов, 1975; Попов, 1983; Рычагов, 1997; Свиточ и др., 2010).

В начале существования пролива коэффициент шероховатости был n = 0,08. При расходе 18 000 м³/с уровень воды достигал 47,2 м н.у.м., а с учётом эффективного испарения — 46,65 м н.у.м. (Таблица 4). Соответствующий расход составил 12 400 м³/с. Это значение близко к максимальному уровню хвалынской трансгрессии (Рис. 11).

3.1.4. Гидравлические расчёты сброса каспийских вод с заполнением осадками

Сценарий с порогом 46 м н.у.м. предполагает частичное заполнение Манычской долины осадками, что изменяет морфометрические параметры русла. Коэффициент шероховатости был n = 0,08 (Рис. 12).

Таблица 2. Результаты гидравлического моделирования сброса каспийских вод через Манычскую долину при пороге стока в 18 м.н.у.м. в районе 16 профиля Попова (1983), село Зунда- Толга.

Уровень воды м.н.у.м.	Коэффициент шероховатости 0.035		
	Расход воды м³/с	Площадь живого сечения кв.м.	Скорость течения м/с
22	1000	20599	0,05
28,1	15000	57858	0,26
28,72	18000	59358	0,27
33	50000	97349	0,51
35	65000	108550	0,6
40	130000	176500	0,91
48	350000	255861	1,36

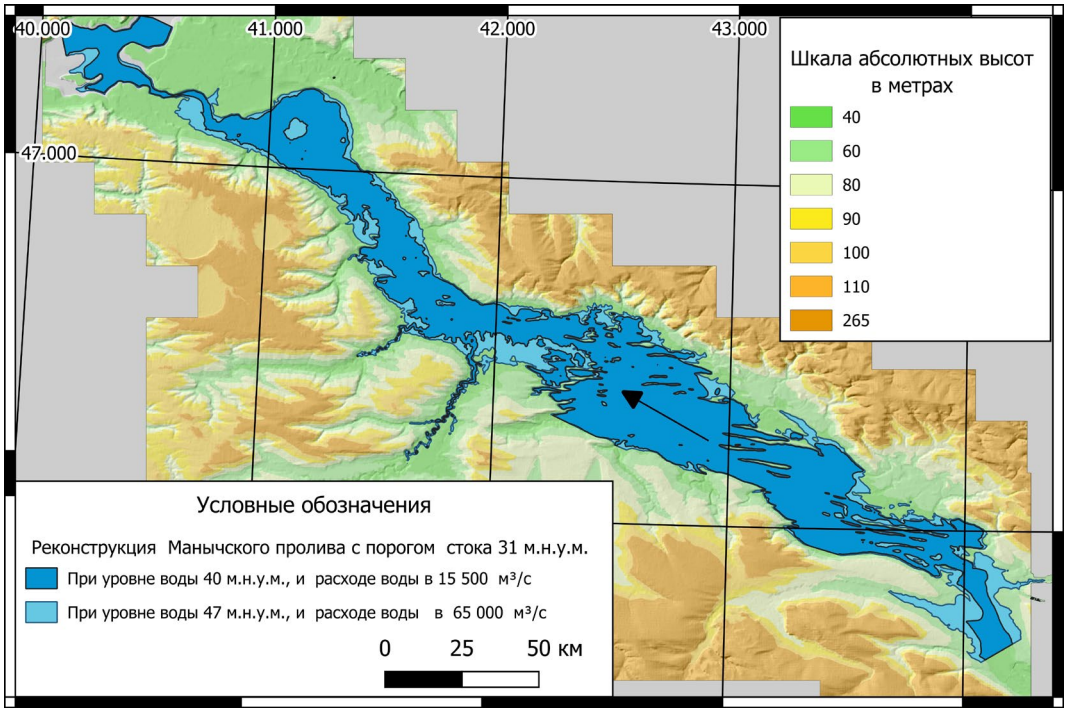

Рис.10. Карта реконструкция Манычского пролива с порогом стока 31 м.н.у.м. и коэффициентом шероховатости 0.08.

При расходе 18 000 м³/с уровень воды в Зунда-Толге составлял 49,7 м н.у.м., а с учётом эффективного испарения — 49,15 м н.у.м. Соответствующий расход составил 12 600 м³/с. Это значение близко к максимальному уровню хвалынской трансгрессии (Таблица 5).

Реконструкции с порогами стока –31, +45 и +46 м н. у. м. являются гипотетическими. Существование данных порогов стока Манычского пролива не подтверждено геологическими доказательствами. Однако более высокий порог стока 31–45 м н. у. м. позволяет обосновать уровень хвалынского бассейна в диапазоне 40–48 м н. у. м. с точки зрения водного баланса Каспия (Рис. 13).

Реконструкция палеорусла Манычского пролива с порогом стока в 18–20 м н. у. м. обоснована, исходя из геологических профилей Г. И. Попова (1983). Если посмотреть продольный профиль Манычского пролива с порогом стока 18 м н. у. м., то увидим следующие закономерности (Рис. 13). В районе Зунда-Толгинского поднятия наблюдается уклон русла. Растет скорость потока (Рис. 14). Что вполне закономерно, так как это самый узкий участок Манычской долины, где в основном преобладала глубинная эрозия. Затем в районе озера Маныч-Гудило происходит выравнивание продольного профиля пролива. Течение становится более спокойным (Рис. 14).

Здесь можно увидеть прислоненные к гудиловским отложениям хвалынские осадки, следовательно, происходила аккумуляция осадков. Сама эрозия не была столь сильной. После Сальского поднятия снова происходит падение русла пролива. Западно-Манычская впадина характеризуется большим перепадом высот и высокими скоростями течения. Данные моделирования подтверждают геологическое строение Западно-Манычской впадины. В отложениях на первой и второй надпойменных террасах фиксируется переотложенная фауна из нижележащих горизонтов, что говорит об активном размыве русла пролива.

Таблица 3. Результаты гидравлического моделирования сброса каспийских вод через Манычскую долину при пороге стока в 31 м..н.у.м., в районе 16 профиля Попова (1983), село Зунда- Толга.

Уровень воды м.н.у.м	Коэффициент шероховатости 0.035		
	Расход воды м³/с	Площадь живого сечения кв.м.	Скорость течения м/с
35	6000	19518	0,31
37,2	14800	35630	0,42
37,82	18000	41068	0,44
41	50000	76828	0,65
42	65000	91164	0,71
48	160000	161572	0,99

Уровень воды м.н.у.м	Коэффициент шероховатости 0.08		
	Расход воды м³/с	Площадь живого сечения кв.м.	Скорость течения м/с
35	3000	21217	0,14
40	15500	62152	0,25
40,55	18000	67872	0,27
46	50000	133918	0,37
47	65000	154190	0,42

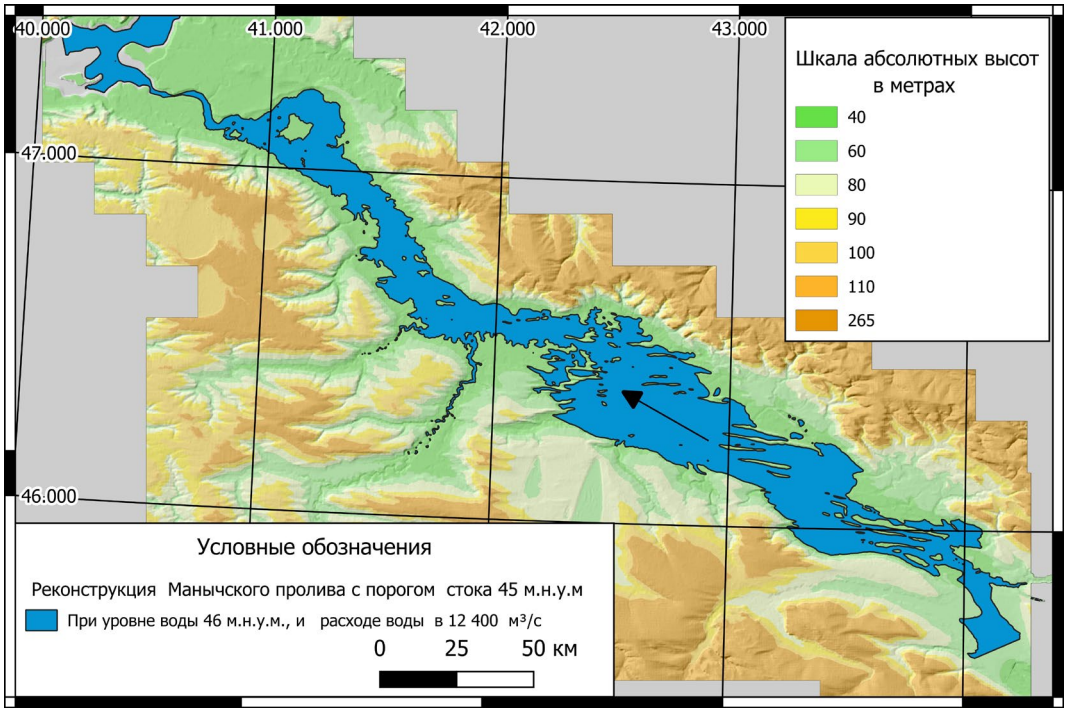

Рис.11. Карта реконструкции Манычского пролива с порогом стока 45 м. абс и коэффициентом шероховатости 0.08.

Однако, несмотря на интенсивную эрозию, продольный профиль Манычского пролива недостаточно выработан, что говорит о кратковременности его существования.

4. Заключение

Гидравлическое моделирование, выполненное в рамках настоящего исследования, позволило реконструировать наиболее вероятные сценарии сброса каспийских вод через Манычскую долину в период хвалынской трансгрессии Каспийского моря. Выделены следующие основные сценарии:

1. При пороге стока 18 м н. у. м. для достижения максимального уровня раннехвалынской трансгрессии (40–48 м н. у. м.) потребовался бы расход воды порядка 130 000–350 000 м³/с. Однако в позднем плейстоцене реки каспийского бассейна никогда не обеспечивали столь высокого стока. Следовательно, подъём уровня Каспийского моря до отметок 40–48 м н. у. м. при пороге стока 18 м н. у. м. следует считать маловероятным.
2. Скорее всего, первоначальный порог стока располагался на более высокой отметке, сформированной за счет дельтовых отложений реки Калаус. Ряд исследователей (Sidorchuk et al., 2011; Попов, 1983; Квасов, 1975) оценивает высоту порога стока около 45 м н. у. м., что согласуется с высотным положением террас в районе дельты Калауса. Результаты гидравлического моделирования показывают, что стока рек в эпоху позднеледниковья было достаточно для поддержания уровня Каспия выше 46 м н. у. м. Вместе с тем на террасах выше 40 м н. у. м. отсутствует малакофауна и не получено радиоуглеродных датировок, в связи с чем вопрос о максимальном уровне хвалынской трансгрессии (48 м н. у. м.) остаётся дискуссионным.
3. Наиболее вероятным представляется сценарий, при котором порог стока располагался на

Таблица 4. Результаты гидравлического моделирования сброса каспийских вод через Манычскую долину при пороге стока в 45 м.н.у.м., в районе 16 профиля Попова (1983), село Зунда- Толга.

Уровень воды м.н.у.м	Коэффициент шероховатости 0.035		
	Расход воды м³/с	Площадь живого сечения кв.м.	Скорость течения м/с
45,61	6000	6642	0,9
46,19	18000	14662	1,23
47,66	50000	38471	1,3
48,37	65000	50467	1,29

Уровень воды м.н.у.м.	Коэффициент шероховатости 0.08		
	Расход воды м³/с	Площадь живого сечения кв.м.	Скорость течения м/с
45,69	3000	7551	0,4
46,65	12400	21955	0,56
47,21	18000	31050	0,58
49,99	50000	78471	0,64
50,81	65000	93099	0,7

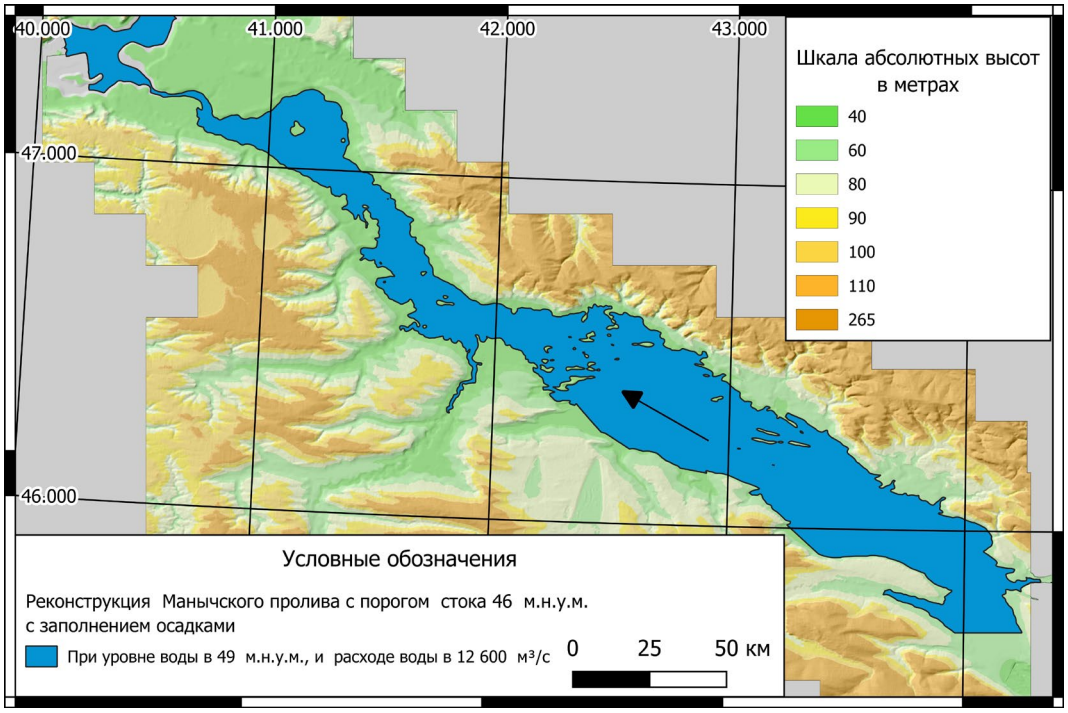

Рис.12. Карта реконструкции Манычского пролива с порогом стока 46 м.н.у.м., с заполнением осадками и коэффициентом шероховатости 0.08.

уровне 31 м н. у. м. Стока рек в хвалынский бассейн Каспия вполне хватило бы, чтобы поддерживать уровень воды в Каспии на уровне 40 м н. у. м. Этот уровень соответствует хвалынской террасе в Ергенях и подтвержден находками малакофауны (Лаврентьев и др., 2024; Свиточ и др., 2017).

4. Дельтовые отложения реки Калаус, по-видимому, подверглись интенсивному размыву водами Манычского пролива, что обусловило постепенное снижение высоты порога до 18 м н. у. м. (Сидорчук и Панин, 2022). В фазе активного размыва расход воды возрастал от 18 000 до 65 000 м³/с. В частности, при расходе 65 000 м³/с и пороге стока 18 м н. у. м., уровень воды в районе Зунда-Толги достигал 35 м н. у. м., что соответствует высотному положению хвалынских террас Каспия (Рычагов, 1997).

5. На протяжении большей части существования Манычского пролива, уровень Каспийского моря удерживался в диапазоне 22–35 м н. у. м., о чём свидетельствуют многочисленные находки хвалынских отложений с характерной фауной и радиоуглеродными датировками в данном интервале высот (Arslanov et al., 2016).

Таким образом, результаты проведённого исследования свидетельствуют о том, что сброс каспийских вод через Манычскую долину в позднем плейстоцене носил поэтапный характер и сопровождался последовательным понижением высоты порога стока. Наиболее вероятными являются сценарии с порогами стока на отметках 31–45 м н. у. м., соответствующие уровням раннехвалынского трансгрессивного максимума.

Результаты гидравлического моделирования, выполненного с использованием программного комплекса HEC-RAS, в целом хорошо согласуются с оценками расхода воды, полученными на основе классических гидравлических расчётов по формуле Шези (Sidorchuk et al., 2011; Сидорчук и Панин, 2022). Тем не менее вопросы высоты порогов стока, динамики их размыва и продолжительности отдельных фаз стока остаются открытыми и требуют дальнейшего междисциплинарного изучения.

Таблица 5. Результаты гидравлического моделирования сброса каспийских вод через Манычскую долину при пороге стока в 46 м.н у м., с заполнением осадков, в районе 16 профиля Попова (1983), село Зунда- Толга.

Уровень воды м.н.у.м.	Коэффициент шероховатости 0.035		
	Расход воды м³/с	Площадь живого сечения кв.м.	Скорость течения м/с
47,93	10000	36491	0,27
48,53	18000	48283	0,37

Уровень воды м.н.у.м.	Коэффициент шероховатости 0.08		
	Расход воды м³/с	Площадь живого сечения кв.м.	Скорость течения м/с
49,15	12600	61179	0,21
49,73	18000	73802	0,24

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Конфликт интересов

Автор заявляет об отсутствии конфликта интересов.

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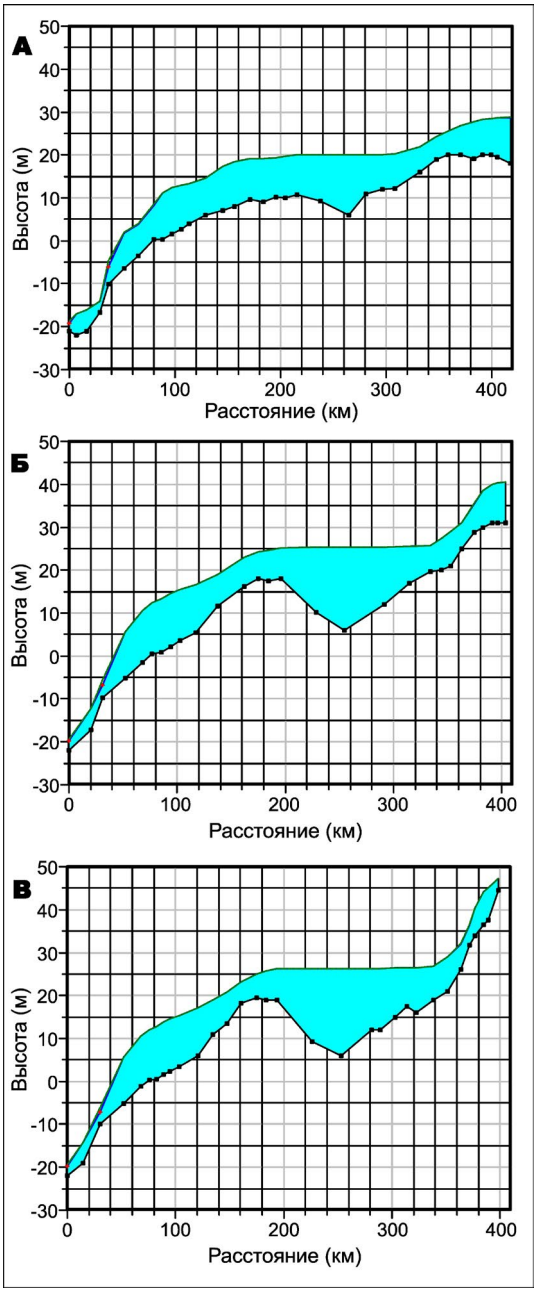

Рис.13. Продольный профиль Манычского пролива с расходом воды 18 000 м³/с.: А — при пороге стока 18 м.н.у.м.; Б — при пороге стока в 31 м.н.у.м.; В — при пороге стока в 45 м.н.у.м.

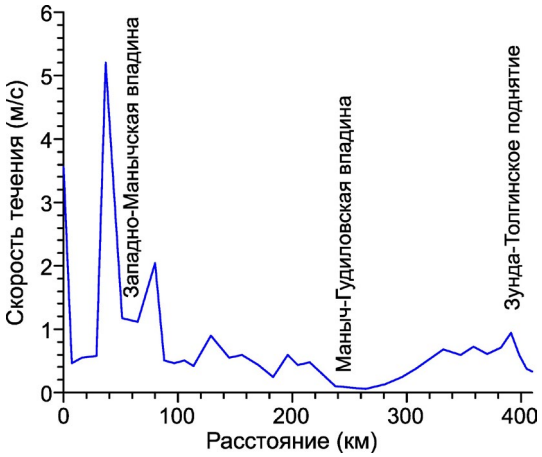

Рис.14. Продольный профиль Манычского пролива с скоростями течения в м/с, при расходе воды в 18 000 м³/с и пороге стока 18 м.н.у.м.

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