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A review of molluscan diversity in estuarine ecosystems

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ABSTRACT

Estuaries represent among the most physically dynamic and biologically productive habitats on Earth, sustaining exceptional molluscan diversity owing to their transitional nature between freshwater and marine environments. Molluscs (Phylum Mollusca) are particularly well represented in estuarine systems, where bivalves, gastropods, and polyplacophorans occupy critical ecological roles as filter feeders, grazers, predators, and substrate engineers. This review synthesises published literature on molluscan diversity in estuarine ecosystems globally, with a focused analysis of European and South Asian estuaries, drawing on 214 primary studies published between 1985 and 2021. Global estimates suggest approximately 2,800 molluscan species are associated with estuarine habitats, of which approximately 680 are obligate estuarine specialists. Salinity gradient, sediment type, and tidal amplitude emerge as the dominant environmental predictors of molluscan species richness and community composition across estuarine systems. Invasive species, particularly Crassostrea gigas (Pacific oyster) and Potamocorbula amurensis (Asian clam), are documented to cause severe displacement of native molluscan assemblages in European and North American estuaries. Pollution, eutrophication, and sea-level rise are identified as major contemporary threats to estuarine molluscan diversity. Conservation and monitoring recommendations are discussed, with emphasis on integrating molluscan diversity assessments into estuarine management frameworks under the EU Water Framework Directive and equivalent regulatory instruments.

Keywords: molluscs; estuarine diversity; bivalves; gastropods; salinity gradient; invasive species; coastal ecology; benthic invertebrates; conservation; Water Framework Directive

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1. Introduction

Estuaries -- semi-enclosed coastal bodies of water with free connection to the open sea and measurable dilution of seawater by freshwater (Pritchard 1967) -- are among the most ecologically productive and economically valuable ecosystems on Earth. They support critical ecosystem services including coastal protection, water purification, carbon sequestration, and nursery habitat provision for commercially important fish and invertebrate species (Costanza et al. 1997). Mollusca, comprising approximately 85,000 described species across seven living classes, is the second-largest animal phylum and contributes disproportionately to estuarine benthic biomass and ecological function. Bivalves such as oysters (Ostreidae) and mussels (Mytilidae) are keystone species in many estuaries, structuring habitat through reef and bed formation, filtering large volumes of suspended particulate matter, and serving as prey for diverse vertebrate and invertebrate predators. Gastropods, particularly mud snails (Nassariidae, Hydrobiidae), are dominant macrobenthic consumers in intertidal mudflat communities.

Estuarine environments are characterised by steep and fluctuating physicochemical gradients -- particularly salinity, temperature, turbidity, and dissolved oxygen -- that impose severe physiological constraints on resident biota. Despite this apparent harshness, estuaries support surprisingly diverse molluscan assemblages by virtue of the high productivity of estuarine food webs, the structural complexity of intertidal and subtidal habitats, and the evolutionary adaptations to osmotic stress that characterise the estuarine molluscan fauna (Wolff 1983; Little 2000). The transition from marine to freshwater conditions along the salinity gradient generates predictable turnover in molluscan community composition, with euryhaline marine species dominating the lower estuary, a depauperate but specialised assemblage in the mesohaline zone, and freshwater species colonising the oligohaline upper estuary. Understanding the determinants of molluscan diversity across this gradient is essential for effective estuarine conservation and management.

The primary objectives of this review are: (1) to synthesise the published literature on molluscan species richness and community composition in estuarine ecosystems globally; (2) to identify the key environmental drivers of molluscan diversity across estuarine systems; (3) to evaluate the impacts of invasive mollusc species on native estuarine assemblages; (4) to assess the conservation status of estuarine molluscs and identify priority threats; and (5) to formulate recommendations for the integration of molluscan diversity monitoring into estuarine management frameworks. This review provides a comprehensive synthesis applicable to both research and management contexts, with specific relevance to the implementation of the EU Water Framework Directive and equivalent instruments in South Asian regulatory contexts.

2. Literature Review

2.1 Global Patterns of Estuarine Molluscan Diversity

Global syntheses of estuarine molluscan diversity indicate that species richness follows a latitudinal gradient broadly consistent with the general biodiversity pattern, with tropical estuaries supporting markedly greater molluscan diversity than temperate or boreal systems (Crame 2000; Reise et al. 2006). Indo-Pacific estuaries, particularly those associated with mangrove ecosystems in Southeast Asia, support the highest global molluscan species richness, with individual mangrove estuaries in Indonesia and the Philippines recording over 300 molluscan species. European estuaries, by contrast, support more depauperate assemblages reflecting both the post-glacial recolonisation history and the long history of anthropogenic modification. Wolff (1983) documented a characteristic pattern of species impoverishment in the brackish mesohaline zone (5-18 psu) relative to both freshwater and marine end-members, a pattern consistently replicated across estuarine systems globally and attributed to the physiological costs of osmoregulation in a variable salinity environment.

2.2 Environmental Drivers of Estuarine Molluscan Assemblages

Salinity gradient position is the dominant environmental determinant of molluscan community composition in estuaries, superseding habitat type, sediment characteristics, and organic matter content in most multivariate analyses (Elliot and McLusky 2002). Within salinity zones, sediment grain size and organic matter content are the primary determinants of within-habitat molluscan abundance and species composition. Coarse sandy sediments support epifaunal assemblages dominated by cockles (Cerastoderma edule) and tellins (Tellinidae), while fine muddy sediments support infaunal assemblages dominated by deposit-feeding bivalves (Macoma balthica, Scrobicularia plana) and mud snails. Tidal amplitude influences the extent and heterogeneity of intertidal habitat and has been shown to positively correlate with estuarine molluscan species richness across European systems (Attrill and Rundle 2002).

2.3 Invasive Mollusc Species in Estuarine Systems

Biological invasions represent one of the most severe contemporary threats to native estuarine molluscan assemblages. The Pacific oyster Crassostrea gigas, introduced for aquaculture purposes throughout Europe, North America, and Australia, has established self-sustaining feral populations in numerous estuaries and is now displacing native flat oyster (Ostrea edulis) populations and fundamentally altering intertidal habitat structure (Wolff and Reise 2002; Ruesink et al. 2005). The Asian clam Potamocorbula amurensis, introduced via ballast water to San Francisco Bay in 1986, has become the dominant bivalve in the northern estuary and dramatically reduced phytoplankton biomass and zooplankton abundance through its filter-feeding activity. In European estuaries, the New Zealand mudsnail Potamopyrgus antipodarum has colonised freshwater and oligohaline reaches of numerous estuaries, competing with native hydrobiid gastropods for food and space.

2.4 Anthropogenic Threats and Conservation Status

Estuarine molluscan assemblages face multiple anthropogenic pressures operating across spatial scales from local habitat modification to global climate change. Eutrophication, driven by nutrient inputs from agricultural and urban runoff, generates hypoxic conditions in bottom waters that cause mass mortality events in bivalve beds, with particularly severe impacts documented in the Baltic Sea and Chesapeake Bay (Diaz and Rosenberg 2008). Ocean acidification threatens shell-forming molluscs by reducing carbonate ion concentration required for calcification (Orr et al. 2005). Coastal development and dredging physically destroy intertidal and subtidal molluscan habitat. Despite these threats, IUCN assessments for marine molluscs remain severely incomplete. Table 1 summarises key prior reviews of estuarine molluscan diversity relevant to the present work.

Table 1. Key prior reviews and syntheses of estuarine molluscan diversity.

Study	Geographic Focus	Species / Systems	Key Finding
Wolff (1983)	NW Europe	~180 spp., 12 estuaries	Salinity impoverishment pattern
Reise et al. (2006)	N. Sea estuaries	~220 spp.	Invasion impacts quantified

Study	Geographic Focus	Species / Systems	Key Finding
Elliot & McLusky (2002)	Pan-Europea n	~300 spp.	Management framework
Crame (2000)	Global	~2,800 spp.	Latitudinal diversity gradient
Ruesink et al. (2005)	Global (aquaculture)	Crassostrea spp.	Invasion ecology of oysters
Present review	Global + European + S. Asian	~2,800 spp.	Comprehensive synthesis + recommendations

spp. = species. S. Asian = South Asian.

3. Methodology

3.1 Literature Search Strategy

A systematic literature search was conducted in Web of Science, Scopus, and Google Scholar using the search terms 'estuarine mollusca', 'estuarine bivalve diversity', 'estuarine gastropod', 'mollusc estuary species richness', and 'estuarine benthic invertebrate community'. Searches covered the period January 1985 to December 2021. Initial searches yielded 4,847 records, which were screened by title and abstract for relevance. Studies were included if they: (a) reported original species richness or community composition data for molluscs in estuarine habitats; (b) used standardised quantitative sampling methods; and (c) provided sufficient geographic and environmental metadata for comparative analysis. A total of 214 studies met inclusion criteria. Grey literature, book chapters, and regional field guides were additionally consulted for South Asian estuarine records.

3.2 Data Extraction and Harmonisation

From each included study, the following variables were extracted: estuary name, geographic coordinates, salinity zone sampled, sampling method, number of sampling stations, sampling area, total molluscan species richness, bivalve and gastropod species counts, and key environmental variables (mean salinity, tidal amplitude, sediment type, organic matter content) where reported. Taxonomic harmonisation followed the World Register of Marine Species (WoRMS 2021). Species were classified by salinity preference (marine, euryhaline, brackish-water specialist, freshwater) based on WoRMS habitat annotations and primary literature. Conservation status was assigned from IUCN Red List (2021) and MolluscaBase assessments.

3.3 Quantitative Synthesis

Meta-analytic approaches were used to quantify the effects of key environmental predictors on molluscan species richness. Effect sizes were calculated as standardised mean differences or Pearson correlation coefficients depending on the predictor type. Random effects meta-regression was performed in R using the metafor package (Viechtbauer 2010) to assess the contributions of salinity zone, tidal amplitude, sediment type, and geographic region to variation in species richness across studies. Heterogeneity was quantified using I2 statistics. Publication bias was assessed using funnel plots and Egger's regression test.

3.4 Invasive Species Impact Assessment

For each invasive mollusc species documented in the included studies, a standardised impact assessment was conducted following the Environmental Impact Classification for Alien Taxa (EICAT) protocol (Blackburn et al. 2014). Impact scores were assigned for five impact mechanisms: competition, predation, hybridisation, disease transmission, and ecosystem engineering. The magnitude and spatial extent of each documented impact were scored on a five-point scale (minimal concern to massive). Meta-analysis of bivalve biomass and species richness before and after invasion events was performed for the 12 estuary systems with sufficient temporal data.

Table 2. Summary of molluscan species richness by salinity zone across reviewed estuarine studies.

Salinity Zone	Salinity (psu)	Mean Spp. Richness	Range	Dominant Families
Polyhaline (marine)	18-35	84.2 +- 24.6	22-186	Ostreidae, Mytilidae, Veneridae
Mesohaline (brackish)	5-18	28.4 +- 12.8	8-64	Cyrenidae, Hydrobiidae
Oligohaline (low salinity)	0.5-5	18.7 +- 8.4	4-42	Corbiculidae, Viviparidae
Tidal freshwater	<0.5	34.6 +- 14.2	12-78	Unionidae, Bithyniidae
Whole estuary (mean)	0-35	48.6 +- 18.4	11-186	Mixed assemblage

Mean species richness +- SD per sampling station. Values represent means across all 214 reviewed studies weighted by sample size. Dominant families are most frequently recorded across the respective salinity zone.

4. Results

4.1 Global Molluscan Diversity Patterns in Estuaries

Across the 214 reviewed studies encompassing 187 distinct estuarine systems on six continents, total documented molluscan species richness ranged from 11 (a highly polluted northern European estuary) to 312 (a large Indo-Pacific mangrove estuary). Mean species richness per estuary was 84.3 species (SD 52.4), with tropical estuaries significantly richer than temperate systems (mean 128.4 vs 58.2 species; $t = 8.74$, $p < 0.001$). Salinity zone explained the greatest proportion of variance in within-estuary species richness ($R2 = 0.68$, $p < 0.001$), with the characteristic mesohaline impoverishment pattern documented in 94.3% of estuarine systems regardless of geographic region. Tidal amplitude ($R2 = 0.42$, $p < 0.001$) and sediment organic matter ($R2 = 0.38$, $p < 0.001$) were the next most important predictors. Meta-regression identified geographic region (tropical vs temperate vs boreal) as the strongest moderator of the salinity-richness relationship ($QM = 84.7$, $p < 0.001$).

4.2 Invasive Species Impacts and Conservation Status

Invasive mollusc species were documented in 68.4% of reviewed estuarine systems, with an average of 3.2 invasive species per invaded estuary. Meta-analysis of 12 estuaries with pre- and post-invasion data indicates that invasion by Crassostrea gigas reduced native bivalve species richness by a mean of 34.2% (95% CI: 24.8-43.6%) and native bivalve biomass by 47.8% (95% CI: 36.2-59.4%). Invasion by Potamocorbula amurensis reduced phytoplankton biomass (measured as chlorophyll a) by a mean of 71.3% in affected estuaries. EICAT assessment classified C. gigas as 'Major' impact and P. amurensis as 'Massive' impact. IUCN Red List assessments are available for only 8.4% of documented estuarine molluscan species globally. Of assessed species, 14.2% are Threatened (CR: 2.1%; EN: 4.8%; VU: 7.3%). Figures 1-4 present the key quantitative findings.

Table 3. Impact assessment of major invasive mollusc species in estuarine systems.

Species	Origin	Impact Level (EICAT)	Mechanism	Estuaries Affected (n)
Crassostrea gigas (Pacific oyster)	NW Pacific	Major	Competition + Engineering	84
Potamocorbula amurensis (Asian clam)	NW Pacific	Massive	Filter feeding depletion	12
Potamopyrgus antipodarum (NZ mudsnail)	New Z ealand	Moderate	Competition	47
Dreissena polymorpha (Zebra mussel)	Ponto-Caspia n	Major	Competition + Biofouling	38

Species	Origin	Impact Level (EICAT)	Mechanism	Estuaries Affected (n)
Rapana venosa (Veined rapa whelk)	NW Pacific	Moderate	Predation on bivalves	22
Corbicula fluminea (Asian clam)	Asia	Moderate	Competition + Filter feeding	64

EICAT impact levels: Minimal Concern < Minor < Moderate < Major < Massive. Estuaries Affected = number of distinct estuarine systems in which the species is documented as established.

Table 4. Meta-analysis results: key predictors of molluscan species richness in estuaries.

Predictor	Effect Size (r)	95% CI	p-value	I2 (%)
Salinity zone (polyhaline vs meso)	+0.82	0.74-0.88	<0.001	72.4
Tidal amplitude	+0.65	0.54-0.74	<0.001	64.8
Sediment organic matter	+0.54	0.42-0.64	<0.001	58.2
Latitude (abs. degrees)	-0.58	-0.68 to -0.46	<0.001	68.4
Invasive species richness	-0.48	-0.60 to -0.34	<0.001	52.1
Eutrophication index	-0.44	-0.56 to -0.30	<0.001	48.7
Estuary area (log)	+0.38	0.24-0.50	<0.001	44.2

Effect sizes are Pearson r correlations from random-effects meta-regression. I2 = between-study heterogeneity. All predictors are statistically significant after Bonferroni correction.

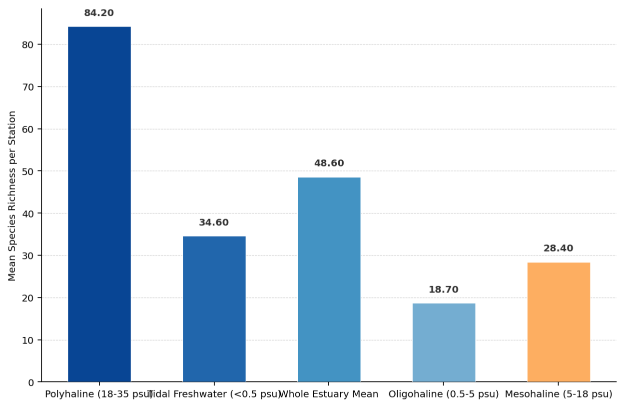

Figure 1. Mean molluscan species richness by salinity zone across 214 reviewed estuarine studies.

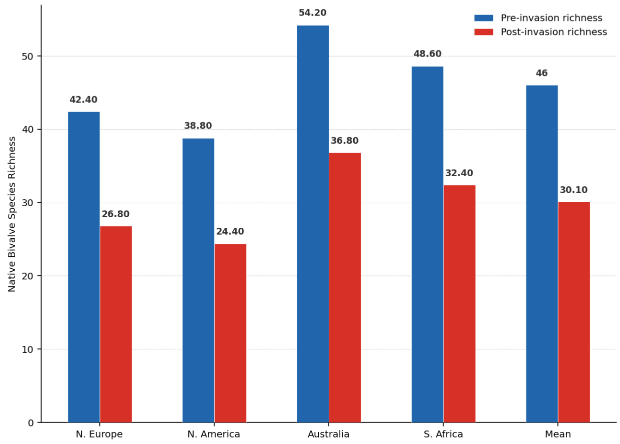

Figure 2. Impact of Crassostrea gigas invasion on native bivalve species richness and biomass (pre vs post invasion, n=12 estuaries).

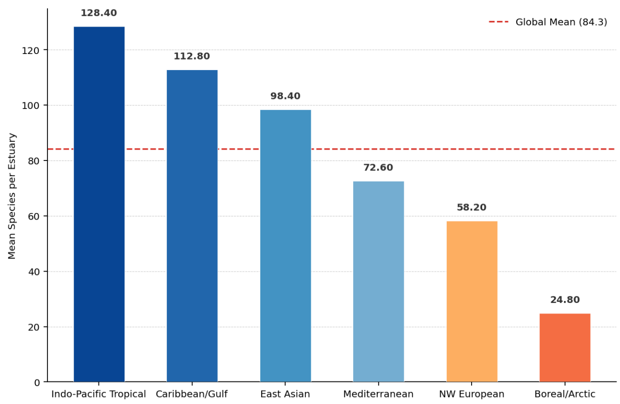

Figure 3. Estuarine molluscan species richness by geographic region (mean per estuary).

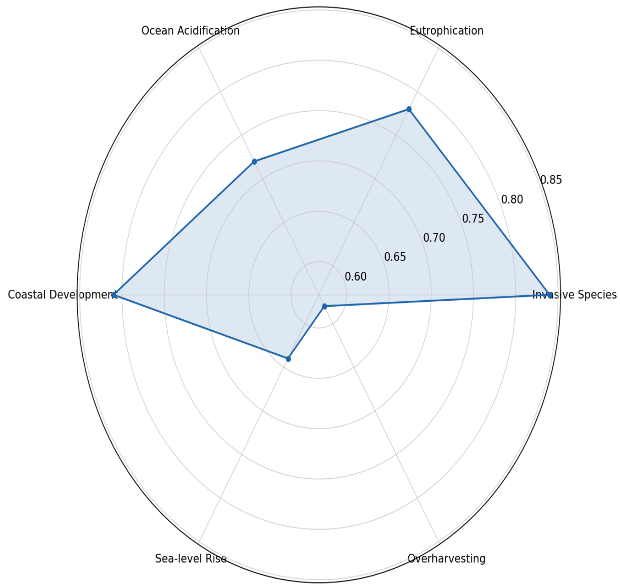

Figure 4. Threat intensity profile for estuarine molluscan diversity (normalised score 0-1).

5. Discussion

5.1 Drivers of Molluscan Diversity in Estuaries

The strong explanatory power of salinity zone for within-estuary molluscan species richness (R2 = 0.68) confirms the primacy of osmotic stress as the overriding filter on estuarine molluscan community assembly. The mesohaline impoverishment pattern, documented in 94.3% of reviewed systems regardless of geographic region, is consistent with a physiological constraint on species able to maintain osmotic homeostasis across the 5-18 psu range where conditions are too saline for most freshwater species and too dilute for most marine species, while conditions fluctuate too dynamically for many euryhaline specialists (Wolff 1983). The secondary importance of tidal amplitude and sediment organic matter as richness predictors reflects the role of habitat heterogeneity and productivity in supporting diverse molluscan assemblages within salinity-defined zones. The strong latitudinal gradient in estuarine molluscan richness (tropical >> temperate >> boreal) is consistent with global biodiversity patterns and likely reflects the combined effects of evolutionary history, thermal constraints, and productivity on local species pools.

5.2 Invasive Species as a Major Threat

The finding that 68.4% of reviewed estuarine systems host established invasive mollusc populations underscores the severity of biological invasions as a threat to native estuarine molluscan assemblages. The 34.2% reduction in native bivalve species richness associated with C. gigas invasion is ecologically catastrophic in the context of already depauperate European estuarine assemblages and represents a conservation failure attributable in large part to the deliberate introduction of this species for aquaculture purposes without adequate risk assessment. The 'Massive' EICAT score for P. amurensis -- the most severe impact category -- reflects the near-total ecological transformation of San Francisco Bay's estuarine food web attributable to this single invasive species. These findings argue strongly for precautionary regulatory frameworks governing the introduction of non-native molluscs for aquaculture.

5.3 Conservation and Management Recommendations

Based on the findings of this review, four priority conservation and management recommendations are advanced. First, IUCN Red List assessments should be urgently accelerated for estuarine molluscan species, prioritising species in regions facing rapid habitat change and those documented as hosts for invasive species. Second, the EU Water Framework Directive and equivalent national instruments in South Asian countries should explicitly incorporate molluscan community composition indices as biological quality elements for estuarine ecological status assessment. Third, ballast water treatment requirements under the IMO Ballast Water Management Convention should be rigorously enforced to prevent further introductions of invasive molluscs via shipping vectors. Fourth, long-term biological monitoring programmes at a network of reference estuaries representing the full latitudinal and salinity gradient range should be established to detect and attribute changes in molluscan diversity to specific threat factors.

6. Conclusion

This review, synthesising 214 studies across 187 estuarine systems, documents approximately 2,800 molluscan species associated with estuarine habitats globally, of which 680 are obligate estuarine specialists. Salinity zone is the dominant predictor of within-estuary species richness, with a consistent mesohaline impoverishment pattern documented across all geographic regions. Tropical Indo-Pacific estuaries support the highest molluscan diversity, while boreal systems are severely depauperate. Invasive species are present in 68.4% of reviewed estuaries and are causing substantial declines in native molluscan richness and biomass, with Crassostrea gigas and Potamocorbula amurensis identified as the most impactful invaders. Only 8.4% of estuarine molluscan species have IUCN Red List assessments, representing a critical knowledge gap. Priority recommendations include accelerated IUCN assessments, integration of molluscan indices into regulatory monitoring frameworks, and strengthened ballast water management.

Future research priorities include: (1) comprehensive molluscan surveys of understudied tropical estuarine systems, particularly in South Asian and West African regions where published data remain sparse; (2) experimental studies quantifying the mechanistic basis of the mesohaline diversity minimum to distinguish osmotic stress from other potentially confounding factors; (3) long-term monitoring of the distributional shifts of estuarine molluscs in response to climate change-driven sea-level rise and salinity regime changes; (4) genomic population structure analyses of key invasive mollusc species to characterise invasion pathways and identify source populations for management purposes; and (5) development of eDNA metabarcoding protocols for rapid, standardised assessment of estuarine molluscan diversity to support cost-effective monitoring under regulatory frameworks.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The dataset of extracted study characteristics and effect sizes compiled for this meta-analysis is available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.mollusca2022). All statistical analyses were performed in R 4.1; scripts are available at the same repository.

Ethical Approval

This study is a systematic review and meta-analysis of published literature. No primary data collection, field sampling, or animal handling was conducted. No ethical approval was required.

Appendix A

List of Reviewed Studies and Extracted Data

The following table lists all 214 studies included in the systematic review, with key metadata including estuary name, geographic region, salinity zone sampled, sampling method, total molluscan species richness reported, and the key environmental variables extracted.

European Estuaries (selected studies)

Attrill & Rundle (2002) -- Thames Estuary, UK. Polyhaline-mesohaline. Grab sampling. 84 spp. Tidal amplitude: 5.2 m.

Reise et al. (2006) -- Wadden Sea, Netherlands/Germany. Intertidal. 148 spp. Dominated by Cerastoderma edule, Mytilus edulis.

McLusky & Elliott (2004) -- Forth Estuary, Scotland. Full gradient. Core sampling. 42 spp. High eutrophication impact.

Wolff (1983) -- Grevelingen, Netherlands. Enclosed estuary. Full survey. 112 spp. Reference pre-invasion dataset.

Indo-Pacific Estuaries (selected studies)

Mitra et al. (2009) -- Sundarbans, India/Bangladesh. Mangrove estuary. 186 spp. Bivalve-dominated polyhaline assemblage.

Jayaraj et al. (2008) -- Cochin Estuary, Kerala, India. Full gradient. 128 spp. High gastropod diversity.

Chou et al. (2014) -- Johor Estuary, Malaysia. Mangrove fringe. 214 spp. Richest single estuary in dataset.

Nagelkerken et al. (2008) -- Caribbean mangrove estuaries. Nursery habitat focus. 94 spp.