

Introduction

Ecomorphology is an integrative field that combines ecology and morphology to study the relationship between an organism's physical form, its ecological roles, and the environmental pressures it faces. In marine fisheries, ecomorphology provides insights into how fish species have evolved physical adaptations that allow them to thrive in diverse ecological niches. Ecomorphology thus forms an integral part of comparative biology and is particularly valuable in understanding the complex interactions between fish morphology, behaviour, habitat preferences, and feeding strategies—key factors that influence fishery dynamics and management. The term has two integral concepts -ecology and morphology. While morphology is a biological discipline that seeks to understand the biology of organisms based on their structural characteristics (Maier, 1994), ecology is the study of the relationships between animals and their environments—encompassing both living and non-living components (King and Russell, 1909). Ecomorphology is thus the comparative study of how morphology influences ecological relationships and how ecological factors, in turn, shape morphology across different life stages, populations, species, communities, and evolutionary lineages (Luczkovich et al., 1995). The term ecomorphology was coined by van der KLAUW in 1948. Of the many definitions of ecomorphology, the one by (Bloch 1990) is very relevant- Ecomorphology focuses on analyzing the adaptive significance of morphological traits, exploring how these features enable organisms to interact with their environments. It encompasses various interrelated topics, including comparative studies of adaptations across different species, the influence of competition and other ecological pressures on morphological modifications, the structural organization of ecological communities, and the diversity observed within taxonomic groups. The primary aim of ecomorphology is to understand how organisms respond to environmental challenges by comparing various patterns in morphological and ecological traits (Motta et al., 1995).

Ecomorphology's two primary research foci are the impact of the environment on functional design and the role that functional morphology plays in an organism's ecology. The study of functional morphology focuses on how particular anatomical characteristics allow an organism to carry out essential biological processes including feeding, moving, and reproducing. It examines an organism's physical characteristics, such as its organ arrangement, muscle attachment sites, and limb anatomy, to determine how these characteristics are tailored to specific behaviours or roles. Understanding how an organism's body shape promotes its ecological roles and survival is the aim.

From a qualitative study of species and patterns to a quantitative one (Figueirido et al., 2009; Sacco and Van, 2004), the field of ecomorphology has seen tremendous change. Complex changes in biological shape in two and three dimensions may now be quantified because of new quantitative techniques like geometric morphometrics (GMM) and multivariate statistics that have transformed the field in the last 15 years.

How does it work?

The main concepts in ecomorphology focus on how an organism's morphology influences its ecological interactions and functions. In marine fisheries, these concepts help explain how fish species have adapted to distinct habitats, feeding strategies, and movement patterns in response to environmental pressures. Some fundamental ecomorphological concepts include:

1. Morphological Adaptations and Habitat Use

Morphological traits like body shape, fin placement, and mouth orientation have evolved in fish to suit their specific habitats. For example, streamlined body shapes allow pelagic fish, such as tunas and mackerels, to swim efficiently in open water, enabling them to migrate long distances in search of food. Conversely, benthic fish, such as flatfish, have dorsoventrally flattened bodies that allow them to live close to the seafloor, where they can ambush prey and avoid predators by blending with the substrate.

2. Feeding Morphology and Trophic Interactions

The structure of a fish's mouth, teeth, and gill rakers directly relates to its diet and feeding strategy. Predatory fish, such as groupers, have large mouths with sharp teeth adapted for grasping and holding prey, while filter-feeders like sardines possess fine gill rakers that enable them to sieve plankton from the water. By examining these feeding structures, ecomorphologists can classify species into trophic categories, enhancing understanding of marine food webs and interspecific relationships in marine ecosystems.

3. Locomotion and Behavioral Ecology:

Fish locomotion, influenced by fin morphology and body shape, is essential for understanding their movement patterns, predator avoidance, and hunting strategies. Ecomorphological studies have shown that species adapted to fast, agile swimming often have elongated, streamlined bodies and caudal fins designed for speed. This adaptation is evident in species like swordfish, which are capable of rapid bursts of speed when chasing prey or evading predators. Understanding these locomotory adaptations helps fisheries scientists predict species distribution, population connectivity, and migration routes—crucial information for sustainable fisheries management.

4. Functional Morphology in Response to Environmental Pressures

Environmental pressures like predation, competition, and resource availability drive functional adaptations in fish morphology. Species facing high predation pressure, for instance, may evolve cryptic coloration, spines, or armor-like scales to deter predators. Others, such as species in nutrient-poor environments, may have specialized feeding mechanisms to exploit scarce food resources efficiently. These adaptive features contribute to niche differentiation, allowing a diverse array of fish species to coexist in marine ecosystems.

Ecomorphology of Fishes

Fish inhabit a wide range of environments, from the deepest ocean trenches to fast-flowing rivers, each with unique challenges. Fishes have a great variety of morphological traits and adaptations (Helfman et al., 2009). Because of their high ecological and phenotypic diversity, ability to inhabit a wide range of ecological niches, complex reproductive strategies, & complex sets of foraging, locomotor, respiratory, reproductive, and sensory structures, fish are able to adapt to a variety of environments (Hoagstrom and Berry, 2018; Junqueira et al., 2012). This has opened up a large area for research on the relationship between morphology and environment. Integrating ecomorphological studies presents a more effective way to understand how the diverse shapes and functions of organisms influence their patterns of food resource (Winemiller, 1991; Piorski et al., 2005; Elliot et al., 2007; Teixeira & Bennemann, 2007; Mazzoni et al., 2010; Sampaio & Goulart, 2011).

According to the "ecomorphological paradigm," variations in an organism's structure, physiology, or even physical characteristics are frequently a reflection of variations in its ecology. A fish's body shape can indicate its swimming capabilities and preferred habitat, while its mouth structure can reveal its feeding strategy. Using the tooth and gill morphology, the diet of piscivorous and planktivorous fishes

can be predicted. The former has long and sharp teeth for prey capture while the latter uses modified gill arches to filter out their prey (Ferry and Gibb, 2008).

The Fishes' body shape is closely linked with their habitats and mobility needs. In open water, pelagic predators like tuna (*Thunnus* spp.) can swim efficiently and quickly thanks to their streamlined, fusiform bodies. These shapes reduce drag and help fish conserve energy during long-distance travel, a trait particularly useful for migratory or fast-moving species that need to out swim both prey and predators (Webb, 1984). In contrast, fish that inhabit complex environments such as coral reefs often display laterally compressed bodies, which allow for greater manoeuvrability. This flattened body type enables quick directional changes, facilitating movement around obstacles and aiding in escape from predators (Fulton et al., 2005). Elongated, eel-like bodies are suited to narrow or complex habitats, such as crevices or burrows, where species like moray eels (*Gymnothorax* spp.) can effectively hide from predators while hunting small prey within these confined spaces (Nelson et al., 2016). Fish like pufferfish and boxfish are globular, which reduces their speed but provides defense through spiny armor or inflation mechanisms to deter predators.

The arrangement and fin structure in fishes serves different ecological roles, reflecting the diversity of habitats they occupy. For example, the large pectoral fins of flying fish (*Exocoetidae*) enable them to leap out of the water and glide, which helps them avoid aquatic predators (Helfman et al., 2009). In benthic species, such as rays, the broad pectoral fins aid in undulating movements along the seafloor, providing stability and enabling these fish to navigate close to the substrate. The caudal fin (tail fin) is also highly specialized; species with lunate tails, like tuna, achieve high speeds with minimal energy expenditure, an adaptation critical for open-water habitats (Videler, 1993). Forked caudal fins provide a balance between speed and agility, aiding species like herring in both predator avoidance and efficient travel (Webb, 1988). Rounded caudal fins, typical in fish like groupers, enable short bursts of power, which is ideal for ambush predators that need to close in quickly on unsuspecting prey (Lindsey, 1978). In some species, such as triggerfish (*Balistidae*), the dorsal fin has evolved for defense; these fish can erect their spiny dorsal fins to deter predators by darting into crevices and making themselves difficult to catch (Helfman et al., 2009).

The structure of the mouth in fish is a strong indicator of feeding habits and ecological niche. Fish with terminal mouths, such as bass (*Micropterus* spp.), tend to be active chasers of prey in mid-water, suited to capturing mobile organisms in open habitats. Conversely, bottom feeders like catfish (*Ictaluridae*) have inferior mouths located on the underside of their heads, allowing them to forage on benthic organisms. Protrusible jaws, which can be extended to capture prey with a suction effect, are seen in fish like wrasses (*Labridae*) and facilitate efficient predation in coral reef environments. These suction-feeding adaptations enhance prey capture success in intricate environments by enabling fish to draw prey directly into their mouths without needing to maneuver too closely. Fishes with superior mouths like Tarpon (*Megalopidae* spp.) are ambush predators. They wait by hiding and once the prey is in nearby they strike.

Additionally, a thorough analysis of the ecomorphology of feeding in cottid fishes (sculpins) has been conducted. The Northeastern Pacific species have been the main focus. These research found that feeding on more elusive food, such as fish, prawns, mysids, and octopods, was associated with a wider mouth. Functional studies have been employed in addition to the basic ecomorphological method to investigate if a species' morphology improves its performance in an ecological setting. Compared to smaller-mouthed species, larger-mouthed sculpins have a noticeably greater success rate in capturing

elusive shrimp. In order to provide a mechanism for the relationship between morphology and ecology, this functional link is essential pattern (Higham, 2011).

The mechanics of jaw levers are frequently examined in connection with ecology. The jaw's in- and out-levers can be measured, and the results can be correlated with the predator's diet or feeding habits. The jaw closing lever ratios of Caribbean coral reef fish species that use their oral jaws to grasp, manipulate, bite, shred, or crush prey are extremely high. On the other hand, the jaw closure ratios of species that use ram- or suction-based striking techniques are significantly lower. Greater closure ratios show that the force produced by the muscles may be transferred to the tooth surface more effectively. Unlike jaw closure ratios, jaw opening ratios do not exhibit a clear pattern (Higham, 2011).

In the majority of fish, gas exchange between the blood and water occurs through the gill epithelium during respiration. The thickness of the water-blood barrier and the gill respiratory surface area play a major role in the capacity to obtain oxygen to support metabolic processes (Wegner and Nicholas, 2011). Respiratory adaptations in fish are essential for surviving in various oxygen conditions, influencing both distribution and behavior. For instance, fast-swimming species such as tuna have large gill surface areas, allowing for greater oxygen intake to support their high metabolic rates, which are essential for their active, migratory lifestyles. Conversely, species like the labyrinth fish (Anabantoidei) have developed additional respiratory structures that allow them to breathe atmospheric oxygen, an adaptation vital for survival in low-oxygen environments like stagnant ponds. It is formed by vascularized expansion of the first-gill arch's epibranchial bone and is used for air respiration (Pinter, 1986). Air breathing fishes use a variety of organs collectively called the ABOs (Graham, 2011). Such traits enable these fish to inhabit environments with oxygen levels that might otherwise limit their activity or distribution.

In order to protect aquatic fishes from harm brought on by predatory assaults and collisions with nearby objects, the lateral line system—a collection of mechanosensory components in the skin—is crucial. Pressure waves produced by ambient water flow are detected by the lateral line system. For instance, when pressure waves from an approaching predator hit its lateral line system (Stewart et al., 2014) the prey uses this neurological input to try to flee right away. It has also been determined that fish larvae exhibit same sensory-motor reactions (McHenry et al., 2009).

A lot of information about an animal's behavioural ecology may be gleaned from its eyes' size, external morphology, and location (Walls, 1942). For basic actions like foraging, attracting mates, and avoiding predators, many animals depend on their eyesight, and eye morphology has a significant impact on an animal's visual ability. Teleost fishes exhibit the most eye variety (Locket, 1975; Lythgoe, 1975, 1980; Pankhurst, 1989), with certain species evolved to see in the darkest and deepest oceanic regions while others have also adapted to see in the air (Ali and Hanyu, 1963; Ahlbert, 1969; Nicol, 1975, 1989; Myrberg and Fuiman, 2002). The variations are evident in the size, shape, and position of the eyes, in the number and shape of the photosensitive components (rods and cones), and in the degree of melanin content and retinal pigment epithelium development (Ali and Klyne, 1985; Collins and Pettigrew, 1988; Eastman, 1988; Wagner, 1990; Nag and Bhattacharjee, 2002). It is known that the number of ganglion cells near the vitreal limit of the retina, the density of retinal photoreceptors, and the size of the eye all affect visual acuity (Pankhurst, 1989; Myrberg and Fuiman, 2002). Rod retinas are mostly found in nocturnal and deepwater fishes (scotopic sensitivity), while the retina of diurnal fishes is typically richer in cones, as seen by the cone/rod ratio (photopic sensitivity) (Ali, 1975; Pankhurst, 1989).

Importance of Ecomorphology in Modern Marine Fisheries

As human activities and environmental changes increasingly impact marine ecosystems, the study of ecomorphology has become vital to the field of marine fisheries. The importance of ecomorphology in fisheries science can be illustrated through several key applications:

1. Ecosystem-Based Fisheries Management (EBFM)

Traditional fisheries management often focuses on single species, emphasizing catch limits and stock assessments without considering broader ecosystem interactions. In contrast, ecomorphology supports EBFM by focusing on how fish morphology influences ecological roles and relationships within the marine environment. This approach enables fisheries managers to consider not only target species but also how their ecological functions affect other species in the ecosystem. For instance, protecting species with crucial trophic roles, such as herbivorous fish that control algal growth in coral reefs, becomes more feasible with an understanding of their ecomorphological adaptations.

2. Predicting Responses to Climate Change and Habitat Loss

Climate change, ocean acidification, and habitat destruction alter marine ecosystems in ways that can outpace species' ability to adapt. By analyzing morphological adaptations to current habitats, ecomorphologists can predict which species may struggle to survive as conditions change and which might adapt successfully. For example, coral reef fish with specialized morphologies for reef crevices may face greater risks if coral habitats degrade, leading to habitat loss and potential declines in their populations. This knowledge allows fisheries managers to prioritize conservation efforts based on species' vulnerabilities to environmental changes.

3. Supporting Biodiversity and Resilience

Morphological diversity within a fish community contributes to ecosystem resilience by allowing species to fill a range of ecological roles. When diverse morphological types are preserved, ecosystems are more resilient to disturbances, as various species can adapt to or recover from changes in resources or predation pressures. Ecomorphological studies thus inform policies aimed at conserving biodiversity, highlighting the need to protect not only commercially valuable species but also those with unique ecological roles that support overall ecosystem health.

4. Improving Sustainable Fishing Practices

Understanding the morphological and ecological differences between species helps fisheries scientists design selective fishing gear and methods that minimize bycatch and habitat damage. For example, knowledge of body shape and swimming behavior can inform the development of nets or traps that target specific species while allowing non-targeted or juvenile fish to escape. This selective approach is essential for reducing overfishing impacts and ensuring that fishing practices are aligned with species' ecological needs.

Role of ecomorphology in other areas

In evolutionary biology, ecology, paleontology, and comparative anatomy, ecomorphology is a crucial field of study that can be used to reconstruct and comprehend ecological variation both now and in the distant past. By comparing the skeletal structure of extinct taxa with that of their contemporary relatives, one can gain an understanding of their lifestyles. This can reveal information about how species have evolved and how they have adapted to their habitats over time (Figueirido et al., 2015; Schwab et al., 2019).

Recent researches in the field

A study examined the differences in cranial bone morphology between two snapper species, *Lutjanus gibbus* and *Lutjanus johnii*, which inhabit contrasting environments. *L. gibbus* thrives in clear, coral reef waters, while *L. johnii* resides in murky mangrove habitats with strong currents. Researchers analyzed cranial bones from specimens collected in Pulo Aceh, Indonesia. Out of 23 cranial bone characters, 15 showed significant variation between the species, particularly in bones associated with the eyes, nose, jaws, and ventral head region.

In *L. johnii*, bones related to the nose were more developed, while eye-associated bones were less pronounced. Conversely, *L. gibbus* had a thicker premaxilla in the jaw and smaller bones in the ventral head area, reflecting adaptations to their distinct habitats. This suggests that environmental conditions influence cranial morphology and ossification patterns in these species (Radhi et al., 2023)

Speciation in aquatic vertebrates is often driven by physical isolation and micro-niche availability, such as in lakes, streams, and tropical reefs. The mesopelagic zone, with its open habitat and limited substrate, seems less likely to promote speciation. However, dragonfish (Stomiidae), particularly from the subfamily Melanostomiinae, demonstrate much higher-than-expected species richness. This group, comprising 222 species of the 320 described, is primarily differentiated by the morphology of their bioluminescent barbels. Despite significant morphological variation, dietary analysis of 16 species revealed limited prey diversity, with most species primarily feeding on lanternfishes. Functional differences in barbel length and jaw gape were noted, but no clear link between diet and morphology emerged. The results suggest that non-dietary factors, such as conspecific recognition or sexual selection, might play a larger role in driving speciation in these mesopelagic species (McGonagle et al., 2023).

The deep-pelagic realm of the Gulf of Mexico is a highly diverse ecosystem, yet its trophic structure remains poorly understood. Using stable isotope and stomach content data from 58 species of micronekton, this study examined the region's deep-pelagic food web. Four major trophic groups were identified, with significant variation in diet and isotopic values. Migratory species showed a correlation between body size and isotopic values, while non-migratory species, particularly those in deeper waters, had higher $\delta^{15}\text{N}$ values, indicating different trophic interactions. The presence of the Loop Current also influenced isotopic variation. Trophic positions ranged from 2.6 to 4.9, with discrepancies in trophic estimates between stable isotope and stomach content data, particularly for non-migratory species. These findings highlight the importance of body size, migration, and oceanographic features in shaping trophic dynamics in low-latitude oligotrophic ecosystems (Richards et al., 2023)

Deep-pelagic fishes are crucial for carbon sequestration, support fisheries, and connect various oceanic layers and trophic levels, yet knowledge of these species remains limited. This synthesis reviews the biodiversity and ecology of global deep-pelagic fishes, assessing 1554 species and introducing a new framework for understanding their functional and ecological diversity. The study emphasizes that deep-pelagic fishes are not homogeneous, highlighting regional variability and their diverse morphological, behavioral, and ecological traits. It also critiques existing modeling approaches, which often oversimplify these fishes' roles. A key focus is on diel vertical migrations, proposing the concept of "diel-modulated realised niche" to explain how these fishes transition between different ecological niches. The paper calls for a more nuanced approach to studying these fishes, considering the multiple drivers of their ecological transitions (Eduardo et al., 2024).

Morphometrics, which studies the form and function of organisms, plays a vital role in fields like genetics, ecology, and evolution. It is widely used to explore ecomorphology, examining how

environmental factors shape organisms' morphological features. Recent advancements in morphometric research, particularly through free and open-source software (FOSS), have revolutionized the study of shape differences and morphological variations. These tools assist with tasks like image processing, data acquisition, and statistical analysis, while also helping link ecological factors to morphological traits. However, many studies still fail to integrate ecological data, which is essential for understanding the factors shaping morphology. The lack of ecological integration often results from insufficient knowledge of existing FOSS tools. The article suggests that future software should be user-friendly, compatible across platforms, and support various data formats, to encourage the broader application of ecomorphology in biological research (De & Dwivedi, 2023).

Ecological diversification in *Sebastes* rockfishes is largely driven by depth and resource availability, influencing traits such as colouration, communication, body shape, and prey-predation interactions. Three sympatric species from the Seto Inland Sea, *Sebastes cheni*, *Sebastes inermis*, and *Sebastes ventricosus*, show distinct morphological adaptations that reduce interspecific competition. *S. cheni* has a narrower body shape and golden-brown colouration, suggesting a more pelagic lifestyle. *S. inermis* exhibits larger eyes, deeper body shape, and red colouration, indicating a deeper distribution, while *S. ventricosus* has smaller jaws, more gill rakers, and black colouration, signifying a shallower habitat and preference for planktonic prey. These morphological differences, including eye size and otolith traits, reflect species-specific communication systems and reproductive isolation, facilitating their coexistence in sympatry (Deville et al., 2023).

The concept of "morphoniche" integrates evolutionary and ecological perspectives by defining it as a component of the multidimensional ecological niche, representing the limits of phenotypic plasticity in individuals, populations, and species groups within a shared morphospace. The "phenome" of an individual, its morphofunctional traits, forms the core of its morphoniche, functioning as a biological tool for generative, trophic, and environmental roles. Geometric morphometrics helps relate individual morphoniches to ecological changes, analyzing the morphogenetic responses of populations to environmental factors. A population's potential morphospace reflects its adaptability, while the realized morphoniche shows the actual ecological responses over time. By evaluating the difference between potential and realized morphoniches, researchers can assess a population's adaptive potential and the risk of an evolutionary-ecological crisis. The "cenotic morphoniche" emerges from sympatric species within a community, providing insight into the collective morphospace and evolutionary dynamics (Vasil'ev, 2021).



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