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Chapter

Population Genetic Structure of Marine Fishes

Fidelina Gonzalez, Patricio Barria, Francisco Ponce and Sergio Mora

Abstract

Research on population genetics structure of marine fishes is increasing because of new technology based on DNA sequencing. This knowledge is necessary for management and conservation of natural population in marine environment. The aim of the chapter is to discuss about how genetic population structure get from DNA, allows us to know about dynamic of life history of species of Teleosts (Actinopterigii) and Chondrichthyes (Elasmobranchii). The analysis is based on taxonomic point of view. We hope to contribute to apply the new advances to management of natural population of fishes and marine wildlife.

Keywords: population genetic structure, life history, Actinopterigii, Elasmobranchii, marine environment

1. Introduction

Marine fishes are highly dynamic organisms that live in an also dynamic environment. Temperature and salinity variations combine to determine the density of seawater. Density governs the vertical movements of water, and density-driven circulation. Life of fishes depends on availability of food, and refugia to complete their lifetime in this environment. Tiger sharks (*Galeorcerdo cuvier*, Galeocerdonidae) moved along about 6–8 km. Thresher sharks (*Alopias vulpinus*, Alopidae) move, at least 400–1900 m, while learning of adult threshers improves the ability to perform directed walks. Blacktip reef sharks (*Carcharhinus melanopterus*, Carcharhinidae) showed high site fidelity and no evidence of oriented movements at large scales and small home ranges [1].

Population structure of marine fishes, otherwise, is determined by genetics or genomics information. Some aspects of this could be expressed in movements of individuals in their lifetime such as philopatry, natal philopatry (return to birth location) or spawning philopatry (return to a previous spawning site used by adults), should be included in stocks management. Natal philopatry improves the probability of offspring to find the best nursery habitats. Aggregation behavior in male and female leopard sharks, *Triakis semifasciata* (Triakidae), strong seasonal philopatry, with 50.0% of females and 60.0% of males moving every year to their aggregation sites [2]. An experiment realized in shark has shown that *Triakis*

semifasciata can use their olfaction for navigation. Tracks of control sharks ended 62.6% closer to shore. Tracks of anosmic sharks (nares occluded with cotton wool) follow tortuous paths, ended 37.2% closer to shore. Detection and discrimination of odors is the function of olfaction, and for navigation [3]. The largest olfactory bulb is found in migratory coastal-pelagic species such as *Carcharodon carcharias* (Lamnidae), *Galeocerdo cuvier*, and *Prionace glauca* (Carcharhinidae) [4]. Gardiner *et al.* [5] have shown that olfaction participates in homing by juvenile *Carcharhinus limbatus* within a shallow bay. Evidence for olfaction-mediated homing in fish larvae, whereas one species showed panmixis, another species showed strong homing. Thus, larvae smelling allow us to choose currents to return to natal home. Therefore, reef populations can develop genetic differences that might lead to reproductive isolation [6], operating mostly in nearshore environments [7].

2. Methodology

To develop this work, we search the information using Pubmed and Taxonomy from NCBI, Google Scholar Databases, and species with barcode in Bold System (http://www.boldsystems.org), and review the references related to DNA obtained from marine fishes using Scholar Google.

3. History life cycles of marine fishes

Fish life histories are necessary to understand how to preserve fish populations for future generations and to make practical regulations for fisheries management (for example, not taking certain species during spawning season or releasing undersized fish). Overexploitation, habitat destruction, pollution, and the uncontrolled introduction of exotic species for mass fish production have led to a decrease in the diversity of species in marine environment. In addition, climate change, which leads to changes in atmospheric temperatures that affect circulation patterns in aquatic environments, results in changes in salinity and dissolved oxygen and affects reproduction cycles of species.

Habitat fragmentation is one of the greatest threats to global biodiversity [8], preventing migratory organisms from completing their life cycles [9] and restricting dispersal and gene flow between populations [10]. The global decline of 76% in abundance of migratory fish over the past 50 years is due to fragmentation of habitat [11].

About 35,000 species of fish have been quantified worldwide. Marine fishes comprise about 60% of fish species in the world. Marine fish have three different areas in their life cycle. The first is for reproduction, the second for juvenile rearing and the third for adult feeding. This implies displacements or movements of different magnitude (migration) among the members of a species forming a panmictic population. Knowing the dynamics of the individuals of a particular population means considering these factors of each species. The interaction between environmental forces and dispersal characteristics is responsible for the population structure patterns of marine fishes. Sequential hermaphroditism defined as individuals first maturing as one sex and later in life transforming into the other sex, modifying population structure patterns. Sex-changing fishes are more spatially structured than gonochoristic (separate sexes) species because of skewed sex ratio. F_{ST} index, test the hypothesis that sex-changing species that are more prone to genetic drift are more genetically structured than gonochoristic species [12].

According to Pla et al. [13] described that functional hermaphroditism has been confirmed in the following orders: Anguilliformes, Aulopiformes, Centrarchiformes, Gobiiformes, Perciformes, Scorpaeniformes, Stomiiformes, and Synbrachiformes. The five families with the higher number of hermaphrodite species were Serranidae (91 spp.), Labridae (63 spp.), Gobiidae (41 spp.), Sparidae (40 spp.), and Scaridae (23 spp.). Sequential hermaphroditism predominated over simultaneous hermaphroditism (305 vs. 65 spp.), 244 are protogyny species, 39 protandric species, and 22 species are bi-directional sequential hermaphroditism. In sequential (sex-changing) hermaphrodite fishes, the sex ratio is usually biased toward the first sex, while reproductive success increases considerably after sex change. Estimated *Ne*, effective population size (*Ne*) in natural populations, the number of individuals that effectively participate in producing the next generation, from two ecologically similar species from the east coast of South Africa, there were *Ne* estimates significantly lower in the protogynous species and no evidence of genetic structuring or significant variation in genetic diversity in the study area [14].

Management and conservation can be greatly informed by considering explicitly how environmental factors influence population genetic structure. A new approach to characterize population connectivity at small spatial scales to conservation and fisheries management for high gene flow species is given by recent advances in oceanographic approaches for larval dispersal [15].

To evaluate genetic connectivity among three subpopulations of *Bothus robinsi* (Pleuronectiformes) Morales-Pulido *et al.* [16] sampled larvae from the Bay of Campeche and the eastern Gulf of Mexico and adults on Florida's continental shelf to test if the larvae tend to mix or display collective dispersal, compare genetic information between larvae and adults. Using ddRadseq (used for SNP discovery and genotyping which is a variation on the RAD sequencing protocol) RAD means restriction site associated DNA markers to genotype 1034 single-nucleotide polymorphic sites (SNPs) from *B. robinsi* larvae, identified morphologically and by DNA barcoding. A long pelagic larval duration of *B. robinsi* and ocean dynamics to transport and mix larvae from all shelf area is enough to produce connectivity, indicating a panmictic population.

Predictions on population-level genetic connectivity and the directionality of effective dispersal, as example, in two seahorses (*Hippocampus*) and three pipefishes (*Syngnathus*), of family Syngnathidae, using genome-wide single-nucleotide polymorphism (SNP) data, it found that follow the predominant ocean circulation patterns in the Gulf of Mexico and northwestern Atlantic [17]. High levels of gene flow and directionality are associated with the pelagic macro-algae *Sargassum* spp.

3.1 DNA molecular markers and main taxonomic group of fishes

To study the population genetics of marine fishes should be necessary to identify the species as the first step. A molecular technique to identify species is DNA barcoding, utilizing mitochondrial gene cytochrome oxidase I. By DNA barcoding is possible to identify species and categorize species for conservation. Mitochondrial Cytochrome c Oxidase subunit I (COI) is a gene of 650 base pairs that codes a protein, important in the cellular respiration and is considered a universal barcode for animals, because of its fast mutation rate, and maternal inheritance, it can be accessed from the DNA libraries data record. DNA barcoding gives information on cryptic species [18]. The benefits of barcoding fishes include species identification, range expansion for known species, and taxonomic identifications where traditional

methods cannot be applied. Specimens with divergent barcode sequences have been confirmed by taxonomic analysis as new species [19]. However, DNA barcoding, with the support of traditional taxonomy has the capability to identify species complexes within populations [20].

More than 25,000 species have already been DNA barcoded. 85% of a total of 1415 species sharks and rays of 12 orders are barcoded (**Table 1**). 95% of a total of 26,133 species grouped in 70 orders of Actinopterigii; a total of 458107sequences stored by orders, and 24,761 species are barcoded, in Bold System. The barcode sequence is a useful tool to identify fish species from any fish, fillet, fin, egg or larva can be matched against reference sequences using barcode of life data (BOLD) system [21] (http://www.boldsystems.org).

MitoFish is a comprehensive and standardized fish mitochondrial genome database of fish mitochondrial genomes (mitogenomes) that includes powerful and precise de novo annotations for mitogenome sequences [22] (http://mitofish.aori.u-tokyo.ac.jp/). Mitogenomic sequence data have resolved fish phylogenies and identifying new fish species [23]. Mitofish database contains 137 mitogenome of species of Elasmobranchii (**Table 1**), and 2316 species of Actinopterigii.

3.2 Cryptic species

Cryptic species require special attention in conservation planning, especially for endangered species complex. Cryptic species are biological entities based on morphological similarities classified as single species, but they possess distinct genetic

Order	Sequences BOLD system	Total species	Species with barcode	Mitofish
Carcharhiniformes	13,136	326	267	55
Heterodontiformes	133	9	7	2
Hexanchiformes	254	6	6	5
Lamniformes	1675	16	15	14
Myliobatiformes	6929	438	376	34
Orectolobiformes	1115	38	34	9
Pristiformes	1572	90	78	0
Pristiophoriformes	68	6	5	1
Rajiformes	6353	261	225	40
Squaliformes	4313	144	118	0
Squatiniformes	488	26	24	8
Torpediniformes	645	55	49	6
Echinorhiniformes	—	—	—	0
Rhinopristiformes	—	—	—	13
Total	36,681	1415	1204	137

Last column includes information about species sequenced mitocondrial DNA in Mitofish.

Table 1.
List of orders of Elasmobranchii, total sequences stored by orders, total species, and species with barcode in Bold system.

lineages and different species might require different conservation strategies [24]. Some species collected from complex ecosystems or different geographical locations showed higher intraspecific genetic distance values due to sympatric or allopatric speciation process. Sympatric speciation, the formation of species in the absence of geographical barriers diverse lineages through selective divergence in Carangoidei [25, 26]. In allopatric speciation, due to geographical barrier that prevent gene flow between populations, same species could be developed into different genetic lineages and develop genetic differences with little morphological change [27].

Analysis of DNA barcoded 2276 specimens belonging to 668 coral reef fish species from Indian and Pacific oceans it proved to be highly effective for the discovery of provisional cryptic diversity [28]. Of the 141 species sampled on each side of the Indo Malaysian Philippine Archipielag, 62 species presented no spatial structure whereas 67 exhibited divergent lineages.

Luciobrotula is a small genus of benthopelagic fishes occurring at depths ranging from 115 to 2300 m in the Atlantic, Indian, and Pacific Oceans, with six species, of the family Ophidiidae (Ophidiformes). *Luciobrotula bartschi* is the only known species in the West Pacific. Wong *et al.* [29] described *L. polylepis* as a new species, previously identified as *L. bartschi*. The genetic distance between the two species is 13.8% on average at the COI locus.

DNA barcoding is a powerful tool to study biodiversity, to increase the knowledge of marine biodiversity. The Southeast Pacific comprises two Large Marine Ecosystems, the Pacific Central American Coastal and the Humboldt Current System show a low representation of barcoded species, more abundant for the Humboldt Current System than the Pacific Central American Coastal. Ramirez *et al.* [30] found for Actinopterygii (30.27%) and Elasmobranchii (24.71%) high level of barcode incongruences for fish using Barcode Index Number (BIN).

In Nigerian fish samples collected from coastal waters, Bolaji *et al.* [31] find four species identified using COI, for the first time, for Nigerian marine environment: *Caranx fischeri* (Carangidae), *Pseudotolithus senegallus* (Sciaenidae), *Lagocephalus guentheri* (Tetraodontidae), and *Sphyraena ensis* (Sphyraenidae).

Using 1314 ultraconserved elements defined as highly conserved regions within the genome that are shared among evolutionarily distant taxa [32], the phylogenomic analysis of Syngnathidae reveals a high biodiversity inside the family [33]. The genus *Corythoichthys* (Syngnathidae) comprises a group of taxonomically complex, widely distributed in the IndoPacific region. To understand the genetic diversity, distribution, and 'species groups' within the genus *Corythoichthys*, a phylogenetic analysis carried out using 52 COI sequences. The analysis confirmed 13 species considered as a single taxon in the IndoPacific realm [34].

The genetic identity of marine species is kept through physiological or behavioral mechanisms that prevent gene flow and hybridization: ecological niche, environmental tolerance, mate recognition, differences in spawning time, reproductive migration, and gamete compatibility may be involved in marine fish species definition [35]. DNA barcoding is a tool to discover cryptic species in Mugilidae necessary for conservation and management of fisheries. Morphological examination of 40 mullets reveals 6 known species but the DNA barcode-based species identify eight operational taxonomic units (OTUs) belonging to five genera (*Crenimugil*, *Ellochelon*, *Mugil*, *Osteomugil*, and *Planiliza*) [36] in Pakistan, a biogeographic area where nearly no mullet species were genetically characterized. A sampling of 245 specimens studied from the Indo-Australian Archipelago found that belonged to five different genera. Some of these are known species, cryptic diversity was found for three of

these species, and eight (30%) probably new species [37]. The population structure of *Mugil cephalus* was investigated across 18 sampling sites in the NE Atlantic Ocean, Mediterranean, and Black Seas, using an 857 bp fragment of mitochondrial (mtDNA) cytochrome b, and 7 nuclear loci. The low nucleotide diversity of mtDNA marker was very low (0.6% divergence) because it is a conservative sequence, indicating a single clade over the entire area. Between the samples from the Black Sea and the samples from other basins, it finds significant mtDNA genetic differentiation observed (Φ_{ST} = 0.17; p = 0.029). Significant genetic differentiation and isolation-by-distance in *M. cephalus* find based on nuclear loci analysis [38].

DNA barcoding using mitochondrial DNA sequences may offer an effective approach to identifying cryptic species and characterizing genetic diversities of deep-sea fish species [39]. DNA barcoding of mesopelagic and demersal fish collected around Japan and southern Taiwan. High intraspecific genetic differentiation showed based on COI sequences of samples of *Chimaera phantasma* (Chimaeridae), *Harpadon microchir* (Synodontidae), and *Pyramodon ventralis* (Carapidae). Moreover, for 19 widespread deep-sea fish species, suggested a high level of genetic differentiation for the northwestern Pacific Ocean, that suggest many cryptic species or regional populations not described yet, in deep-sea fishes [40].

To identify development stages of lifetime for some species, the eggs of 15 species collected at 40 stations distributed across and around the Gulf of Mexico. The cluster analysis identified eight groups that yielded percomorph eggs, a neritic community, an oceanic community, and a transitional community in the shelf break. The coastal-pelagic species would have mixed neritic–oceanic distributions. Of the 1144 eggs barcoded, 709 (62%) identified 62 species belong to 42 families, and 20 taxa identified to genus or subfamily level [41].

3.3 Mitochondrial DNA control region. Subpopulation.

The lack of a known repair mechanism for mutations that arise during replication of mitochondrial DNA allows higher rate of evolution than nuclear genome. The initiation of replication of mitochondrial DNA occurs in the control region (about 1 KB). Control region of mitochondrial DNA is a good marker for analyzing population connectivity, defining conservation units, identifying migration routes of fishes, using in many phylogenetic and population genetic studies because of high copy number, and its maternal and haploid mode of inheritance [42].

Flounders provided evidence of a genetic structure between the sampling sites from Southwest Atlantic coast using a fragment of the mitochondrial DNA of the control region and seven microsatellite loci. *Paralichthys orbignyanus* displayed a lower to moderate contemporary genetic structure among all samples except between Lagoa dos Patos (Brazil) to San Matias Gulf (Argentina), explained probably by limited gene flow associated with a consistent larvae retention in all sampling sites, congruent with the prevailing littoral drift [43].

The mitochondrial DNA control region of 91 individuals from six populations Japanese flounder *Paralichthys olivaceus* (Paralichthyidae), which is endemic to the Northwest Pacific. The analysis of 233 sequences, from four populations, showed high nucleotide diversity (0.032 ± 0.016) and haplotype diversity (0.996 ± 0.001). The geographical distribution and genetic population structure of *P. olivaceus* is explained by ocean currents and climate change. The peripheral population in the East China Sea had the relatively lowest genetic diversity and highest differentiation [44].

Biological parameters, geopolitical boundaries, and the existence of fisheries management units do not match genetic populations for marine fisheries management. The contribution of genetic and genomic data allows to define management units. *Pagellus bogaraveo* (Sparidae) is a sparid in the northeast Atlantic, with three stock units. The northern stock collapsed (1975–1985). The Mediterranean and Azores are two different units. A significant population structure found for the entire sample area (AMOVA: F_{ST} = 0.052, p < 0,001) attributed to the individuals from the Azores, which showed significant differences with the remaining five sites. Mitochondrial control region corroborates the results obtained using nuclear markers (i.e. microsatellites) [45]. Consistent results get from mitochondrial and nuclear markers [46]. The differentiation of the Azorean population is common to other species of the Northeast Atlantic, *Labrus bergylta* (Labridae) [47], *Aphanopus carbo* (Aphanopodinae) [48], *Coryphoblennius galerita* (Blenniidae) [49] and *Diplodus vulgaris* (Sparidae) [50].

Lumpfish (*Cyclopterus lumpus*, Cyclopteridae), a transatlantic marine fish, show high dispersal, and gene-flow, displaying large population sizes. Nevertheless, this species may have a natal homing behavior and local populations with adaptive differences because of the observed high levels of population structuring throughout the Atlantic. Analysis using SNP methodological strategies by Jansson et al. [51] identified genetic evidence of local population substructures [51].

3.4 Conservation of marine fishes

Climate change and anthropogenic activity affect marine biodiversity in the Persian Arabian Gulf. Assessment following the International Union for Conservation of Nature (IUCN) Red List methodology, of 471 species of marine bony fishes in the Gulf, informed about the threatened marine bony fishes. Based on available data all species, threats include 47% of marine bony fishes related to fisheries and harvesting, and 32% of marine fish species related to coastal development and loss of habitat, acute in nearshore areas where spatial analyses indicated high species richness [52].

Fisheries resource management in the Persian Arabian Gulf has been inadequate but, only 22 Gulf fish species have been listed as threatened or Near Threatened due to impacts from overexploitation. Classified as a primary threat 120 species with large-scale exploitation, 105 species listed as Least Concern including species with a small maximum size, short lifespan, and high reproductive output; for example, six of the eight clupeids commonly found in fisheries were listed as Least Concern [52].

3.5 New technologies and future development

Marine ecosystems are currently subjected to a range of exploitation rates. Management actions have controlled reductions in exploitation rates in some regions, but a fraction of stocks collapsed. Local context could define the selection the best management tools. A combination of traditional approaches (catch quotas, community management) coupled with strategically placed fishing closures, changing selective fishing gear, holds much promise for restoring marine fisheries and ecosystems [53, 54].

Recently advances in environmental DNA (eDNA) originates from cellular material shed by organisms in aquatic or terrestrial environments is revolutionizing fish biodiversity monitoring. To improve the sensitivity and reliability of fish eDNA analyses are recommended the available universal primers used to amplify barcoding sequences from fish eDNA and combined use of different gene marker such as pair of

primers of conservative sequences of following genes, such as12SrDNA, 16SrDNA, Cytochrome b, Cytochrome oxidase 1, and databases [55]. The first step in improving the accuracy and efficiency of eDNA detection is optimized a technical procedure for eDNA-based detection with high specificity to identify the COI gene [56].

Based on metabarcoding of the 16S mitochondrial gene for fish and the 18S nuclear gene for macroinvertebrates of Manly Lagoon, a polluted estuary in eastern Australia DiBattista et al. [57] identified seasonal differences in fish and macroinvertebrate community composition, as well as species richness to examine temporal and spatial changes in the aquatic community, which correlated (in some cases) with the environmental parameters of sea surface temperature and freshwater input. Several known migratory fish species contributed significantly to the overall patterns observed (fish assemblages shifting in response to environmental drivers in polluted estuaries).

A new tool for knowing the spatio-temporal population structure of fish species and diversity is the massive sequencing of genetic markers, such as the use of single-nucleotide polymorphisms (SNP) obtained by DNA sequencing associated with the restriction site by RADseq. They find in the genome and define a thousand loci [58, 59, 60].

The overexploitation of shallow-water fish stocks has led to increasing fishing pressure on deep-sea species. Genetic structure of *Pagellus bogaraveo* find no variation in *cyt-b* and low genetic variation in *D-loop* sequences, nucleotide diversity was extremely low (p = 0.002) for mitochondrial DNA in fish and haplotype diversities (h = 0.5919), effective population size must have been reduced to very low numbers, indicate that *P. bogaraveo* may have undergone a severe bottleneck in the past, as other Atlantic species of fish, possibly originated from the last glaciation [61].

Hydrographic or topographic barriers prevent dispersal of adults and/or larvae in deep-sea fish species between populations at regional and oceanographic scales. Analysis of population structure using D-loop and microsatellite indicates significant genetic differentiation between populations at a regional level. Using SNPs obtained by RADseq, Francisco *et al.* [46, 62] identified different populations of *Pagellus bogaraveo* in the Atlantic Ocean. The results of this investigation suggest the need to integrate this type of information in stock management.

A marine fish in the North Pacific, *Gadus macrocephalus* (Gadidae), experienced shifts in biomass and distribution linked to climate change [62]. During the spawning season of fish collected around the Korean Peninsula using DNA (RAD) sequencing and individual assignment defined small and isolated peripheral populations, often remnants of glacial refugia in high gene flow marine species. Populations relatively small of *Gadus macrocephalus* on Korean coasts were highly differentiated (F_{ST} = 0.025–0.042). Data suggest asymmetrical dispersal and gene flow, potentially involving adaptive alleles, between peripheral populations inhabiting markedly different thermal regimes. Fisher *et al.* (2022) [63] suggest the conservation value of peripheral populations [64, 65]. A loss of genetic diversity that includes adaptive variation important for response to environmental change [65]. Adaptive alleles in small peripheral populations of *Gadus macrocephalus* demonstrate contemporary migration from warm- to cold-adapted populations, Peripheral populations should therefore be conserved and maintained as an important genetic resource.

Eleginops maclovinus (Eleginopsidae), is a marine protandric fish, male in the early stages of life live [66, 67], in estuarine habitats, and female in the later stages, when it is pelagic, live near the coast. They tend to live at the mouths of rivers, adults are not morphologically hydrodynamics, spawning and developing in this environment [68]. The dynamic and heterogeneous landscape in Patagonia, can harbor an important

but cryptic genetic population structure using restriction site-associated DNA (RAD) sequencing. In five locations sampled, distributed across a salinity cline from Northern Patagonia, Canales *et al.* [69] identified a spatial structuration with gene flow and spatial selection by environmental association. Neutral loci gave two genetic group meanwhile adaptive loci gave three genetic groups. The effective population sizes ranged from 572 to 14,454 and were influenced by locality.

Analysis of specimens of *Boreogadus saida* (Gadidae) collected in the Canadian Arctic Archipelago would set potential barriers to gene flow between the Canada West group and Canada East. Differentiation patterns can be explored by the application of single-nucleotide polymorphism markers (SNPs) [70]. Detected population differentiation of *B. saida* over circumpolar and regional scales. Patterns of gene flow can be influence by geography, river discharge, prevailing currents, bathymetry, water properties, and prey availability. Direction of gene flow has important implications for expansion of southern alleles, prevailing currents may be promoting northward range expansions [71].

The high trophic level oceanodromous species undertake migrations of significant distances across the oceans to feed, or to breed, and have wide geographic distributions, such as tuna. Therefore, these species live both within the exclusive economic zones and outside these zones. Pelagic species live primarily in the open ocean and spend part of their life cycle in nearshore waters [72]. Microsatellites and SNP arrays do not identify population structure and fish populations from different ocean basins. However, stock genomics research using RAD sequencing can give genetic differentiation in *Thunnus albacares* (Scombridae) [73–75] *Thunnus alalunga* (Scombridae) [76, 77], *Acanthocybium solandri* (Scombridae) [78], and *Kajikia audax* (Istiophoridae) [79].

4. Conclusion

The new advances in DNA technology and bioinformatics allow to increase the knowledge, as show in this chapter, both fish biology and population genetics, therefore, to contribute to improving the management of natural population of fishes and marine wildlife.

Conflict of interest

The authors declare no conflict of interest.

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