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Life history of marine fishes and their implications for the future oceans

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Abstract: Through natural selection, the environment shapes the survival and reproductive traits of species, including marine fishes. The particular set of life history traits a fish species possesses determine its location in a trilateral continuum of life history strategies. These strategies can be used to understand the dominant biological trade-offs affecting that species, in addition to the gradients of environmental disturbance, variability, and predictability to which it is subjected. Life history strategies can be further subdivided into functional groups differentiated by habitat and feeding preferences. Large predatory fishes can be separated into pelagic specialists and demersal generalists, which are influenced by the separation of primary production into pelagic and benthic secondary production. This life history framework and functional type understanding suggest multiple alterations to fish populations under climate change, including shorter lifespans, smaller maximum body sizes, reduced fecundity, greater susceptibility to climate variation impacts, and increased reliance on pelagic food chains.

Key Words: reproduction, lifespan, trophodynamics, pelagic, demersal, benthic, environmental variability

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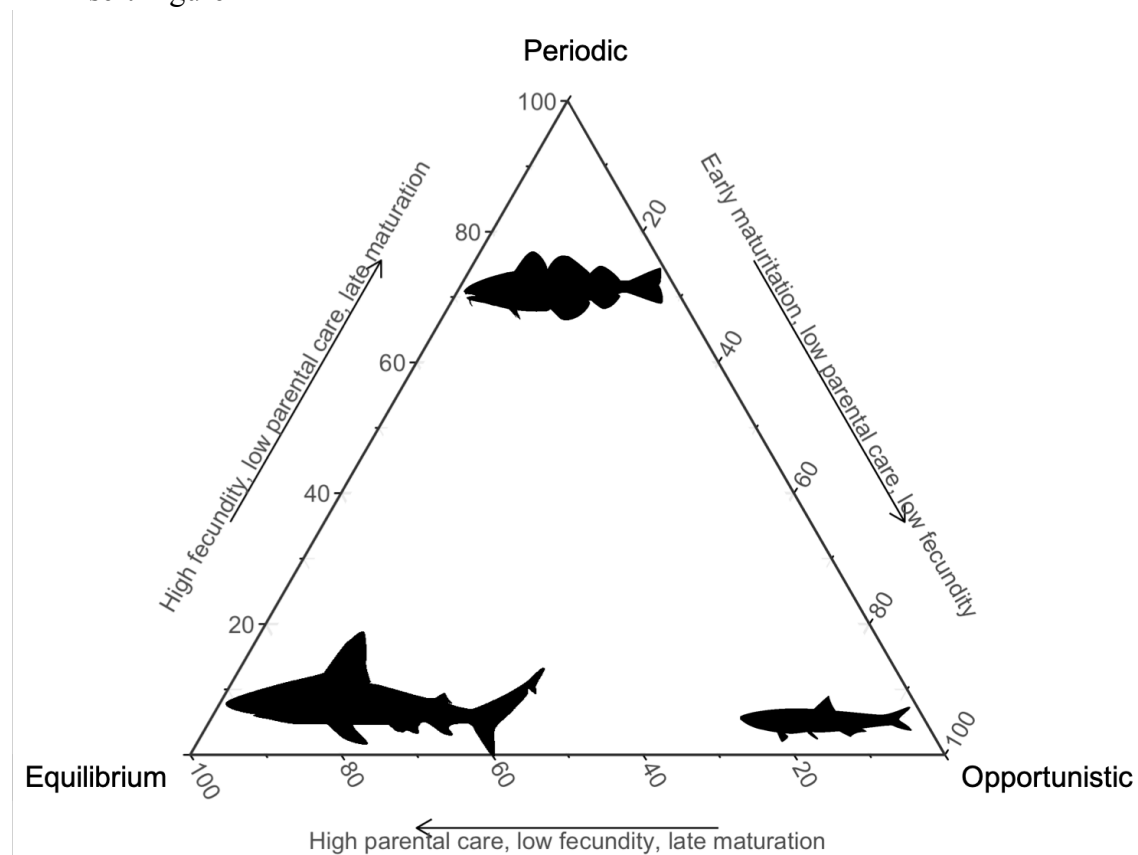
1. Life history strategies of fishes

Life history refers to the pattern of survival and reproduction events during the life of an organism. Life history traits include maximum body size, longevity, age at maturity, and fecundity. Life history theory espouses that these traits have been shaped by natural selection to optimize trade-offs related to growth, reproduction, and survival. Thus, organisms that have the same phylogeny share similar traits. Conversely, unrelated organisms occasionally evolve similar traits independently.

Winemiller and Rose [1] evaluated patterns in fish life history traits across species to create an organizing framework. This framework consists of the Equilibrium, Periodic, and Opportunistic (E-P-O) niche scheme, three endpoint strategies of correlated life history traits (Figure 1). Equilibrium species were categorized by moderate to long generation time, low fecundity, and high investment per offspring. Examples of commercial fish species include spiny dogfish and longnose skate. Periodic species were

denoted by long generation time, high fecundity, and low investment per offspring – species like Atlantic cod, halibut, and tuna. The Opportunistic strategy consisted of fishes with short generation times, low batch fecundity, and low investment per offspring, such as sardine, anchovy, and mackerel. These endpoints are a trilateral continuum based on biological constraints and different fish species could theoretically lie anywhere in this space.

*** Insert Figure 1 ***



Caption: The life history endpoint strategies of Winemiller and Rose (1992) as a triangular continuum of traits.

Credit: Fish silhouettes courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

The environment has shaped the particular life history traits of any given fish. Because life history traits ultimately determine population dynamics, the E-P-O framework developed by Winemiller and Rose [1] can be used to predict a population's response to different types of disturbances. The E-P-O niche scheme was mapped onto a 2D life history plane by Winemiller [2] that described the gradients of environmental disturbance, variability, and predictability associated with each life history strategy. The Opportunistic group is a colonizing strategy that thrives in environments with high amounts of disturbance and low levels of predictability of resources and mortality [2]. As the scale and predictability of spatiotemporal environmental variability increases, the Periodic life history strategy is favored [2]. Conversely, Equilibrium life history

strategies persist in stable environments with high levels of competition and predation [2].

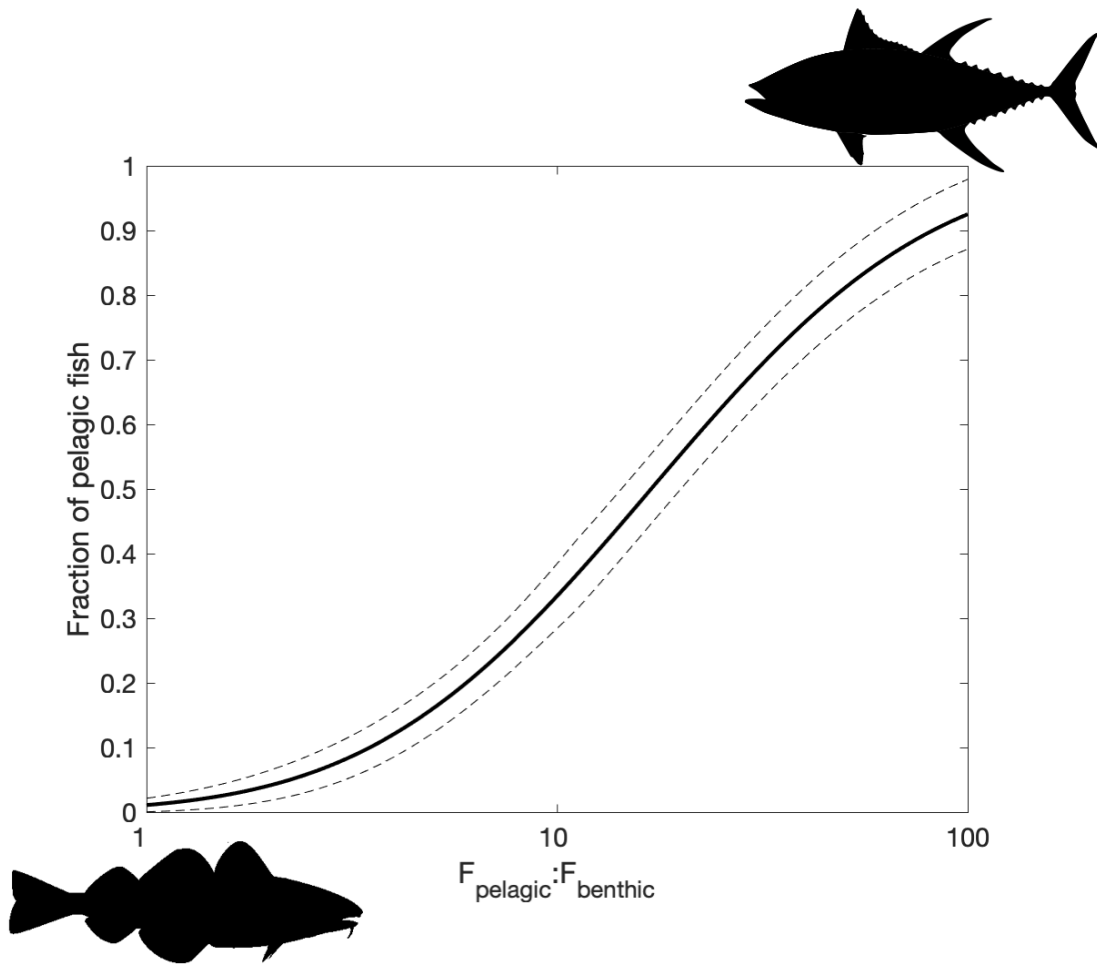
Winemiller and Rose's [1] analysis consisted of 216 North American freshwater and marine fishes, and they noted that marine species tended towards the Periodic endpoint. In this case, it seems unlikely that the small differences in traits could be used for understanding population dynamics. The analysis of Winemiller and Rose [1] was extended globally to include marine species of commercially harvested fish stocks [3]. The results show that when examined alone, marine fish species also encapsulate the triangular continuum, but do not fill the space entirely.

2. Dominance of large predatory fishes

Life history distinctions may not provide enough information given that the majority of marine fishes fall within the Periodic category, but they differ in their socioeconomic value and ecosystem role. In the marine environment, the Opportunists are often planktivorous forage fishes that serve as prey to higher predators, like the Periodic and Equilibrium fishes. These life history strategies can be further divided into various functional groups defined by habitat and feeding preferences. For example, large predatory Periodic fishes can be separated into pelagic and demersal species. Large pelagic fishes inhabit epipelagic and mesopelagic environments, often making large migrations in search of prey [4]. These fishes reach large maximum sizes and often possess homeothermic adaptations to support their higher metabolic rates and fast swimming speeds commensurate with their large migratory abilities [4,5]. Demersal fishes also attain large sizes, but tend to be slower growing and moving compared to the large pelagics [6]. They live near the seafloor and are capable of feeding both on benthic fauna and on pelagic animals [7,8]. In this vein, demersals are more "generalist" predators, while large pelagics are "specialists." These large predatory fishes seldom coexist in the same habitat, with large pelagics dominating in the tropics and subtropics [5] and demersals in temperate and polar environments [9].

Empirical studies have found that net primary productivity (NPP) alone is a weak predictor of regional variations in total fish biomass [10-12]. Rather, the production of fish biomass is closely tied to the separation of NPP into pelagic and benthic secondary production and the total amounts of these two types [11,12]. van Denderen et al. [13] expanded this work by hypothesizing that the ratio of the two pathways from NPP to fishes influences which functional type dominates. Indeed, the ratio of the fraction of NPP that remained in the pelagic (F_{pelagic}) to the fraction of NPP that was exported to the seafloor (F_{benthic}) explained the majority of the deviance in the relative biomass of large pelagic fish versus demersals in fishery landings [13]. When the amounts of pelagic and benthic resources are similar, the generalist demersals are able to outcompete the large pelagic specialists by feeding on both resource pools while the large pelagics only have access to one. Large pelagics proliferate as the ratio of pelagic to benthic resources increases (Figure 2). Mechanistic food web models have also verified this statistical relationship [13,14].

*** Insert Figure 2 ***



Caption: Relationship of the fraction of pelagic fish in fishery landings of combined pelagic and demersal fishes with the ratio of pelagic (F_{pelagic}) vs. benthic (F_{benthic}) fractions of net primary production.

Credit: Based on van Denderen et al. (2018) Figure 3. Fish silhouettes courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

This partitioning of production explains the latitudinal patterns in the distributions of large pelagic fish and demersal fish. In oligotrophic, continuously stratified regions like the subtropical gyres, the majority of NPP is recycled within the mixed layer via microbial pathways that support microzooplankton grazers in the pelagic zone. In contrast, the light-limited high latitudes experience strong but short blooms in NPP with high interannual variability. The variability in bloom timing can lead to a mismatch between NPP and the zooplankton grazer population, which has been reduced to low levels via deep winter mixing, resulting in a fraction of ungrazed NPP available for export [15]. Temperature additionally explains the latitudinal patterns in pelagic vs. benthic resources, and thus large pelagic vs. demersal fish, through its effect of increasing remineralization rates during export thereby reducing the amount of NPP that reaches the seafloor [16,17].

3. Expectations under climate change

It is well known that global air and ocean temperatures are increasing due to anthropogenic greenhouse gas emissions [18]. Higher temperatures favor large pelagics over demersal via two mechanisms: increasing remineralization rates and increasing stratification, both of which act to reduce export. One related measure to export production is the zooplankton-phytoplankton coupling metric, ZPC, of Stock et al. [19], which reflects the proportion of total primary production that is consumed by zooplankton. Global biogeochemistry projections (2051–2100) under a high emissions scenario (RCP8.5) compared to mean contemporary simulations (1951–2000) indicate that ZPC generally increases with climate change [19]. These increases are particularly large in mid and high latitude regions where climate change leads to shoaling of the winter mixed layer depth [19]. On average, the regions with strong increases in ZPC demonstrate increases in zooplankton ingestion rates and decreases in the loss of phytoplankton via aggregation, thus suggesting an increase in the ratio of pelagic resources to benthic resources. Following the results of van Denderen et al. [13] and Petrik et al. [14], these increases in ZPC would lead to a higher fraction of large pelagic fishes in regions that historically have been dominated by demersal predators. There will, of course, be other constraints on the abundance of large pelagics fishes at high latitudes under climate change. These include the effects of temperature on metabolic physiology in addition to whether there is enough total productivity to support higher trophic levels.

Despite their dissimilarities in prey and habitat preferences, large pelagic and demersal fishes exemplify the Periodic life history strategy selected for in seasonally variable environments. It has long been hypothesized by fisheries oceanographers that the survival of larvae and their recruitment to the adult population is influenced by environmental variability (e.g. [19]). Spawning events should evolve to produce larvae that temporally or spatially match the ideal oceanographic conditions for survival, such as plankton blooms or retentive circulation, however the variability of these features often leads to failures [21-23]. Thus, the long lifespans of Periodic fishes are an adaptation to variable recruitment success where longevity serves the purpose of repeated recruitment attempts [24,25] rather than attaining the large sizes of a top predator like the Equilibrium species. Furthermore, their high fecundity also increases the chance that some proportion of offspring will encounter favorable conditions.

However, the E-P-O framework uses mean life history traits for each species, but these traits are plastic and a range of phenotypes may be present within each fish stock [26,27]. There is evidence that fishing pressure and climate change have altered the life history traits of populations, such as age at maturity [28] and maximum size [29]. For example, fishing has depleted many long-lived, large, higher trophic level fishes that have been replaced by faster growing, earlier maturing species of lesser trophic level [30]. Similarly, temperature rise has increased the occurrence of species with Opportunistic and Periodic strategies increased along European margins [31].

In general, fishing pressure has selected for smaller sizes and earlier maturity ages, which decreases reproductive capacity of population [32]. Additionally, fishing truncates the age and size structure of populations [33]. These changes act to increase the influence of recruitment success and environmental conditions on the populations, especially for fishes whose reproductive traits vary with age, such as the Periodic cod,

haddock, plaice, and winter flounder [34]. Firstly, older fishes produce more larvae with increased growth rates and starvation tolerance [33] that may be able to survive in a broader range of environmental conditions. Thus, when these spawners are removed from the population, survival of the larvae produced by the younger population is more variable due to the need for meeting a narrower range of environmental conditions each year. Secondly, spawning time often varies with age [33] such that a population with an intact age structure spreads the risk over a greater period of time so there is a greater probability of larvae temporally matching the ideal conditions for survival. The shifting of populations from “bet-hedging” Periodic strategies to Opportunistic life histories will be further exacerbated by the asymmetric effects of climate change on the timing of spring blooms and spawning. Spawn timing is largely affected by temperature, whereas the spring bloom is affected by additional factors like mixed layer depth, such that climate change could increase the proportion of mismatches. This is particularly significant for populations that spawn in specific geographic locations [35,36].

4. Conclusions

Climate change has the potential to drastically alter marine ecosystems [37]. The warming that has occurred over the past several decades produced observable consequences for marine organisms including smaller body sizes, faster maturation rates, vertical displacements, and shifts in geographic ranges [29,38,39]. These changes directly influence predator-prey relationships, including fishing (humans as predators), that depend on size ratios and overlapping habitats. Managing the conservation and sustainable fishing of marine resources on a species-by-species basis under multiple, often interacting, impacts will not be straightforward. Fortunately, life history theory in combination with a trophodynamic understanding of functional types provide frameworks for anticipating the effects of disturbance, including climate change. Thusly, these frameworks serve as potentially powerful tools for guiding ecosystem-based fisheries management.

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