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Review

Scientific Methods to Understand Fish Population Dynamics and Support Sustainable Fisheries Management

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Abstract: Fisheries play a significant role in the livelihoods of the world population, while the dependence on fisheries is acute in developing countries. Fisheries are consequently a critical element for meeting the sustainable development (SDG) and FAO goals to reduce poverty, hunger and improve health and well-being. However, 90% of global marine fish stocks are fully or over-exploited. The amount of biologically unsustainable stocks increased from 10% in 1975 to 33% in 2015. Freshwater ecosystems are the most endangered ecosystems and freshwater fish stocks are worldwide in a state of crisis. The continuous fish stock decline indicates that the world is still far from achieving SDG 14 (Life Below Water), FAO's Blue Growth Initiative goal and SDG 15 (Life on Land, including freshwater systems). Failure to effectively manage world fish stocks can have disastrous effects on biodiversity and the livelihoods and socio-economic conditions of millions of people. Therefore, management strategies that successfully conserve the stocks and provide optimal sustainable yields are urgently needed. However, successful management is only possible when the necessary data are obtained and decision-makers are well informed. The main problem for the management of fisheries, particularly in developing countries, is the lack of information on the past and current status of the fish stocks. Sound data collection and validation methods are, therefore, important. Stock assessment models, which support sustainable fisheries, require life history traits as input parameters. In order to provide accurate estimates of these life history traits, standardized methods for otolith preparation and validation of the rate of growth zone deposition are essential. This review aims to assist researchers and fisheries managers, working on marine and freshwater fish species, in understanding concepts and processes related to stock assessment and population dynamics. Although most examples and case studies originate from developing countries in the African continent, the review remains of great value to many other countries.

Keywords: life history traits; methods comparison; population imbalance; stock assessment

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1. Introduction

Human connections to fisheries have developed over thousands of years, underlining the notable contribution of fish and fisheries to human well-being. Globally, millions of people directly or indirectly depend on fisheries for their employment, income and food security [1–3]. This dependence is acute in developing countries, particularly for poor and marginalized people [4,5]. The opening up of global markets for fish and fisheries products have created multiple opportunities to increase employment and income from fisheries [6]. Total employment in fisheries grew increasingly from 28 million in 1995 to 39 million in 2010 [3] (Figure 1). In 2016, more than 40 million people were involved in fisheries, with 79% and 13% of these 40 million people living in Asia and Africa, respectively [3]. The involvement of people in fisheries in developing countries has been growing steadily, while it has been declining in most developed countries [7], indicating that fisheries play a significant role in developing countries. Whereas men are primarily involved in fishing, women are heavily involved in fisheries-related activities such as processing and trade [8]. In developing countries, particularly in Asia and Africa, millions of women are involved in fish processing, marketing, making and repairing nets, making baskets, pots, and baiting hooks [7].

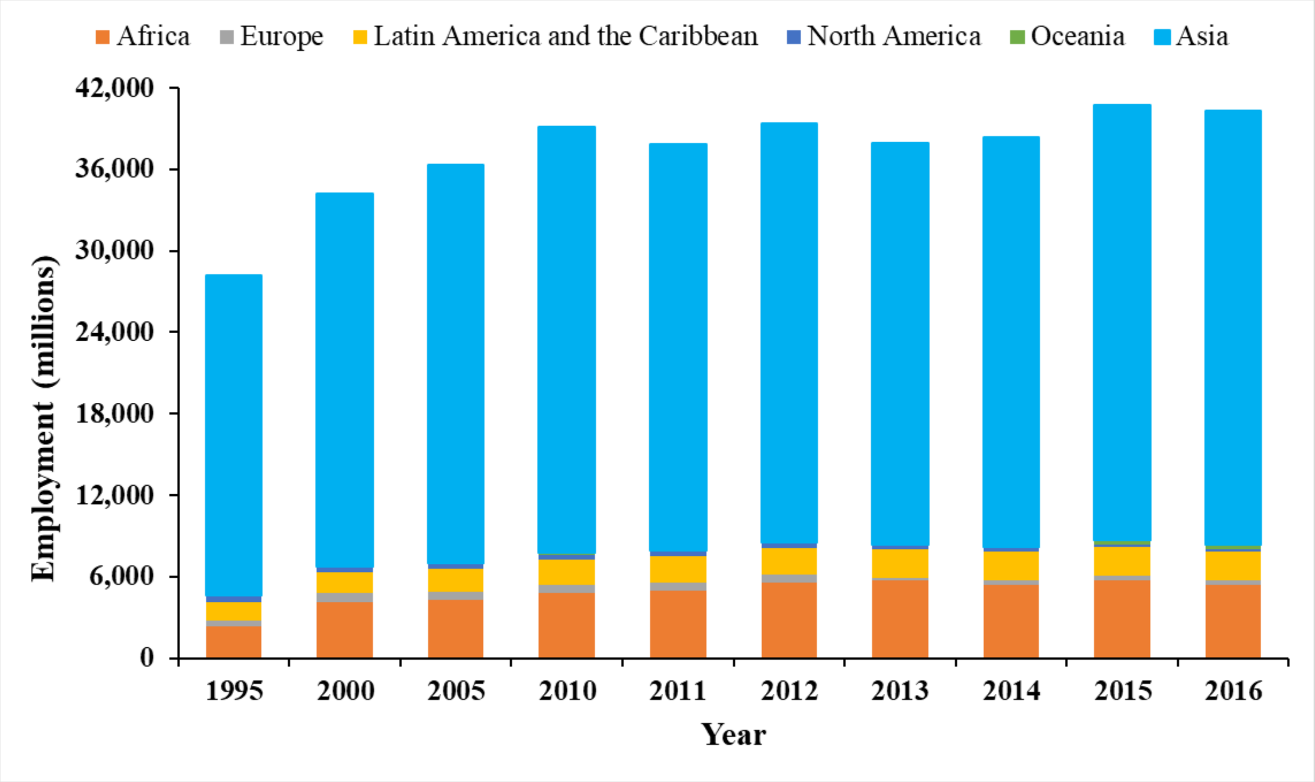


Figure 1. The global role of the fisheries sector for employment (Source: [3]).

Fisheries have an important economic contribution worldwide. Fisheries products are among the most traded food items and play a vital role in the global and local economy. For example, in 2016, approximately 60 million tonnes of fish and fish products (35% of global fish production) entered international trade in various forms [3]. This represents a total increase of 245% compared to 1976, but if we consider the trade in fish for human consumption alone the increase is more than 500% [3]. The value of global fish products also grew significantly from USD 8 billion in 1976 to USD 152 billion in 2017 [3]. This value surpasses the combined value of the net exports of rice, coffee, tea, tobacco and meat of that same year [3]. Fisheries play an important role in the national economies of many developing countries through the generation of foreign exchange derived from international trade. Fish production exports from developing countries account for approximately 60% of the total fish production being traded internationally [7]. Fish trade by developing countries increased from less than USD 4 billion in 1980 to USD 18 billion in 2001 [9]. Thus, fisheries are playing an increasingly important role in the national economy of many developing countries. Additionally, since the majority of the people involved in fisheries are from developing countries, fisheries are essential to keep households and communities out of poverty and improved fisheries management has the potential to further reduce poverty. The rural poor and marginalized people employed in fisheries could use the income earned from the sector to buy basic needs for living and to send their children to school. Fisheries have several valuable socio-cultural aspects. Understanding the socio-cultural values associated with fish and fisheries is, therefore, vital for effective management of the resources [10]. Ignoring these values could reduce the social acceptability of the management options [11].

Of the seven billion people in the world, one billion are officially designated as starving [12] and two billion people suffer from micronutrient deficiency [13]. Although the improvement of agriculture practices has been identified as essential to overcome the looming food security crisis, fisheries can also make a significant contribution [14]. Fish is an important and affordable source of protein, essential micronutrients, and fatty acids, especially for people in developing countries [15,16]. Fish consumption has been associated with various human benefits such as child mortality reduction, and maternal health improvement [7]. The annual global fish production for human consumption has increased from 67% of the total fish production in the 1960s to 88% in 2016 [3]. Fish accounted for 17% of animal protein consumed by the world population [3], the majority of which was consumed in low-income food-deficit countries [1,17,18]. Generally, fisheries are important to address hunger, micronutrient deficiencies and food insecurity [1], underlining its vital role in meeting the sustainable development goals (SDGs 1 = no poverty, 2 = zero hunger, 3 = good health and well-being) and FAO’s goal of a world without hunger and malnutrition.

Despite the significant contribution of fisheries to livelihoods, employment and income, many of the global fish stocks have been declining drastically. Successful management of the fish resources is therefore crucial. Failure to effectively manage world fish stocks can have disastrous effects on biodiversity and the livelihoods and socio-economic conditions of millions of people who are strongly dependent on these resources. Management strategies that successfully conserve the stocks and provide optimal sustainable yields are urgently needed. Successful management is possible when the necessary data such as age, growth, mortality and maximum yield are obtained, processed and interpreted and decision-makers are well informed. Fisheries managers, particularly from developing countries, are faced with many challenges due to lack of information on the past and current status of fisheries and the fish stocks. Although stock assessment modelling is necessary (i) to provide answers to questions about the current status of the stock, (ii) to predict the effect of current and future management measures and (iii) to support sustainable fisheries by providing fisheries managers with necessary advice to make informed decisions (Figure 2), such studies are limited in developing countries. To understand the factors affecting fish population imbalance, a good understanding of the wide range of age determination and validation techniques is required. They provide valuable input parameters for further stock assessment evaluation. However, the majority of young researchers in developing countries have limited skills and knowledge on how to select and prepare ageing hard structures and to validate measurements. Although there have been several well-documented methodological studies in developed countries that can be used as a reference, most of them are not open access. This hinders fish resources managers and young researchers in developing countries from accessing these documents. Therefore, the aim of this study is to provide an accessible review to fisheries managers and young researchers from developing countries. The review focuses on the factors that affect fish population imbalance, the different ageing hard structures, optimal otolith preparation and age validation techniques and their limitations and advantages. The review provides essential information to illustrate the need for reliable methods for life history trait estimation and evidence-based fisheries management. Therefore, this review aims to assist researchers and fisheries managers, working on marine and freshwater fish species, in understanding concepts and processes related to stock assessment and population dynamics. Although most examples and case studies originate from developing countries in the African continent, the review remains of great value to many other countries.

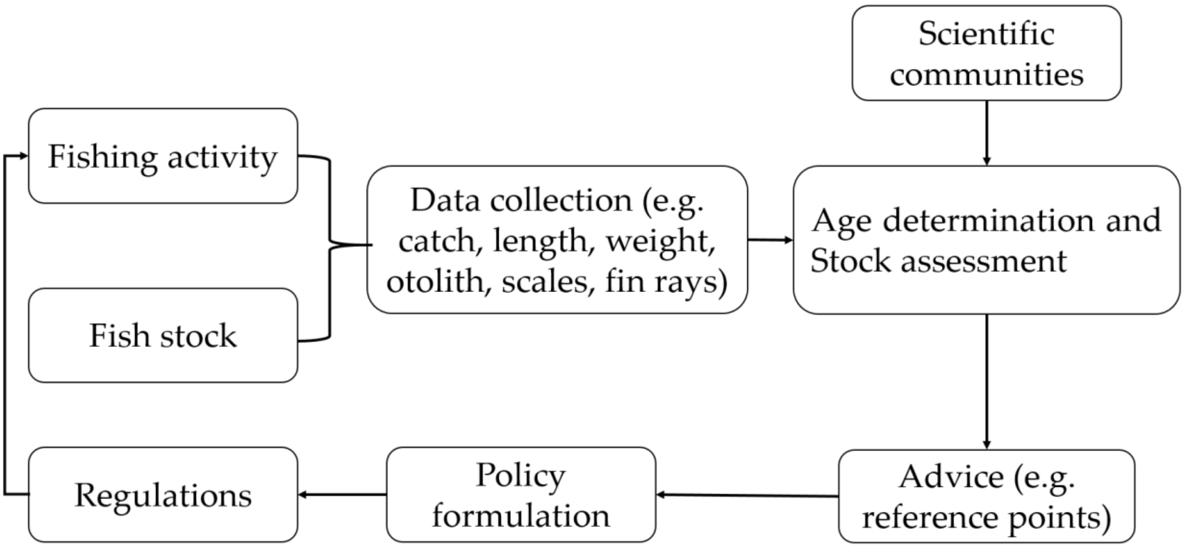
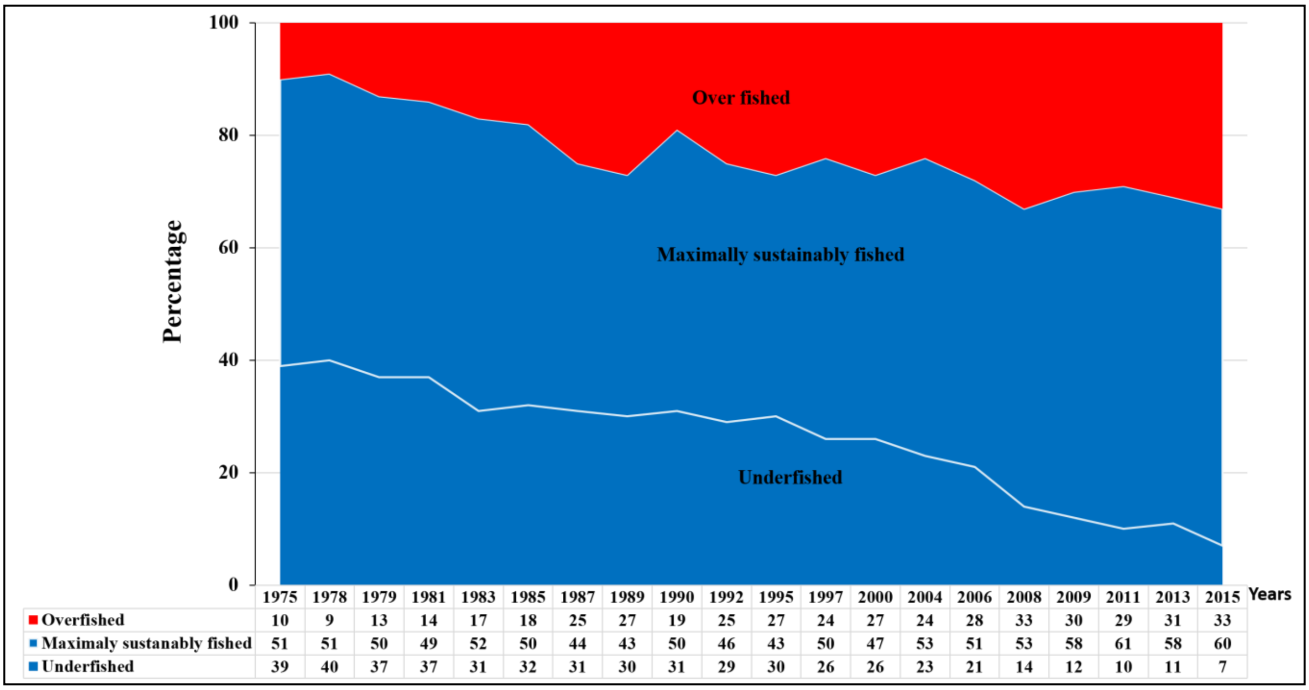


Figure 2. The process of fisheries data collection for age determination methods and stock assessment modelling to provide important advice to develop regulations and policies for sustainable fisheries management.

2. Global Fish Stock Status

Global fish stocks have been declining drastically. This decline has been attributed to several pressures, particularly the rapid increase of fishing efforts to feed the rapidly increasing human population [3]. Currently, 90% of global marine fish stocks are fully or over-exploited [3]. The size of biologically sustainable marine fish stocks (i.e., maximally sustainably fished and underfished stocks) decreased from 90% in 1975 to 67% in 2015, while the size of biologically unsustainable stocks (i.e., overfished stocks) increased from 10% in 1975 to 33% in 2015 [3] (Figure 3). Since there are no new fishing grounds to be exploited [3,19] and the current world human population is predicted to exceed nine billion by 2050, there will likely be more pressure on the stocks.



	1975	1978	1979	1981	1983	1985	1987	1989	1990	1992	1995	1997	2000	2004	2006	2008	2009	2011	2013	2015
🟥 Overfished	10	9	13	14	17	18	25	27	19	25	27	24	27	24	28	33	30	29	31	33
🟦 Maximaly sustanably fished	51	51	50	49	52	50	44	43	50	46	43	50	47	53	51	53	58	61	58	60
🟦 Underfished	39	40	37	37	31	32	31	30	31	29	30	26	26	23	21	14	12	10	11	7

Figure 3. The trend of the global marine fish stock (source: [3]).

Freshwater ecosystems, one of the most important life-support systems on Earth, are the most endangered ecosystems in the world [20]. Freshwater ecosystems are vulnerable to changes in the basin [21,22] originating from agriculture, mining, urbanization and dam and diversion weirs construction [23]. Anthropogenic pressures cause changes in the physical, chemical and/or biological components of the freshwater ecosystems when the carrying capacity of ecosystems decreases below the ability to absorb stress. Freshwater fish stocks are in a state of crisis worldwide [24]. The perceived increase is caused by changes in the monitoring and measuring rather than actual changes in fisheries production [3]. This is corroborated by the drastic decline in abundance and diversity of the different freshwater fish species due to the increased anthropogenic pressures [20,25–33]. Furthermore, ≥65% of the inland water habitats are moderately or highly threatened [27], suggesting that some of the fish species inhabiting these systems are at high risk of extinction. According to World Wide Fund for Nature (WWF [34]), the current rate of fish population decline in freshwater systems is two times the rate for marine systems.

There are many examples of excessive stressors with negative consequences. For example, the catches, diversity and composition of the fish communities, particularly the most commercially valuable species, in many African lakes such as Lake Malawi, Lake Tanganyika, Lake Victoria and Lake Tana have markedly declined due to overexploitation, illegal fishing, the introduction of exotic species and environmental degradation [31,33,35–38]. A recent assessment by the International Union for Conservation of Nature (IUCN) revealed that 9% of the 458 fish species inhabiting Lake Malawi are at high risk of extinction [39]. Studies indicated that in Lake Malawi, long-living, slow-growing and late-maturing species have been depleted [40–44] while the biomass of the endemic *Oreochromis* species (chambo), has been declining rapidly [45,46]. There are strong signs of overfishing for chambo, the most valuable component of the lake fishery [47]. The chambo fishery in Lake Malawi has declined from 5000 tonnes per year in 1992 to less than 2000 tonnes per year in 1999 [48]. Similarly, in response to intensified pressures, like eutrophication and overfishing, fish stocks in Lake Victoria have changed both in composition and abundance [49]. Currently, more than 76% of the fish species in Lake Victoria face extinction [50]. The abundance and diversity of fish species in Lake Turkana drastically declined due to degradation of the littoral habitats and flood pulse breeding areas caused by upstream development and climate change [51]. Fisheries in the major river basins such as the Zambezi River system have experienced drastic declines in catch rates, changes in fish communities and loss of valuable species [52]. Most of the fish communities in the inland waters of Ethiopia are showing signs of overfishing [25,53–55]. Anthropogenic pressures in and around the inland waters negatively affect the survival of fish species in Ethiopia. For example, the abundance and size of the fish populations in Lake Tana have been declining drastically due to overexploitation, agriculture and dam constructions [31–33]. As a result, the catch per unit effort (CPUE) of the endemic *Labeobarbus* in the lake decreased from 63 kg/trip in 1991–1993 [56] to 2 kg/trip in 2016–17 [55]. Currently, five *Labeobarbus* species are already reported as IUCN red-listed species [57]. This number will likely increase even more in the near future as the present status of many species have not been evaluated yet. Furthermore, the predominance of small-sized species with little economic importance over large-sized species with high economic importance has been reported [53]. This suggests overfishing of the system. Due to overfishing, the proportion of large and valuable species decreases in favour of small and less valuable species [58]. Therefore, the continuous fish stock decline, particularly in developing countries indicates that the world is far from achieving the SDGs. Especially, SDGs target 14.4 to end illegal, unreported and unregulated (IUU) fishing by 2020 will not be met at all. Additionally, the world human population is rapidly increasing, leading to a higher demand for fish, which poses a hurdle for the FAO’s Blue Growth Initiative goal. This goal aims to maximize the goods and services provided by the different ecosystem types without compromising the social and economic benefits the systems offer [3].

3. Dynamics in Fish Population Size and Life History Traits

3.1. Factors Affecting Fish Population Imbalance

Fish population dynamics are primarily affected by three factors: (1) recruitment, (2) growth and (3) mortality rates [59]. The recruitment is defined as the number of individuals born within a given period. Growth is the increase in length and weight of the individuals of a population in a given period of time, and mortality is the number of individuals removed from the population within a given period of time (Figure 4). Recruitment and growth increase the fish population in number and biomass, while mortality, due to fishing and/or natural causes, decreases the population both in number and biomass. Illegal, unreported and unregulated (IUU) fishing increases fishing mortality and has adverse effects on the abundance and size composition of fish populations. Fishers often target the spawning biomass, causing high mortality rates which in turn leads to drastic reductions in the abundance of recruits and mega-spawners. Furthermore, small mesh sizes, typically used for illegal fishing, are known to have negative effects on the size distribution and maturation of fish [60,61]. For example, the majority of the specimens of *Labeobarbus* species in Lake Tana caught using ≤ 8 cm mesh size gillnets had fork length less than the size at first maturation ($FL_{50\%}$) [55]. The dominance of immature individuals ($<FL_{50\%}$) in the catch confirms the expected negative effect of small mesh size gillnets. Additionally, specimens of *Labeobarbus* with ≥ 40 cm fork length (FL) were more often recorded in the late 2000s [62,63] than in 2016/17 [55]. The absence of large-sized specimens (mega-spawners) is the result of destructive fishing activities targeting the spawning biomass and causing environmental degradation. Climate change also has the potential to affect freshwater fish resources, especially the mega spawners [64–67]. The reduction of mega-spawners in a stock is detrimental to the long-term survival of fish populations due to (i) their high fecundity, which creates a greater chance of survival to larvae [68,69], (ii) their ability to serve as reservoirs and distributors of desirable genes [70], and (iii) their ability to act as a natural safeguard against subsequent recruitment failure [71,72]. The presence of enough mega-spawners can be used as a simple estimator of the resilience of stocks against random disturbance events [70]. The presence of 30–40% of mega-spawners in stock indicates a healthy size and age structure of the population, while < 20% could be a matter of concern [70]. In general, the fish population decreases if the addition to the population by recruitment and growth is smaller than the removal from the population due to mortality. Thus, the current drastic decrease in the global fish population suggests that mortality (fishing and/or natural) is exceeding recruitment and growth. Understanding the major factors that cause fish population imbalance is therefore vital for a sustainable exploitation of fisheries.

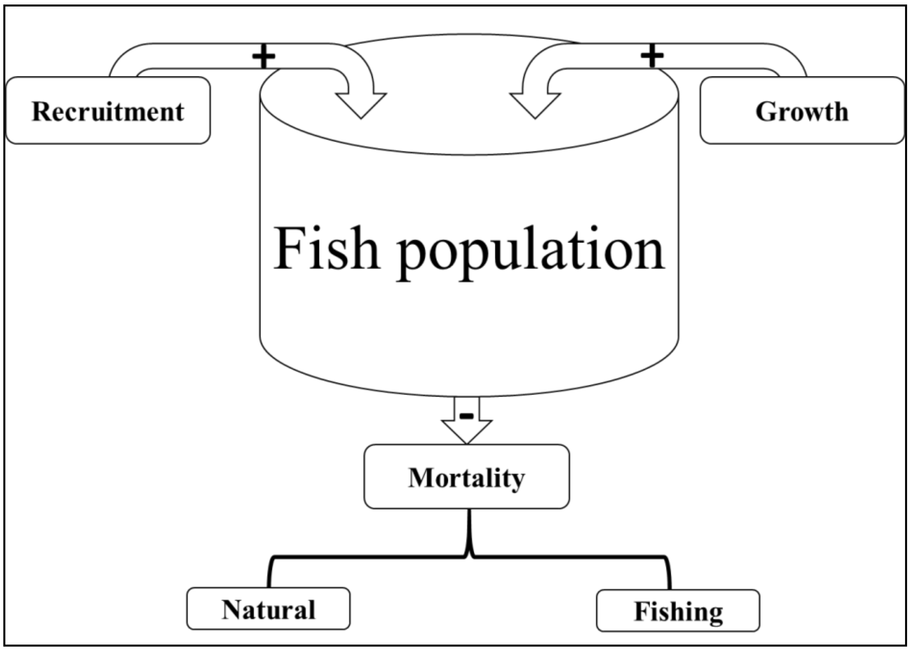


Figure 4. Illustration of the fish population dynamics. The "+" sign indicates an addition to the population, while the "−" sign indicates removal from the population.

Size structure indices are useful to evaluate the status of the fish population and identify the pressures that affect the population dynamics [73–76]. For example, analysis of length-weight relationships for a species can provide fundamental insights into the ecology, population dynamics, and management of that species. Understanding how the weight of fish changes as a function of length is useful to predict weight from the length of the fish and determine the growth type and relative condition of the fish population. Use of the size structure indices as potential indicators of fish population imbalance has gained popularity because of their connections with recruitment, growth and mortality [73,75,77]. For example, the proportion of small size individuals in the population might be higher than the proportion of large size individuals due to high recruitment, slow growth and/or high mortality rates of large size classes and vice versa [73,74].

3.2. Life History Traits as a Basis for Stock Assessment and Fisheries Management

The current world human population is rapidly increasing, although the world fish stocks have been declining drastically and there are no new fishing grounds to be exploited [3,19]. The rapid world human population increase will likely cause high fish consumption demand which in turn will increase the pressures on the stocks. Fisheries managers are facing many challenges as fish stocks continue to decline and IUU fishing undermines the sustainability of fisheries. The main problem of fisheries managers, particularly in developing countries, is the lack of appropriate fisheries data for accurate stock assessment modelling. Stock assessment models provide answers to questions about the current condition of the stock and allow for predictions about how the stock will respond to current and future management measures. Additionally, stock assessment supports sustainable fisheries by providing fisheries managers with vital advice to make informed decisions. However, stock assessment models require life history traits such as age, growth and mortality rates as input parameters [78–80]. In fisheries science, age is one of the most influential life history traits that is primarily used to estimate life history traits such as age at maturity, growth rate, mortality rate and population analysis [79]. The importance of life history traits for fisheries assessment and management is presented in Table 1 [59].

Table 1. The importance of life history traits for assessment and management use.

Life History Traits	Assessment and Management Use
Age data (i.e., individual age)	Used to determine the age at first maturity and to estimate growth parameters
Age and length at first maturity	Used to establish a minimum size limit to ensure that individual fish can reproduce at least once before being harvested
Maximum age (i.e., longevity)	Used to estimate the natural mortality rate and set the maximum age in the stock assessment models
Asymptotic length ($L\infty$)	Used to set size limits (i.e., restrict mesh sizes and prohibit fishing gears)
Growth rate (K)	Indicates how fast the fish will reach the fisher's minimum size limit
Mortality rates (i.e., natural and fishing) and spawning behaviour	Highlights the area and time of increased vulnerability to harvest and can be used for seasonal or area closures to protect the spawning biomass
Sex ratio	Used to understand the relationship between individuals, the reproductive potential of the species and the state of the population
Habitat preference	Helps to identify areas for protection

In fisheries science, the collection, preparation, and interpretation of different hard structures provide a means for age estimation [81]. Otoliths, scales and fin rays are the most commonly used hard structures for age estimation [79,82]. The choice of the most suitable hard structure for estimating age is guided by several factors: (1) the ease of obtaining the hard structure, (2) growth of the structure itself and the formation of growth zones on the structure, (3) difficulties in preparation of the hard structure and growth zones interpretation and (4) accuracy and precision of the age estimates derived from the hard structures [80]. Therefore, understanding the advantages and limitations of each structure (i.e., otoliths, scales and fin rays) is indispensable to make the correct choice. In the next sections these structures are discussed more in depth.

3.3. Advantages and Limitations of the Hard Structures Used for Age Estimation

3.3.1. Otoliths

Otoliths are calcium carbonate structures that aid in balance and hearing of fish [81]. Additionally, otoliths record a remarkable amount of information about the life history traits of the fish and the environments they are living in [83]. To better understand and manage the fish population, this information should be carefully assessed, interpreted and incorporated into fisheries management decision-making. Of the three existing types of otoliths, sagittal otoliths are used for the age estimation of most fish species [84–86], but asteriscus otoliths are the most suitable structure for the Cyprinidae family [87–89]. The calcium carbonate that is used to form the otoliths originates from the water and from the food of the fish. This process is influenced by fish metabolism. During seasons with adequate average temperatures and sufficient food availability, fish grow at a relatively fast rate causing formed rings to be widely spaced. However, during the colder months where there is limited food supply, particularly for fish species in temperate regions, growth is restricted leading to narrow ring formation. As a result, alternate opaque and translucent growth zones are formed, which are considered to have been formed in one year (i.e., annulus). The age estimates of the fish can be obtained by counting the number of annuli deposited on otoliths. Regardless of its effort and cost, ageing accuracy is much higher for analysis of growth zone deposition on otoliths compared to the length and otolith size-based methods [90].

The use of otoliths for precise and accurate age estimation has several advantages: (1) otoliths grow continuously and form annuli even when the body growth slows down and the asymptotic length has been reached, (2) metabolically they are inert and not subject to resorption, (3) otolith growth varies between seasons leading to the formation of annual increments that can be used for age estimation, and (4) annuli reabsorption does not appear to occur during periods of food limitation or stress [79,88,91]. However, the use of otoliths also has limitations [92]. Age estimation using otolith is laborious, time-consuming, expensive and is dependent on the skills and experience of readers, which limits the sample size and prevents researchers with limited skills and experience to use otolith for age estimation [93,94]. Additionally, otoliths require sacrificing fish, which makes this approach difficult to be applied for threatened species or small populations [95].

3.3.2. Scales

The age of fish can also be determined by scales as the successive rings (circuli) are formed as the fish grow. The ctenoid and cycloid scales are most often used for estimating fish age [84]. Although scales from the whole part of the fish can be used, those that are found on the shoulder between the head and the dorsal fin are generally the best because of their relatively large size and low sensitivity to damage [80,84]. Traditionally, due to their non-lethal nature, scales have long been considered the most efficient and suitable structure for age determination, but more recent studies have revealed them to be inaccurate [96–99]. The limitations of scales to yield precise and accurate age estimates have been found most severe for slow-growing and older fish [79,98,99]. Scales have various inconsistencies, which make them difficult to read and interpret visually [100]. For example, well-defined marks on one scale might be absent on the neighbouring scales of the same fish [100]. Scales have several additional limitations: The first limitation is the dependency of scale growth and patterns of the circuli formation on fish growth. The variability in fish growth (i.e., between young and old fish) affects the scale growth and the appearance of the circuli. Scale growth is minimal or non-existent after the onset of maturity, particularly when fish growth is very low or ceases [84]. Thus, this causes underestimation of the actual fish age, particularly in older fish. In older fish, the circuli at the edge of the scale can be crowded making the circuli interpretation difficult. The second limitation is resorption causing some reworking or breaking of the circuli, leading to misinterpretation. The third limitation is transparency, which makes the circuli difficult to observe. The fourth limitation is that damaged or removed scales can be regenerated, resulting in growth patterns that do not accurately reflect the age of fish. The fifth limitation is that either some fish have no recognizable pattern on their scales or entirely lack scales. Therefore, when scales are used for age determination, either the age of all groups in the population should be validated, which is difficult if not impossible, or an alternative aging method should be used for older individuals in the population [80,84].

3.3.3. Fin Rays

Compared to otoliths and scales, fin rays are not frequently used for age estimation. However, the suitability of fin rays for some fish species is reported by some researchers [101–104]. The most commonly used fin rays are the dorsal, pectoral, and, pelvic fins [84]. Age estimates from fin rays have higher precision and accuracy compared to the estimates from scales [96,105,106]. Most importantly, using fin rays does not require the fish to be sacrificed [107,108] and the annuli remain representative for the age of older fish [109,110]. However, the low precision and accuracy of these structures have also been reported [111–113]. Fin rays provide inaccurate age estimates due to the following reasons: (1) difficult to read and interpret annular marks, (2) early marks are sometimes obscured by the vascular core of the fin rays, (3) irregular and unexpected spacing of annuli on the fin rays sections, which suggests resorption at different rates in different years, (4) difficult to distinguish between the true and false annulus and to correctly identify the first annulus, and (5) its preparation requires special technical skills [100,112,113].

4. Precision and Accuracy of Otolith Preparation Methods

Although there are several calcified structures available for age estimation [79,82], otoliths often provide the most precise and accurate age estimates [79,114]. However, age estimation based on the analysis of otolith growth zones involves judgment and subjective interpretation [79,81,115]. The subjective interpretation of otoliths contributes to two major sources of errors involving both processing and interpretation [79,116]. The first source of error relates directly to the nature of the otolith structure being interpreted. In this regard, otoliths must satisfy the criteria outlined in [117]: (1) otoliths must display growth increments that can be quantitatively resolved, (2) the formation of growth zones must conform to a regular and determinable time scale, and (3) otoliths must grow continuously throughout the lifespan of the fish. The second source of error can be traced back to the preparation of otoliths, interpretability of growth zones and reader experience [79,116,118,119]. The interpretation error can be minimized by describing a standardized, precise and accurate otolith preparation method and by training the age readers [79,116,118,119]. If the otolith images used for age estimation have the clearest view of the growth zones, core and edge, the bias between age readers should be minimal. It is, therefore, useful to describe the most adequate preparation method for each species. To this end, different otolith preparation methods such as transverse sections, staining, burn-and-breaking, polishing and whole otolith submerging in different substances including water and glycerol have been compared in attempt to describe the best method. Additionally, bias among hard structures such as scales, otoliths and fin rays has been compared to select the most appropriate structure. Such comparisons are especially important to approximate the accuracy of age estimates [84,120]. The precision and bias among different aging methods and age readers are usually done using statistical methods, graphical approaches, precision indices and qualitative expressions. Average percentage error (APE) [121] and coefficient of variation (CV) [122] are widely used and the most suitable and statistically sound measurements of precision [79]. The APE and CV are computed by the following formula:

$$\mathrm{APE} = \frac{100}{\mathrm{N}}\sum_{\mathrm{J}-1}^{\mathrm{N}}\left(\frac{1}{\mathrm{R}}\sum_{\mathrm{i}-1}^{\mathrm{R}}\frac{\left|\mathrm{X_{ij}} - \mathrm{X_j}\right|}{\mathrm{X_j}}\right) \tag{1}$$

$$\mathrm{CV} = \frac{100}{\mathrm{N}}\sum_{\mathrm{J}-1}^{\mathrm{N}}\left(\frac{\sqrt{\sum_{i=1}^{R}\frac{\left(\mathrm{X_{ij}} - \mathrm{X_j}\right)^2}{R-1}}}{\mathrm{X_j}}\right) \tag{2}$$

where N is the number of fish aged, R is the number of times fish are aged, X_{ij} is the ith age determination for the jth fish, and X_j is the average estimated age of the jth fish.

Although there is no rule of thumb, Campana [79] suggested CV ≤ 7.6% and APE ≤ 5.5% as reference values. The method with the smallest APE and CV values is, therefore, the most optimal method. The systematic bias between age readers, aging structures and aging time (i.e., if the reading is made two times by the same reader) can be described using a test of symmetry and it is best described through an examination of an age-agreement table [123]. The age estimates from the most experienced reader or the structure thought to be the most accurate should be used as the column variable in the age-agreement table. If the reading is made two times by the same reader, the first reading should appear as the column variable. Although several statistical methods were capable of detecting systematic aging differences, they were incapable of detecting both linear and non-linear biases in aging [115]. Some statistical methods, for example, were not sensitive enough to detect if the ages of younger fish were systematically over-aged or if the ages of older fish were systematically under-aged. To address this problem, Campana, et al. [115] introduced the age-bias plot to visually assess the differences in paired age estimates from two structures, two readers, or one reader at two times. Later, Ogle [124] modified the original age-bias plot in several ways. For the age-bias plot, one set of age estimates serve as reference age (x-axis). The age estimates that are thought to be most accurate are usually used as reference age. Thus, when the bias between age readers has comparable age estimates, the estimates of the most experienced reader should be used as reference age, whereas if the bias between two preparation methods or structures is compared, age estimates from the method or structure that is thought to be the most accurate should be used as reference age. However, the first reading should be used as reference age, if two readings from the same reader are made. Additionally, other factors such as qualitative expression may be involved as well. A quality control criteria (i.e., Q1 = readable otoliths with minimum bias, Q2 = readable otoliths with moderate bias and Q3 = unreadable otoliths) should be used to analyse readers' confidence. The method with the highest number of otoliths under Q1 has a higher readers' confidence than the other methods. The processing time and reading time should also be recorded. If there is no difference in precision and accuracy, the method that has the shortest processing time, the shortest reading time and the highest reader's confidence should be considered as the most optimal method.

The process of growth zone deposition on otoliths is affected by biological and environmental factors [125]. The rate of growth zone deposition on otoliths is either annual or biannual. Therefore, in age estimation studies, validation of the rate of growth zone deposition is essential. Although several methods to validate age or the rate of growth zone deposition are available, mainly marginal increment analysis and edge analysis are used [79]. For more detailed information, see literature elsewhere [79,81,84,115,124].

In developed countries, significant and extensive work has been done to standardize otolith preparation methods, validate age or the rate of growth zone deposition and estimate life history traits of fish [83,87,118,121,126–136]. Such studies are limited in developing countries such as African countries. Except for the limited efforts in South African and Ethiopian water bodies [85,86,89,137–146], many fish species in the African water bodies including the Great African Lakes remain poorly studied. Concerning the description of optimal otolith preparation methods, validation of the rate of growth zone deposition and estimation of life history traits. The present lack of information on life history traits of different fish species hinders scientists and fisheries managers from refining optimal strategies for their conservation. Thus, detailed information on the description of the optimal otolith preparation method and validation of the rate of growth zone deposition is crucial. The widely used methods to validate the rate of growth zone deposition are discussed in the next section.

5. Validation of the Rate of Growth Zone Deposition

Validation of the rate of growth zone deposition is indispensable for accurate age estimation. There are several validation methods including advanced methods such as radiochemical and bomb radiocarbon dating. However, since these advanced methods are very expensive and difficult to apply for short-living species, mark-recapture of chemically tagged fish, marginal increment analysis and edge analysis are often used to validate the rate of growth zone deposition [79]. In this section only these widely used methods are discussed, for information about the other validation methods see Campana [79], Green, et al. [81], Andrews, et al. [130] and Piddocke, et al. [147]. A summary of the different methods used to validate age or the rate of growth zone deposition is presented in Table 2.

Table 2. Advantages, limitations, precision, sample size and cost of the different methods used to validate age or the rate of growth zone deposition. Methods are listed regardless of any scientific value. (Source: [79,147]).

Methods	Advantages	Disadvantages	Precision	Sample Size	Cost
Mark-recapture	Validates the frequency of post-tagging growth increments.	Low or non-existent of recaptured fish at liberty (>1 year).	±1 year	>1	Minimal excluding cost of tagging cruise

		Difficulty to identify a post-mark annulus			
Marginal increment analysis and Edge analysis	Validates frequency of growth increments formation.	Applicable to fast-growing or young fish. A year-round sample is required.	±1 year	>100	Minimal other than a fish collection
Radiometric	Validates absolute age. Applicable to any recently collected data. Suitable to long-lived fish	Can only distinguish between widely divergent age estimates	±25–50%	10–50	~$1000 per age category
Radiocarbon	Validate both absolute age and frequency of growth increments. Suitable for long lived fish. Does not require recently collected sample.	Some of the fish in the sample must be hatched before 1965.	±1–3 years	20–30	$700–$1000 per otolith

5.1. Mark-Recapture of Chemically Tagged Fish

At the moment this method is one of the best and most cost-effective methods available to validate the rate of growth zone formation [79]. It can be applied through various methods such as injection, immersion and feeding. Injection is the most common technique for tagging wild fish [148–150]. Fish species that are captured from the wild are injected with calcium-binding chemicals such as oxytetracycline (OTC), alizarine, calcein and strontium immediately at the time of tagging [125]. These chemicals are incorporated into otoliths shortly after injection. The permanent mark is visible under fluorescent light in the growth zone being formed at the time of tagging [79]. The rate of growth zone deposition can be determined based on the number of growth zones deposited distally to the mark in the recaptured fish and the time at liberty. If the difference in the time of injection and liberty is one year and one growth zone is deposited during this time, it means that the studied fish species deposited one growth zone per year. However, if two growth zones are deposited, it means the rate of growth zone deposition is biannual. This method has been applied to validate the periodicity of growth zone deposition in several fish species [141,143–145,151–154]. The growth zones being validated are formed while the fish is growing in the natural environment. This method is time-consuming, technically difficult to apply and the recovery rates of the tagged fish are usually low [155]. Additionally, since the numbers of growth zones formed after tagging are low, a wrong conclusion can be made on the rate of growth zone deposition, if one of the growth zones is misinterpreted.

5.2. Marginal Increment Analysis

Marginal increment analysis (MIA, linear-circular model) is the most widely used validation method due to its modest sampling requirements and low cost [79]. The MIA is based on the observed incremental patterns of growth zones throughout the year and assumes that the outermost increment displays a yearly sinusoidal cycle when plotted against months of capture [156,157]. It uses the ratio of the width of the last growing zone and the width of the last fully completed growth zone (MIR) as a dependent variable and months of capture as an independent variable [158–160]. The marginal increment ratio (MIR) is, therefore, computed as follows [161].

$$\mathrm{MIR} = \frac{\mathrm{R} - \mathrm{r_n}}{\mathrm{r_n} - \mathrm{r_{n-1}}} \tag{3}$$

where R is the distance from the core to the outermost of the edge, r_n is the distance from the core to the end of the growing zone and r_{n-1} is the distance from the core to the end of the last fully formed growth zone.

When the MIR value is equal to one, it indicates the completion of growth zone formation. Although the MIA is a useful method, especially when supported by other validation methods [159], it is also susceptible to bias and misinterpretation if not applied rigorously [79]. The approach has several limitations. The extended time of sample collection (monthly at least for one year), high possibility to collect small sample size per size classes within each month, difficulties to objectively classify the edge types and substantial inter-individual variation in marginal increment appearance [79,147]. These limitations are more pronounced in older fish where growth increments become very thin and packed together [118,162]. Therefore, when MIA is applied as age validation, the following protocols should be applied. (1) samples must be completely randomized when assigned to the examiner, (2) a minimum of two complete cycles need to be examined, in accordance with accepted methods for detecting cycles, and (3) the results must be interpreted objectively [79]. All the described protocols and encountered limitations for this technique here are also applicable for the edge analysis approach described below [79].

5.3. Edge Analysis

Similar to the MIA, edge analysis (EA, binary-circular model) is also based on examination of the marginal increments. Its dependent variable is binary, the otolith edge types either opaque or translucent, while the month of capture is the independent variable. Analysis of the EA can, therefore, verify the hypothesis that growth zone deposition is either annual or biannual. This approach assumes that the density of the outermost margin (i.e., proportion of the translucent zone) exhibits a sinusoidal cycle when plotted against the months of capture [79]. Several researchers found this approach useful for validating the periodicity of growth zone deposition [89,143,161,163]. For example, the Edge analysis revealed an annual growth zone deposition for *Labeobarbus platydorsus* in Lake Tana [140] (Figure 5). Although the EA approach is cheap and logically simple, it is susceptible to bias and misinterpretation if not applied rigorously [79].

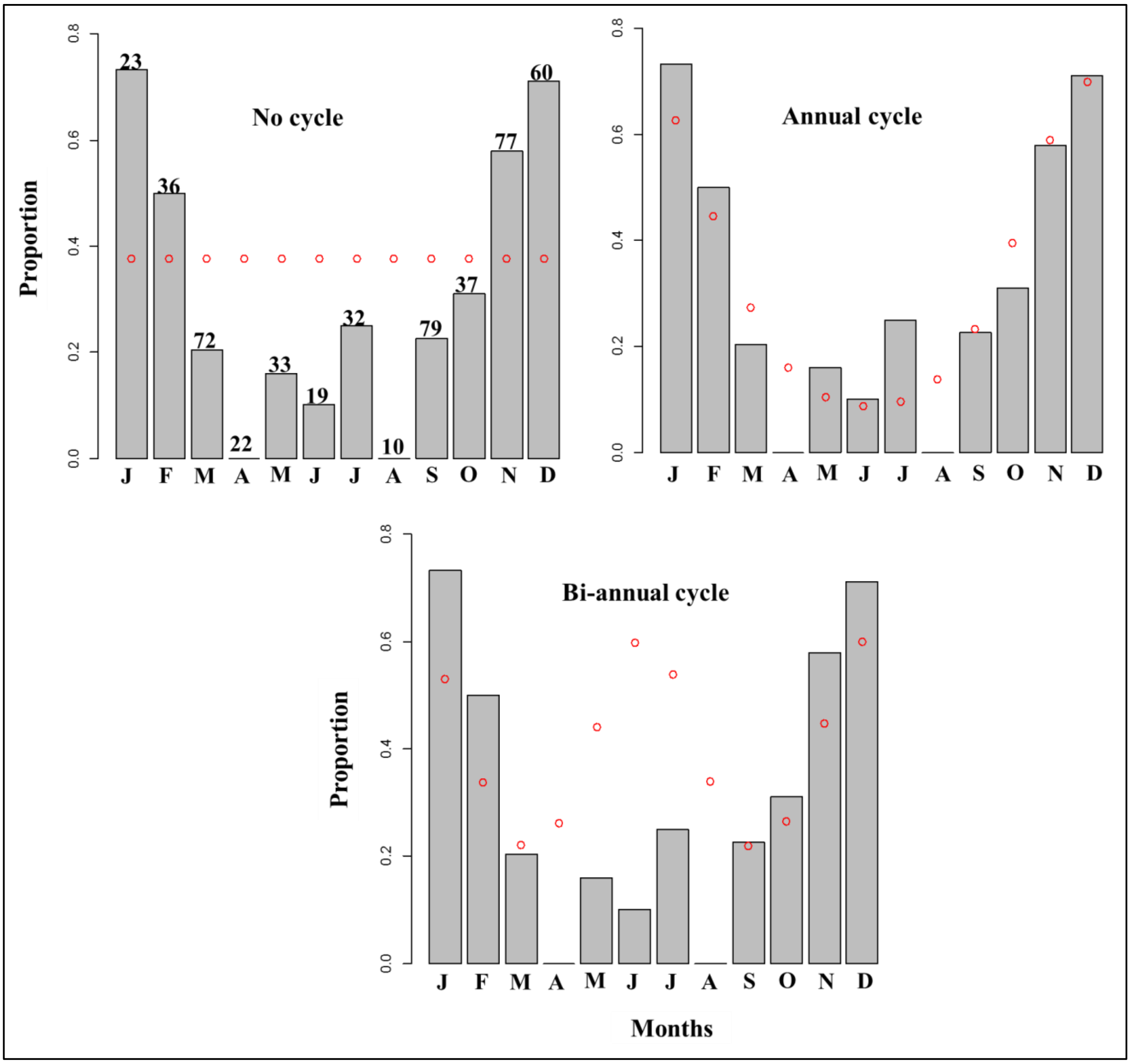


Figure 5. The proportion of asteriscus otoliths with a translucent growth zone on the edge for *Labeobarbus platydorsus* based on samples collected between May 2016 and April 2017 in Lake Tana, Ethiopia [140]. The bar graph denotes the proportion of the translucent growth zone and the open dot line represents the predicted model results. The numbers above the bars in the no cycle model are total sample size and the same sample size is used for the other models. The annual cycle mode best fit the data.

6. Conclusions

Fisheries management strategies must be developed to ensure that stocks are harvested at sustainable levels. Fisheries managers rely on age estimates to develop effective and sustainable management options. Accurate and precise age estimates can be obtained if and only if an appropriate otolith preparation method is described and the rate of growth zone deposition is properly validated. Age estimates combined with data such as fish length, weight and reproductive condition can be used to describe the structure and dynamics of the population considered to comprise the harvested stock. For example, longevity and growth rates are estimated using length and age data, while the combination of sex and reproductive condition with growth data are used to describe the age-fecundity relationship and sex-specific growth. Mortality rates are also computed by combining age estimates with counts of the number of fish per age class in a sample. These analyses provide researchers and fisheries managers with a range of information to derive sustainable harvest strategies through stock assessment evaluations. In order to avoid complete stock collapse, fisheries catch should not exceed the maximum sustainable yield of the stock (MSY). The MSY is an important tool to quantify the goal of a fishery and allows fisheries managers to evaluate the performance of the fishery. The comparison of the assessed state of the fish stock with the values of the fisheries reference points such as MSY supports the managers to make informed decisions. Thus, fisheries reference points should be calculated as correctly as possible. The most popular and widely used model to estimate the MSY is the yield-per-recruitment model, introduced by Beverton and Holt [164]. Understanding the population dynamics, age determination techniques, and the estimation of life history traits allow policymakers and fisheries managers to optimize future conservation strategies (Figure 6). Furthermore, monitoring and evaluating the effects of the major pressures such as pollution, habitat degradation and over utilization of aquatic resources is vital to provide insights into the changes of aquatic ecosystems and indicate their status (Figure 6).

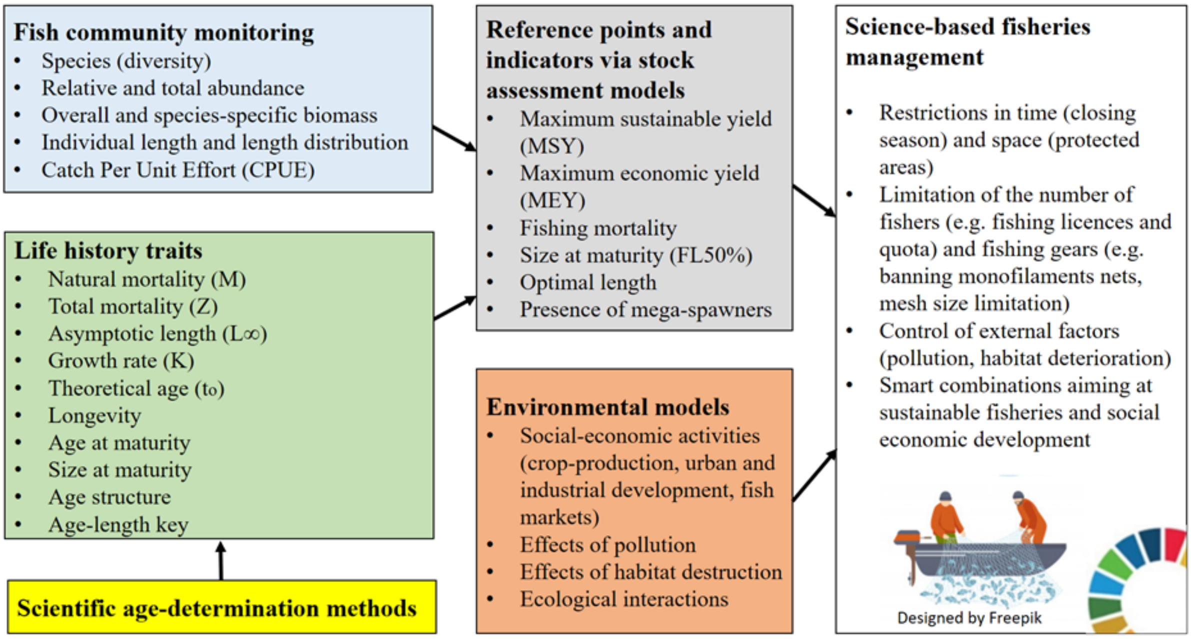


Figure 6. Schematic representation of fish community monitoring, fish stock assessment and environmental modelling to develop science-based fisheries management.

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