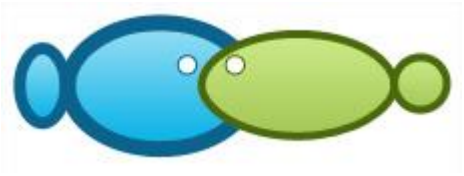

Spawning grounds literature review: spawning success factors

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Abstract. Information regarding factors that influence the success of fish spawning is important to understand and thoroughly study it. The initial step of the study was to conduct a literature review regarding the factors that can influence the success of fish spawning, which is a key factor in production and natural restocking. This study presents a literature review related to fish spawning grounds which are among the main factors in achieving sustainable principles. Fish resources can be recovered, but the rate of recovery alone is not balanced with the utilization. This study provides information on fish spawning ground, environmental conditions, reproduction, fish survival, and spawning success inhibiting factors. Fish spawning grounds are influenced by environmental conditions such as temperature and current characteristics. Apart from environmental conditions, spawning and fish survival are also influenced by increased swimming energy expenditures, increased vulnerability to predation, fishing exploitation, changes in biotic conditions, external pressure, population size and natural and fishing mortality rates. Future fish resource management needs to consider the spatial variability related to fish responses to the changing environmental conditions.
Key Words: environmental conditions, fish survival, reproduction, spawning ground.

Introduction. To achieve sustainable management of aquatic resources, it is essential to balance current needs with future ones. Water resource management must prioritize the well-being of people while also considering environmental sustainability. It is crucial to ensure that consumption aligns with the availability of sustainable resources. Fish resources in aquatic environments play a crucial role in maintaining the ecosystem's balance due to their high trophic level and their ability to serve as indicators of ecological balance (Suen et al 2009). As top predators, fish provide an integrative view of the environment, making them the most suitable indicator species (Wu et al 2014; Zhao et al 2015). Fish resource management involves regulating the utilization and maintenance of fish resources to maximize benefits while ensuring their long-term sustainability. The abundance of fish resources currently exceeds the number of fish needed, but fisheries management is necessary to ensure their sustainability. Regulating fishing activities is crucial for ensuring the long-term sustainability of fish resources (Ernawati et al 2017). The fish capture needs to be carried out carefully so that the rate of fishing does not exceed the recovery capacity.

Spawning ground protection is one of the principles of sustainable efforts in the utilization of aquatic resources. The spawning ground allows marine organisms to carry out their reproductive cycle or breed optimally in that area. Reproduction is the key to the survival of organisms. Temperature intervals have an influence on the success rate of the process of hatching eggs and the development of fish larvae (Muhling et al 2010; Reglero et al 2018; Llopiz & Hobday 2015; Muhling et al 2013). Appropriate water temperature encourages the presence of fish for optimal spawning (Huang & Huang

2015). Temperature functions as a driving force that motivates fish spawning behavior (King et al 2016; Dewi et al 2023). In addition to water temperature, currents also play a major role in spawning success rates by increasing or inhibiting larval retention in spawning areas (Domingues et al 2016; Lindo-Atichati et al 2012; Muhling et al 2010). Lincoln et al (2024) presented an individual density distribution map which shows that the behavior of larvae in spawning and their distribution is greatly influenced by variable currents driven by the wind. Chen et al (2015) found that fish spawning activity was sensitive to currents during the spawning period. Eggs distribution is greatly influenced by currents because of their small size. Increased currents both spatially and temporally greatly influence the fish migration and spawning activity, the egg abundance (Koster et al 2018; Xu et al 2015) and the availability of a suitable spawning habitat (King et al 2016; Li et al 2019; Chen et al 2020). One good research method for studying fish spawning is by looking at the spatial patterns of fish spawning. The distribution of egg diameters can indicate fish spawning patterns and locations. Ignoring the impact of environmental changes in fisheries management strategies can have negative impacts on fish survival (Pan et al 2023). Indirectly, the ecological status of waters is related to a series of hydrological patterns that occur spatially and temporally (Barbalic & Kuspilic 2015). Information about ecology can help determine potential areas for fish spawning grounds (Bezerra et al 2021). Therefore, the influence of the environment on the life cycle of fish resources is an important factor determining the management and conservation strategies.

Management and conservation of migratory resources in wide waters requires good knowledge, especially regarding movements and habitats along the life cycle stages, in particular the appropriate environment for spawning and hatching of fish populations (Wang et al 2014; Raja et al 2016). Even though fish resources are recoverable, the rate of recovery should be managed properly. This research investigates the fish spawning ground as a preliminary step for a management method to maintain the sustainability of fish resources in the waters.

Fish spawning ground. Spawning is an important stage in the recruitment of fish resources in waters. Spawning behavior is important to understand, especially in fish that have high commercial value or which are affected by an intense fishing pressure over time (Sadovy de Mitcheson et al 2013; IUCN 2020). The in situ research identifying deep breeding areas is still scarce, which contributes to increase the risk of species extinction, in particular when the dynamics of fish reproduction is disturbed due to overfishing (Bezerra et al 2021; Ferreira et al 2014). Most of the available research is limited to information from divers and fishermen (Giglio et al 2016; Bueno et al 2016).

Research on the causes of suboptimal recruitment related to the spawning, nursery and feeding ground was also conducted (ICES 2018). Fish behavior during the spawning phase is influenced by two factors, both internal and external. Several fish species form spawning aggregations in the same area every year, possibly due to the suitability of the water area for a successful spawning (Surette et al 2015). Species that form aggregations are generally very vulnerable to exploitation because they are often targeted by fishing activities, thereby impacting the population density and reproductive success (Sadovy de Mitcheson 2016). Identifying fish spawning areas and periods is critical for understanding population dynamics and connectivity, and for establishing effective management strategies (Sadovy de Mitcheson 2016; Sala et al 2021). Fish spawning grounds are in located near the coast (Lincoln et al 2024). Protection of spawning stocks and a better understanding of the factors driving spawning success are critical to the future sustainability of fisheries resources. Conservation efforts to maintain the sustainability of spawning and nursery grounds need to be carried out consistently. Literature studies related to this matter are the first step in conservation efforts.

To conserve fisheries, it is essential to protect spawning aggregation areas. One effective approach is to make temporal and/or spatial recommendations, as these areas can be predicted in space and time (Gruss et al 2014).

Environmental conditions. The environment is a place where organisms survive and grow, carrying out every cycle in their life. Fish species intolerant of sudden changes in fluctuating environmental conditions have shown a global decrease in spawning intensity, as demonstrated by numerous studies (Wang et al 2014; King et al 2016). Phenological changes have been proven to have an influence on shifts in trophic interactions, primary reproductive patterns, population distribution, migration times and routes, and spawning times (Cohen et al 2018). Water temperature is known to substantially affect the spawning activity of fish: the appropriate temperature drives the spawning behavior of aquatic organisms they (Kayaba et al 2010; King et al 2015). The effect of temperature on fish growth is also influenced by the intensity of sunlight entering the water. Water temperature is also very important for the development of fish gonads (Dorts et al 2012). Fish species have a specific range for spawning and survival. Spawning occurs when the water temperature rises above the lower limit (Wang et al 2014). Fish spawning patterns are generally determined by climate change, environmental conditions and spawning period, duration and migration (Bal et al 2017; Asch et al 2019; Langan et al 2021). The timing and duration of fish spawning have an important impact on the recruitment, survival and distribution of species in waters (Asch et al 2019; Kanamori et al 2019). Changes in the distribution of fish spawning sites are common in waters (Goertler at al 2021; Pan et al 2020). The duration of the fish spawning season is inversely proportional to the vulnerability. This means that fish species that have a short spawning period will more easily experience a population decline (Sadovy de Mitcheson & Erisman 2012). The duration of spawning and the fish behavior can determine the spawning period. In addition, large fish tend to have a longer spawning season (Hixon at al 2014).

Temperature is a critical environmental factor that originates from the solar energy. In aquatic ecosystems, temperature fluctuates daily and annually, primarily following the pattern of air temperature in the surrounding environment, sunlight intensity, geographical location, shade, and internal water conditions such as turbidity, depth, current speed, and organic material accumulation at the bottom of the waters. The solubility of various types of gases in the air as well as all the biological activities in waters are greatly influenced by temperature.

Fish are cold-blooded animals, whose body temperature always adjusts to the surrounding temperature. Furthermore, it is also said that fish have the ability to recognize and choose certain temperature ranges that provide the opportunity to carry out a maximum of activity. The influence of water temperature on fish behavior is most clearly visible during spawning. Sea water temperature can trigger and speed up or slow down the pace of spawning in some types of fish. Water temperature and currents during and after spawning are the most important factors determining the "offspring vigor" and larval survival in the most commercially important fish species. Extreme temperatures in spawning grounds during the spawning season can force fish to spawn in other areas. Long-term temperature changes can influence the migration from a spawning ground. Several previous studies have shown that fish migration and spawning are related to temperature (Crozier & Hutchings 2014; Lombardo et al 2020). Peer & Miller (2014) reported that fish spawning behavior responds to every marginal change in temperature (by 1°C). Fish spawning can occur more quickly due to warmer temperatures. Sea surface temperature is considered the main trigger for spawning (Lincoln et al 2024). However, a study of freshwater fish showed the possibility of both a positive or negative correlation between spawning and water temperature. The response of fish to changes in temperature within a population is not always homogeneous, it can also be influenced by the spawning areas (Pan et al 2023). Therefore, integrating the several environmental parameters of fish spawning will provide a better predictability (Yang et al 2021).

The highest probability of the presence of fish larvae is at a temperature of 26°C (Muhling et al 2010). Each species has a homeostatic range of conditions that are appropriate for growth and development (Todorovic et al 2019). Tuna species, for instance, have a tolerance range to a wide range of environmental conditions (Arrizabalaga et al 2015). The preferred spawning temperature for fish is usually cooler than the optimal temperature for larval growth (Reglero et al 2018). A good area for spawning is one of the most important factors in fisheries resource management efforts.

Effective fishery resource management is crucial as fish are the primary source of nutrition for the community (Bell et al 2009). Remote sensing technology can be used to analyze maps of aquatic habitats for studying resource management (Kostylev et al 2001). Spatial-based fisheries management through the study of environmental conditions is a highly effective method for ensuring the sustainability of aquatic resources (Karametsidis et al 2023).

Reproduction. Organisms of every species go through a reproductive phase in their life. Reproduction is a natural process for a species to ensure its sustainability in nature (Asriyana & Halili 2021). Reproduction is a breeding process that occurs in organisms in order to maintain the survival of the species. Reproduction is influenced by internal and external factors, internal factors include gonad development and fish sexuality, while external factors include the presence of the opposite sex, temperature, good spawning areas and the presence of substrate in the waters. Identifying the relationship between reproduction and biotic and abiotic parameters in each fish species and then comparing the similarities could be useful for realizing appropriate adjustments to the environmental conditions, in order to increase multispecies fish spawning. Each fish species has its own conditions suitable for spawning (Yang et al 2021). More detailed research on each species will produce a more accurate picture, and identify common parameters that may affect different types of fish. Spawning will produce fish larvae whose growth will preserve fish species.

River ecosystems can support a variety of fish species due to the fluctuations in flow, frequency, duration, time, and rate of change in river flow that stimulate fish spawning (Zhang et al 2015; Zhang et al 2018; Li et al 2019). An appropriate area can greatly support the success of spawning and the survival of fish eggs or larvae, during the spawning season (Liu et al 2011). Survival and reproduction are fundamental aspects of life, and an organism's ability to achieve them is a measure of its fitness. This makes survival a crucial indicator of an organism's overall health and well-being. Reproduction is a crucial stage in the life cycle of fish, and it is essential for the survival of the species.

Flying fish are a highly valuable species that demand attention. Not only are they a significant food source, but their eggs are also in high demand due to their exceptional nutritional content. Flying fish lay these eggs and attach them to floating objects (Casazza et al 2005). This is thought to be due to the positive effect of warmer surface temperatures on the egg development (Uygun & Hossucu 2018), protecting the eggs during the critical early phase of their life (Stevens et al 2003).

Fish survival. The survival of fish is very dependent on the conditions of the waters where it lives. Species maintain their survival by reproducing and preserving their offspring to avoid becoming extinct. Several things can affect the survival of organisms, namely adaptation, reproduction and natural selection.

Quantification of fish spawning habitats and connectivity between habitats is important for the conservation and management of fishery resources. The survival of fish eggs can be affected by predation, physical movement or stress (Schmidt et al 2020). The survival of fish eggs after spawning shows a positive influence from environmental conditions such as waves and water temperature (Wang et al 2014). Besides, increased swimming energy expenditure, increased vulnerability to predation and fishing exploitation, changes in biotic conditions, external pressure, population size and natural and fishing mortality rates can also affect fish spawning areas and migration (Secor et al 2020). Changes in environmental conditions can result in more competitive spawning, as older or larger fish can dominate suitable spawning areas. This causes less competitive fish to migrate towards the coastal zone for exploring new spawning habitats (Pan et al 2023).

The survival of aquatic organisms is supported by the existence of places for foraging and sheltering, such as sea grass, seaweed, coral reefs and others. Seagrass beds provide shelter for aquatic organisms. The structure of seagrass plants that are firmly embedded in the seabed is an ideal place for attaching fish eggs and larvae. Most small fish also spend their lives in seagrass beds before going to deeper seas.

The availability of good shelter greatly affects the survival of fish, fish larvae or eggs, especially in demersal fish species. Several studies of coral reefs have focused on their function as a habitat that affects fish abundance (Lima et al 2019). The availability of quality aquatic habitats affects the increase in the recruitment and survival of fish and other aquatic organisms (Hylkema et al 2023). The spatial complexity of coral reefs offers shelter for a variety of fauna. Coral reefs have great benefits, both ecologically and economically, as a habitat for various species.

Spawning success inhibiting factors. The spawning process of fish is influenced by both internal factors and habitat. The distribution of spawning larvae is determined by meteorological, oceanographic, and biological factors. Annual variations in these factors impact the success or failure of larval recruitment (Beraud et al 2018), which affects spawning success. The strong interannual variations are likely due to the co-habitation of all possible spawning contingents in the spawning ground. The presence of both resident and migratory fish increases sensitivity to climate change, resulting in a high degree of variability in spawning onset time from year to year (Pan et al 2023; Gahagan et al 2015).

Indirectly, the success of the fish spawning process can have an impact on the population of organisms in the waters and the related information is needed for fisheries management (Lloret et al 2014). Fish body conditions are influenced by many factors such as food availability (Hidalgo et al 2009; Rueda et al 2019), the impact of fishing (Hiddink et al 2016; Rueda et al 2015), density (Casini et al 2016; Kjesbu et al 2014; Rueda et al 2015), various environmental factors such as water temperature (Laurel et al 2016; Veron et al 2020), salinity (Rueda et al 2015) and primary productivity (Rueda et al 2015; Veron et al 2020). All actors involved in fisheries play a crucial role in maintaining the balance of fish resources in the waters. Researchers conduct regular research related to resource management, the government implements regulations related to management, and fishermen make significant contributions to the preservation of resources in their area. To maintain resource balance, fishermen can take several actions. They should use environmentally friendly fishing gear, avoid overfishing, protect the marine environment, and understand the principles of wise fishing. By taking these actions, fishermen can ensure that they are contributing to the sustainability of the fishing industry.

External factors such as fishing, pollution, and development pose a threat to the life cycle of fish, including the spawning process (Miranda-Chumacero et al 2020). The presence of suspended sediments in the water can hinder successful fish spawning by attaching to fish eggs and affecting their buoyancy. Suspended sediments in the water column can cause water to become turbid, which can significantly impact the physiology, behavior, and reproduction of numerous marine organisms (Wenger et al 2017; Magris & Ban 2019; Corell et al 2023).

Suspended sediments in waters can affect the physiological activities of the aquatic organisms' life cycle, especially the stages of spawning, egg development and fish larvae growth (Li et al 2020; Qiu et al 2019). Fish eggs and larvae are the most sensitive stages of fish life, making it crucial to intensively protect them. Ensuring the sustainable growth of fish larvae is essential for optimal fish production and the sustainability of its resources (Wenger et al 2017). Biophysical modeling is used by many researchers to support the understanding of the factors driving larval recruitment and dispersal pathways. This modeling is used to simulate the potential dispersal of marine larvae from spawning areas, based on the oceanographic conditions and larval migration behavior (Beraud et al 2018; Cabral et al 2021). Modelling involves a high degree of uncertainty, but its predictions can cover spatial and temporal scales that cannot be generated empirically, making it highly relevant in studying the birth, origins, and connectivity of populations. The Larval Dispersal Model is one of the latest models, which tracks particle trajectories to estimate larval distribution patterns that describe fish spawning grounds with great accuracy (Lincoln et al 2024).

Conclusions. Fish spawning grounds are influenced by environmental conditions such as temperature and current conditions. Apart from environmental conditions, spawning and fish survival are also influenced by increased swimming expenditures, increased vulnerability to predation, fishing exploitation, changes in biotic conditions, external pressure, population size and natural and fishing mortality rates. Future fish resource management needs to consider the spatial variability related to fish responses to the changing environmental conditions. Environmental conditions' impact on spawning behavior and fish populations in aquatic environments can be understood through literature studies and survey data.

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