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A century of parasitology in fisheries and aquaculture

J.T. Timi[1] and K. Buchmann[2]

[1]Laboratorio de Ictioparasitología, Instituto de Investigaciones Marinas y Costeras (IIMyC), Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata- Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Funes 3350, (7600) Mar del Plata, Argentina and [2]Laboratory of Aquatic Pathobiology, Department of Veterinary and Animal Sciences, Faculty of Health and Medical Sciences, University of Copenhagen, Frederiksberg C., Denmark

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Author for correspondence:
J. T. Timi,
E-mail: jtimi@mdp.edu.ar

Abstract

Fish parasitological research associated with fisheries and aquaculture has expanded remarkably over the past century. The application of parasites as biological tags has been one of the fields in which fish parasitology has generated new insight into fish migration and stock assessments worldwide. It is a well-established discipline whose methodological issues are regularly reviewed and updated. Therefore, no concepts or case-studies will be repeated here; instead, we summarize some of the main recent findings and achievements of this methodology. These include the extension of its use in hosts other than bony fishes; the improvements in the selection of parasite tags; the recognition of the host traits affecting the use of parasite tags; and the increasingly recognized need for integrative, multidisciplinary studies combining parasites with classical methods and modern techniques, such as otolith microchemistry and genetics. Archaeological evidence points to the existence of parasitic problems associated with aquaculture activities more than a thousand years ago. However, the main surge of research within aquaculture parasitology occurred with the impressive development of aquaculture over the past century. Protozoan and metazoan parasites, causing disease in domesticated fish in confined environments, have attracted the interest of parasitologists and, due to their economic importance, funding was made available for basic and applied research. This has resulted in a profusion of basic knowledge about parasite biology, physiology, parasite–host interactions, life cycles and biochemistry. Due to the need for effective control methods, various solutions targeting host–parasite interactions (immune responses and host finding), genetics and pharmacological aspects have been in focus.

Introduction

According to the Food and Agriculture Organization of the United Nations (2022), fisheries and aquaculture – whose production totalled 214 million tonnes in 2020 – will play an increasingly important role in providing food and nutrition to a growing world population in the future. Recent Food and Agriculture Organization of the United Nations statistics show significant increases in the consumption of aquatic foods worldwide. As aquaculture is a prominent actor in this growth, we must face the challenge and secure sustainability in future developments. On the other hand, fishery resources are continuing to decline due to overfishing, pollution, inadequate management and other factors, although the number of landings of biologically sustainable stocks is rising. Therefore, the expansion of the paramount contribution of fisheries and aquaculture to global food security and nutrition will require ‘transformative changes in policy, management, innovation, and investment to achieve sustainable, inclusive and equitable global fisheries and aquaculture’ (Food and Agriculture Organization of the United Nations, 2022).

Parasites in fish represent a high diversity of taxa, are ubiquitous components of biological systems and establish obligate interactions with their hosts. They affect the physiology, morphology, reproduction and behaviour of their hosts, and their presence illustrates the host distribution and population structure (Cantatore & Timi, 2015). Therefore, these factors may play a prominent role in the changes needed in the near future for aquaculture and fisheries. These roles, as played over the past century, are reviewed and updated in this review.

When the *Journal of Helminthology* was launched a century ago, fish parasitology was a growing field, but had a predominantly descriptive perspective (i.e. Hesse, 1923; Khalil, 1923; Kobayashi, 1923). Yet its relationship to fisheries and aquaculture remained minor or unexplored. At present, parasitism is increasingly recognized as having significant impacts on host individuals, populations, communities and even ecosystems resulting from the tight host–parasite reciprocal adaptations that allow parasites to exploit the specific biological features of their hosts to ensure their transmission and survival and the maintenance of viable populations (Timi & Poulin, 2020). These characteristics make parasites suitable tools as biological markers to provide information on the diet, movements, population and stock structure of their hosts (Williams *et al.*, 1992; MacKenzie & Abaunza, 2014), a methodology increasingly applicable to fishery management and monitoring (Timi & MacKenzie, 2015; Pita *et al.*, 2016). The historic development of the use of parasites' tags in fish stock studies, as well as its limitations, benefits, advantages and disadvantages have been comprehensively reviewed in many articles, especially recently (Timi & MacKenzie, 2015; Pascual *et al.*, 2016). Thus, only recent advances will be discussed here, along with the value of parasite genetics in assessing the host population structure and as indicators of the success of protective measures to restore or preserve aquatic resources. The past century has also presented strong scientific evidence that fish parasites in wild fish stocks challenge fish quality (Mohamed *et al.*, 2020) and may constitute a human health hazard (Strøm *et al.*, 2015; Nordholm *et al.*, 2020). The occurrence of zoonotic nematodes (Mattiucci *et al.*, 2004, 2018; Buchmann & Mehrdana, 2016; Gay *et al.*, 2018) and trematodes (Skov *et al.*, 2009; Madsen *et al.*, 2022) poses a major problem for the fish processing industry, as the removal of worms before they reach the consumer is labour-intensive and undermines profitability. However, the medical importance and influence on human health will not be discussed further in this work. In contrast, the impact of parasites on fish health in aquaculture will be mentioned, due to the potentially pathogenic effect of many parasite taxa. Protozoans, myxozoans, monogeneans, cestodes, digeneans and crustacean parasites have a major impact on global finfish and shellfish aquaculture and constitute a key constraint to production, sustainability and economic viability (Shinn *et al.*, 2015). Selected problem parasites, which have attracted special attention in the aquaculture industry over the past century, will be treated and discussed in the following sections. Therefore, in this review, our aim is to synthesize the major developments and trends in parasitological research on fisheries and aquaculture carried out over the past century.

Parasites in fisheries

Parasites as natural tags in fisheries, an update

One of the most frequent overlaps between fishery and parasitology is the use of parasite tags for identifying the population structure or stock composition of exploited resources. This science may contribute significantly to fish biology, considering that only about 25% of the global catch currently comes from numerically assessed stocks (Food and Agriculture Organization of the United Nations, 2020). Fisheries lacking formal assessment account for more than 80% of the global catch (Costello *et al.*, 2012), which indicates an increasing need for alternative and complementary methods of detailed stock assessment as a prerequisite for rebuilding plans and effective management of most resources.

At present, parasite tags are one of the variety of approaches used to identify and classify stocks, which also include catch data, life-history characteristics, mark–recapture, otolith microchemistry, morphology and genetics (Begg & Waldman, 1999; Cadrin *et al.*, 2005). A growing number of studies use parasites as indicators (Timi & MacKenzie, 2015), as they may identify variations and differentiating parameters of parasite populations and communities.

Nearly a century has passed since Herrington *et al.* (1939) used parasites to investigate the stock structure of a marine fish for the first time. Since then, the use of parasite biological approaches has become a reliable, well-established subdiscipline of parasitology (Poulin & Kamiya, 2015) that has deserved the publication of two special issues of specialized journals devoted to the subject (Lewis, 2007; Timi & MacKenzie, 2015).

At present there is a consensus on a series of methodological guidelines, which are periodically reviewed and adjusted, although with a variable degree of application at global scale (Timi & MacKenzie, 2015). These reviews discuss and update the criteria for the selection of suitable tags, their advantages and disadvantages, the biological target systems and the perspectives of the study (population structure, migrations and recruitment) for different groups of parasites' geographical regions (Kabata, 1963; Sindermann, 1983; MacKenzie, 1983, 1987, 1993, 1999, 2002; Lester, 1990; Moser, 1991; Williams *et al.*, 1992; MacKenzie & Abaunza, 1998, 2014; Mosquera *et al.*, 2003; Timi, 2007; Abaunza *et al.*, 2008a; Lester & MacKenzie, 2009; Baldwin *et al.*, 2012; Catalano *et al*, 2014; Cantatore & Timi, 2015; George-Nascimento & Oliva, 2015; Lester & Moore, 2015; MacKenzie & Hemmingsen, 2015; Marcogliese & Jacobson, 2015; Reed, 2015; Timi & MacKenzie, 2015; Pascual *et al.*, 2016). This compilation of literature provides an 'evolutionary view' of the development undergone by the use of parasites as biological markers for the study of fish populations or stocks that resulted in an increasingly efficient and reliable methodology. Therefore, there is no need to repeat their concepts and case studies here. Instead, this review will summarize some of the main recent findings of that research derived from the use of parasite tags and which aims to improve, reinforce or complement this methodology. These topics include: (a) the extension of the use of parasite indicators to host groups other than bony fishes; (b) the increasing interest in selecting those parasites' groups of guilds, suitable for each kind and scale of study; (c) the host traits driving the structure and composition of parasite assemblages and their effects on their use as natural tags; and (d) the increasingly recognized need for integrative, multidisciplinary studies.

Parasite tags in studies of non-teleost hosts

Parasites can be used as indicators of diverse ecological features even for fragile or difficult to mark species, such as many invertebrates (Williams *et al.*, 1992). The exploitation of aquatic invertebrates largely relies on extractive activities in natural populations, which require strict management measures to ensure sustainability. However, despite the economic relevance of many of these fisheries, that is, squids, scallops, prawns, lobsters, oysters and the knowledge about their parasites, few studies have used parasitological evidence for stock or population assessment. According to Timi & MacKenzie (2015), the vast majority of published papers on parasite tags deal with teleost fish as hosts, with only a minor proportion of studies on elasmobranchs and invertebrates of commercial interest. This situation has not changed in recent years, with only four new publications on elasmobranchs (Isbert *et al.*, 2015; Irigoitia *et al.*, 2017, 2022; Gérard *et al.*, 2022) being issued since that revision. Yet no new research has been conducted on exploited invertebrates, despite the value of natural tags having been recognized for many years (Williams *et al.*, 1992; Pascual & Hochberg, 1996). The present development and acceptance of this methodology may promote research on natural tags of many groups of exploited invertebrates to assist in ensuring a suitable management and sustainable exploitation of these resources.

Improvements in the selection of parasite tags

A series of criteria for selecting ideal parasite tags have been articulated and refined over the years (Kabata, 1963; MacKenzie, 1983, 1987; Sindermann, 1983; Williams *et al.*, 1992), although parasites that meet all of them are not frequently found (MacKenzie & Abaunza, 2014). Among the suitable characteristics, the residence time of a parasite in the subject host is one of the key features worth considering (Lester & MacKenzie, 2009). Indeed, it is suggested that parasites should persist in the host for a long period, that is, at least one year for stock identification and recruitment studies, whereas species with life spans of less than one year are acceptable for studies of seasonal migrations (MacKenzie & Abaunza, 2014). Some recent studies have tested these recommendations by comparing long-lived vs. short-lived parasite guilds, with results confirming the validity of these criteria. For example, long-lived larval endoparasites of red porgy *Pagrus pagrus* were able to discriminate among stocks along the Atlantic coast of South America, whereas short-lived guilds (ectoparasites and gastrointestinal endoparasites) exhibited significant differences even among samples belonging to a single stock (Soares *et al.*, 2018). Similar results were obtained for the *Sympterigia bonapartii*, a seasonally migratory skate from the same region. However, in that case, variations of transient parasites were related to the migratory behaviour of the fish, constituting, therefore, suitable markers for fish migration (Irigoitia *et al.*, 2017). In addition, temporal and or short-scale spatial variations in parasitism have been subjected to methodological analyses to avoid the possible occurrence of pseudoreplication problems (Ferrer-Castelló *et al.*, 2007; Espinola-Novelo & Oliva, 2016).

Effect of host traits on the application of parasite tags

The role of host traits in the value of fish parasites as tags has been also under methodological scrutiny. Since long-lived parasites are recommended as biological tags for most studies, and cumulative patterns with fish age and/or size are common to them (Timi *et al.*, 2010, 2011), prevalence and abundance tend to increase with host traits such as size, mass, age and even sex. Consequently, there is a need to evaluate their value as descriptors of the host population structure of stocks. In this context, Braicovich *et al.* (2016) conducted a comparative analysis of the effect of host variables on the parasite abundance and species richness in *Percophis brasiliensis* caught in the Argentine Sea. Length and sex consistently appeared in the most parsimonious models, suggesting that fish length seems to be a slightly better predictor than age or mass. Thus, these authors confirmed that fish size is a suitable measure of growth and recommended restricting the comparisons to fish of similar length or incorporating length as covariate when comparing parasite burdens. Host sex should be also considered for sexually dimorphic fish in terms of morphology, behaviour or growth rates.

Beyond the effect of characteristics of individual fish on their parasite burdens, evolutionary and ecological traits may exert considerable influence on comparative analyses. For example, Levy *et al.* (2019) demonstrated that parasites can be excellent models for comparative research in assessments of fine-scale population structure when site fidelity and strong adaptations to local conditions prevail and/or where physical heterogeneity needs to be revealed (Levy *et al.*, 2019).

The interaction between host traits (such as size or age) and ecology must be considered in some studies. For example, for migratory species whose foraging and spawning habitats alternate seasonally during their life cycles, ontogenetic changes in the structure of parasite assemblages must be taken into account since, due to cumulative patterns, host-length differences can lead to a misinterpretation of the patterns, especially when migrations are asynchronous among cohorts. This was observed for *Umbrina canosai* migrating between the coastal waters of southern Brazil and northern Argentina (Canel *et al.*, 2021). Thus, differences in parasite assemblages were more clearly observed in young fish, indicating possible variations in migratory routes, distance travelled and/or latitude reached, depending on environmental conditions and age. Consequently, it is advisable to consider the differences among fish length classes when using parasite tags for resources with temporally and spatially variable migratory patterns, especially when different cohorts are compared.

Need for integrative multidisciplinary studies

Among the most recent literature, the need for integrative studies applying simultaneously different, but complementary techniques for stock identification has been a recurrent topic for improving fishery management tools (McClelland *et al.*, 2005; Abaunza *et al.*, 2008b; Niklitschek *et al.*, 2010; Baldwin *et al.*, 2012; Mattiucci *et al.*, 2015; Van der Lingen *et al.*, 2015; Welch *et al.*, 2015; de Moor *et al.*, 2017; Brickle *et al.*, 2021; Zhang *et al.*, 2021). In general, higher discriminatory power and increased accuracy of stock assignment may result from combining different sources of information, including host genetics, otolith microchemistry and parasites (Baldwin *et al.*, 2012; Brickle *et al.*, 2021; Zhang *et al.*, 2021). These advantages also include the elucidation through the complementarity of connectivity patterns of host populations across different spatial and temporal scales (Taillebois *et al.*, 2017).

Parasite genetic data and fisheries

Genetic markers are used for complementing and resolving taxonomic issues, thus helping to achieve higher taxonomic resolutions in ecological studies. Poor taxonomic resolutions may mask undetected biodiversity, probably leading to biases in ecological analyses where accurate estimates of species richness or species co-occurrences matter (Poulin & Leung, 2010). For example, the genetic identification of several species of larval *Anisakis* spp. has contributed to the identification of stocks of the European hake (*Merluccius merluccius*) in Atlantic and Mediterranean waters (Mattiucci *et al.*, 2004), of Atlantic horse mackerel, *Trachurus trachurus* (Mattiucci *et al.*, 2008) and of the skipjack tuna *Katsuwonus pelamis* in the north-west Pacific (Takano *et al.*, 2021). Similarly, the genetic identification of larval *Anisakis* spp. confirmed the relative contribution of oceanographically contrasting masses of waters to the parasite fauna of the silvery John dory *Zenopsis conchifer*, living in a transitional zone (Lanfranchi *et al.*, 2016, 2018).

Beyond the value for parasite systematics, the development of molecular and computational tools for population genetics and phylogenetics has fuelled an enormous advancement of parasite ecology, including the use of molecular data on parasites to infer diverse aspects of the ecology of their hosts and reconstruct their evolutionary and demographic histories (Nieberding & Olivieri, 2007; Archie *et al.*, 2009). For example, the use of genetic markers to assess population structures has been applied to parasites relevant for aquaculture, such as the sea louse *Lepeophtheirus salmonis*, and has improved the understanding of its dispersal capabilities and control in farmed salmonids (Glover *et al.*, 2011; Messmer *et al.*, 2011).

Selected genetic markers comprise innate tags whose advantages are that all members of a population are inherently marked and do not affect the behaviour or survival of the organisms. Furthermore, information may be obtained on conservation issues, the identification of catch origins and migratory routes (Antoniou & Magoulas, 2014). The use of genetic information to ascertain population membership of individuals includes a variety of approaches known as assignment methods, also used to identify the number of populations coexisting in a given area, mixed-stock analysis or the origin of migrant individuals (Manel *et al.*, 2005; Criscione *et al.*, 2006).

In fisheries, both mitochondrial and nuclear genetic markers are commonly used for such purposes (Antoniou & Magoulas, 2014), but unfortunately such assignments are often inaccurate when there is little or no neutral genetic differentiation among source populations, outlining the need for alternative methods (Criscione *et al.*, 2006). Independently of techniques utilized for the study of the geographical distribution of genetic lineages, phylogeographic patterns between species linked by a parasitic relationship may be congruent in time and space for specific, obligate parasites (Nieberding *et al.*, 2004). The usefulness of genetic data on parasites species to assign fish to source populations was initially proposed by Beverley-Burton (1978) after comparing the frequencies of allozymes in *Anisakis simplex* parasitizing Atlantic salmon. After this and early in the 21st century, the use of parasite genetic signatures to assess host populations and regions of origin was recommended and viewed as a promissory perspective (Manel *et al.*, 2002). Nevertheless, despite the potential of parasite genetics to identify many aspects of host phylogeography and population structure, molecular methodologies have not been widely applied to fish parasites relevant to fisheries in general (Criscione *et al.*, 2005) and as markers of fish stocks (Pascual *et al.*, 2016).

The underlying idea of this methodology is that if a parasite is genetically subdivided more finely than its host, then the genotypes of the parasite in question could potentially be used to assign hosts to their population of origin with higher probabilities than by using the host genotypes (Criscione *et al.*, 2005). Support for this concept is the fact that the rate of molecular evolution is faster in parasite DNA and RNA, relative to that within the homologous loci of their hosts, which yields genetic sequences that are comparatively better sources of data (Whiteman & Parker, 2005). Furthermore, in addition to differences in mutation rates, the shorter generation time of most parasites relative to their hosts accelerates the evolutionary processes, allowing favourable genotypes of the population obtained by mutation, recombination or migration, to rapidly increase in frequency, rendering powerful inferential tools (Gandon & Michalakis, 2002; Whiteman & Parker, 2005). Additionally, a parasite can be more genetically structured than its host due to the different rates of gene flow of effective population sizes between them, because not all hosts are infected and because parasites may be locally adapted at a higher level compared to their hosts (Criscione *et al.*, 2006).

The first study to test the hypothesis that parasite genotypes are more accurate in assigning hosts to source populations than the host genotypes themselves was carried out using microsatellite markers to compare the accuracy of assignment back to known source populations between steelhead trout *Oncorhynchus mykiss* and its strictly freshwater parasitic trematode *Plagioporus shawi* (Criscione *et al.*, 2006). These authors showed that the genotypes of the parasite had fourfold greater odds of correct assignment than host genotypes. This highlighted how the genotypes of the parasites are more accurate than host genotypes when assigning individuals to their population of origin. They may also be useful for identifying individuals from protected areas, and for tracing dispersal patterns or feeding grounds for migratory species.

More recently, several authors have studied the population genetic structure of a parasite species to infer that of its fish host along a geographical range, using mitochondrial genetic markers (table 1). Most studies have been carried out for larval *Anisakis* spp. on fish, with the exception of a study on cetaceans (Marigo *et al.*, 2013). The success in identifying the population structure varied with the identity of both host and parasite species, the host ecology, the region of origin and the geographical scale. Indeed, this success relied on the selection of an appropriate scale of sampling to account for the different life histories and geographical distribution of the species being studied (Cross *et al.*, 2007). According to Baldwin *et al.* (2012), the features and approaches necessary for selecting parasite molecular markers include: (a) ease of recovery and identification; (b) the use of more than one genetic marker to verify that a parasite species is cryptic; (c) an assessment of mutation rates for specific genetic marker types; and (d) temporal and geographical stability in a parasite population to enable long-term monitoring.

In addition to those factors driving the population structure of parasites – such as evolutionary and ecological history, mode of reproduction and transmission, host dispersal, and life-cycle complexity – anthropogenic factors, such as biological invasions, environmental perturbation, global warming and extractive activities, may affect the parasite faunas (Zarlenga *et al.*, 2014). In particular, stressors such as overfishing can reduce the host population size (Wood *et al.*, 2010), with a concomitant reduction in parasite populations and the genetic diversity within them. Thus, a minimal genetic structure among geographically isolated populations may be interpreted as a hallmark of human activity (Zarlenga *et al.*, 2014). Nevertheless, little has been done to correlate habitat degradation with genetic diversity among parasites' populations, although clear-cut examples are available about the effects of habitat disturbance on the genetic diversity of anisakid nematode populations (Mattiucci & Nascetti, 2007, 2008). The values of genetic variability of different anisakid genera (i.e. *Anisakis*, *Contracaecum* and *Pseudoterranova*) were significantly higher in Austral populations than in Boreal regions in coincidence with a lower degree of habitat disturbance in southern populations (Mattiucci *et al.*, 2017). Increased overfishing, the by-catch of cetaceans, the hunting and disease mortality of seals, sea water pollution and acidification in Boreal regions reduce host population sizes, which reduces the population of lower anisakid and heightens the probability of genetic drift phenomena in the parasite gene pools (Mattiucci *et al.*, 2015). Therefore, comparisons of genetic variability among parasite populations inhabiting ecosystems with a different degree of disruption may be applied to an evaluation of the effect of overfishing or, alternatively, of protection measures for many fisheries.

Phylogeographic analysis of parasites, as well as those variations in their genetic diversity resulting from the effect of anthropogenic stressors, represent valuable and reliable sources of information to be integrated into multidisciplinary studies dealing with a holistic approach to fisheries management and stock identification (Begg & Waldman, 1999), aiming for the long-term maintenance and sustainability of fishery resources.

Phylogeographic analysis of both parasites and their fish host, performed on the same genes, are promissory tools to be included in multidisciplinary studies on stock structure

Table 1. Studies using genetic markers (mitochondrial genes) to assess population structure of marine parasites of relevance in fisheries.

Host	Parasite	Region	Genetic marker	Results/conclusions	Source
Fishes					
Clupea harengus	*Anisakis simplex* (Nematoda: Anisakidae)	north-west coast of Scotland	cytochrome oxidase 1 (mtDNA cox1)	very high haplotype and low nucleotide diversities. Large within population differences with localized temporal stability	Cross *et al.* (2007)
Sardinops sagax	*Anisakis pegreffii*, *A. simplex* 'C' and *A. simplex* s.s.	California Current upwelling zone, United States	cytochrome c oxidase 2 (mtDNA cox2)	panmictic distribution of the larval *Anisakis* spp. due to presumed migratory pathways of the intermediate and definitive hosts	Baldwin *et al.* (2011)
Seriola lalandi	*Zeuxapta seriolae* (Monogenea: Heteraxinidae)	northern Chilean coast and Eastern Island	mtDNA cox1	geographical genetic structure, two populations both with high haplotype diversity	Sepúlveda & González (2015)
Sebastes mentella	*A. simplex*	three stations at the North-East Atlantic	mtDNA cox2	lack of geographical structuring (panmyxia)	Klapper *et al.* (2016)
Clupea harengus	*A. simplex*	Norwegian, Baltic and North Seas, English Channel	mtDNA cox1	differences in haplotype frequencies from the different areas, indicating genetic sub-structuring of *A. simplex*	Mattiucci *et al.* (2018)
Cetaceans					
Pontoporia blainvillei (Cetacea)	*Synthesium pontoporiae* (Digenea: Brachycladiidae)	Brazilian and Argentine coasts	concatenated nicotinamide adenine dinucleotide dehydrogenase subunit 3 (ND3) and mtDNA cox1	lack of population structure (panmixia) and population expansion due to high mobility of intermediate hosts or to small sample size	Marigo *et al.* (2013)

(Mattiucci *et al.*, 2015). Such co-phylogeographic studies, under the 'magnifying glass hypothesis' (the increased chance of tracking the genealogical history of the host with genetic data of the parasite) (Huyse *et al.*, 2017; Geraerts *et al.*, 2022), along with the recent advances in next-generation DNA sequencing technologies and the genome-wide genotyping applications to fish parasites, will undoubtedly be of paramount relevance to fisheries and aquaculture in the near future.

Parasites as indicators of the success of Marine Protected Areas (MPAs)

Fishing practices and aquaculture, in combination with many other anthropogenic factors, have led to a rapid and radical degradation of marine ecosystems. This may drive considerable and complex changes in the physical structure, chemistry, biology and ecological functioning of oceans (Lubchenco *et al.*, 2003). Some of the signs of such alterations, related to fisheries, include abrupt changes in species composition, habitat degradation, epidemics, mass mortalities and the collapse of fisheries (Lubchenco *et al.*, 2003).

An effective mechanism for preventing or reversing these widespread declines and for protecting, maintaining and restoring ecosystems is the implementation of MPAs, a key management tool employed worldwide to conserve biodiversity and sustain fisheries (Pelletier *et al.*, 2008; Watson *et al.*, 2014). Indeed, MPAs allow for the recovery of depleted stocks of exploited species and provide a source of individuals for fished areas (Lubchenco *et al.*, 2003).

Although most MPAs allow some extractive activities such as fishing, by protecting both biota and their biophysical environments, they offer an ecosystem-based approach to conservation or fisheries management (Lubchenco *et al.*, 2003). An efficient management of MPAs requires continuous feedback on the objectives achieved and the suitable indicators for assessing the efficacy of using them (Pomeroy *et al.*, 2005). Numerous studies have provided a broad dataset on the biological effects of reserve protection for a wide range of geographical locations and organisms (Lester *et al.*, 2009). On average, positive effects of reserve protection on the biomass have been reported, such as increases in density, species richness and the size of organisms within their boundaries (Lester *et al.*, 2009). However, there is considerable variation in the responses documented across reserves (Lester *et al.*, 2009), which requires further and permanent improvement of the evaluation of their ecological effects (Claudet & Guidetti, 2010).

Recent analyses (Sala & Giakoumi, 2018) showed that the biomass of whole fish assemblages in marine reserves is, on average, 670% greater than in adjacent unprotected areas, and 343% greater than in partly protected MPAs. This suggests that reserves contribute to the restoration of the complexity of ecosystems through trophic cascades once the abundance of large animals recovers sufficiently. Given the dependence of parasites on the population density of all hosts involved in their life cycles, as well as on the complexity of food webs for those trophically transmitted species (Wood *et al.*, 2010), differences in free living communities due to protective measures are expected to have a correlate in parasite communities.

An example was provided by Huspeni & Lafferty (2004), who evaluated the success of an ecological restoration project at a degraded site, the Carpinteria Salt Marsh in California, United States, in a before–after, control–impact study using larval digeneans infecting the California horn snail, *Cerithidea californica*. Over a period of six years, trematode prevalence nearly quadrupled and species richness doubled at restored sites, whereas both factors remained unchanged at control sites. These authors attributed these changes to the use of the restored habitats by birds.

At present, several studies have evaluated the success of MPAs using fish parasites as biological indicators (table 2), most of which recorded increased abundance, species richness and/or diversity of different parasite taxa, resulting from the protection measures and varying with their characteristics. Only a few exceptions were unable to detect changes in parasite loads (Loot *et al.*, 2005; Ternengo *et al.*, 2009). Most of these studies have also evaluated the effect of MPAs on fish parasites by comparing protected and unprotected areas, with the exception of Braicovich *et al.* (2021), who compared temporal changes in the composition and structure of parasite communities of *P. brasiliensis*. The hosts were caught at the beginning of the implementation of protection measures (temporal and spatial closures to fishery) and after a period of 13 years in a coastal region of northern Argentina (table 2).

Temporal evaluation of changes due to MPAs should be complementary to that of spatial evaluation, since either biotic or abiotic factors can affect the structure of parasite populations and assemblages, even at an exceedingly small scale (Levy *et al.*, 2019). Therefore, the most reliable results are expected when using a sampling scheme comparing 'before and after'. When complemented by simultaneous sampling 'inside and outside' the MPAs, this will permit the identification of any possible regional change from local variations occurring as a consequence of the protection measures.

As fishing activities reduce the density of fish and other hosts and may affect the fish populations (selectively removing large fish), they may reduce food web complexity and drive a decline in parasite burdens (Wood *et al*, 2010). The protection of these environments, therefore, is expected to restore the systems to their original state or at least return them as closely as possible to their original conditions, explaining the majority of the observed increases in the levels of parasitism in the studies listed in table 2. However, under certain circumstances, reserves can pose threats to conservation by increasing the density and, thus, the transmission of parasites, especially through enhanced contact rates in small, overcrowded or highly diverse reserves where organisms may be more vulnerable to infection (Ezenwa, 2004; McCallum *et al.*, 2005; Lebarbenchon *et al.*, 2007). For example, for parasites with heteroxenous life cycles, the diversity and abundance in intermediate and/or paratenic hosts should consequently increase with the diversity and abundance of definitive hosts (Hechinger & Lafferty, 2005).

Beyond the use of parasites as indicators of the success of MPAs, their possibly detrimental effects, together with that of other pathogens, have received virtually no attention (McCallum *et al.*, 2005; Wootton *et al.*, 2012) and should be included in any cost–benefit analysis of marine reserves to improve their efficacy and subsequent management strategies (Wootton *et al.*, 2012).

Parasites in aquaculture

Historical reports on parasites and aquaculture

Although the production of plants and animals in the aquatic environment (aquaculture) has greatly expanded over the past century in general and the last fifty years in particular (Food and Agriculture Organization of the United Nations, 2022), this food production method is not novel. Chinese reports have described the production of various cyprinid fish species in freshwater pond culture systems since the early days, at least 8000 years ago (Costa-Pierce, 2022). It is also from these ancient aquacultures that the first reports of fish parasites appeared (Lom & Dykova, 1992). Asia is still the main producer of aquacultured fish (Food and Agriculture Organization of the United Nations, 2022), and the other main players in this region, historically and currently, are Indonesia (Rimmer *et al.*, 2013), India (Kumar *et al.*, 2015) and Vietnam (De Silva & Phuong, 2011). In Africa, archaeological evidence points to early fish-keeping in small ponds in ancient Egypt (Costa-Pierce, 2022), associated with exceedingly early reports of the occurrence of fish pathogens (Snieszko, 1975), whereas large-scale farming developed much later in East Africa (Dadzie, 1992; Mwainge *et al.*, 2021). In South America, Brazilian aquaculture dates back to the 17th century (Valenti *et al.*, 2021), but the main focus of South American aquaculture parasitology developed much later in Chile with the advent of salmonid mariculture necessitating a focus on the ectoparasitic crustacean *Caligus rogercressei*. United States and Canadian mariculture industries similarly urged fish parasitologists to target *L. salmonis* in their research (Burka *et al.*, 2012). The North American catfish farming industry (Engle *et al.*, 2022) was also a cradle for aquaculture parasitology. Russian aquaculture dates back several centuries. Although the culture of cyprinids has been in focus, major technological steps have been taken within sturgeon production since the 1860s (Vasilyeva *et al.*, 2019). In Europe, archaeological evidence points to the existence of primitive fish-keeping facilities already 6000 years ago (Costa-Pierce, 2022), but more organized production systems appeared later on when carp aquaculture was organized in the Roman Empire from 100 BC to AD 500. The artificial reproduction of trout was developed during the 18th century, and production facilities were subsequently established in several European countries and in North America. Despite the ancient history of aquaculture, large scale production was established far later. The intensification of production systems mainly arose over the past century, a period in which aquacultured fish from both freshwater and marine systems have gained increasingly greater economic importance (Food and Agriculture Organization of the United Nations, 2022).

Intensification of fish parasitology with the development of aquaculture

Along with the aquaculture intensification process, the study of parasitic diseases became indispensable due to the role of the diseases as a production-limiting factor. Ancient reports on diseases, although not strongly documented, date back to 330 BC. (Snieszko, 1975), and classical zoologists with an interest in parasites, such as Müller (1776) and Abildgaard (1794a, b), described a range of parasites in fish. Although the stringency and level of detail in their descriptions lag behind modern systematics, their contributions remain valid. The impact of parasites on productivity was not a major issue until commercial aquaculture developed, however.

The spread of natural infections (caused by viral, bacterial, protozoan and metazoan pathogens) of wild fish to domesticated fish species was largely uncharacterized and unknown before the intensification process. The impact of infections on cultured fish kept in high densities became increasingly visible. The pathogens

Table 2. Studies on fish parasites as indicators of success of Marine Protected Areas (MPAs).

Fish host	Parasite/s	Region	Comparisons	Results/conclusions	Source
Gobius bucchichii	five helminth species	Cerbère-Banyuls Marine Reserve, France	in and around MPA	fish in protected area harboured more parasites	Sasal *et al.* (1996)
Diplodus sargus	11 species of *Lamellodiscus* (Monogenea)	Cerbère-Banyuls Marine Reserve, France	inside and outside of MPA	increased abundance of *Lamellodiscus elegans* in protected area	Sasal *et al.* (2004)
63 fish species	102 digenean species	Scandola Nature Reserve off Corsica	MPA with other regions of the Mediterranean and Black Sea	digenean diversity in MPA far greater than in other parts of the Mediterranean	Bartoli *et al.* (2005)
Sicyases sanguineous and two moluscan species	*Proctoeces lintoni* (Digenea)	Chilean coast	four sites differing in harvest intensity	increased parasitism in molluscs in MPA, no differences in fish	Loot *et al.* (2005)
five fish species	helminths and arthropods	Line Islands chain, central Pacific	pristine vs. heavily fished coral atolls	parasite species richness, prevalence and abundance higher at pristine site	Lafferty *et al.* (2008)
six fish species	whole community	Bonifacio Strait Marine Reserve (Corsica Island)	one zone outside the MPA, and three zones in areas of reinforced protection	parasite distribution not influenced by the protection status of the site	Ternengo *et al.* (2009)
Boops boops	whole community	Balearic Sea, Santa Pola Bay and the Gulf of Oran	two zones with different fishing pressure on *B. boops*	higher species richness and abundance in parasite component communities at unfished site. More species with lower prevalence in fished site	Marzoug *et al.* (2012)
Cheilodactylus variegatus, *Aplodactylus punctatus* and two invertebrates	gill parasites of fish, a digenean of molluscs and a crab of sea urchins	Central Chile	three MPAs and three open access areas	substantially greater density of nearly all parasite species in MPAs, one gill monogenean more abundant in fish from MPAs	Wood *et al.* (2013)
seven species of coral reef fishes	whole community	Line Islands archipelago, central Pacific	three fished vs. three unfished islands	overall parasite species richness depressed on fished islands, response of parasite abundance varied among taxa: directly transmitted parasites more abundant on fished islands, the opposite for trophically transmitted parasites	Wood *et al.* (2014)
Diplodus sargus sargus	whole community	Western Mediterranean	three sites outside MPA, two at buffer area and two inside MPA (no-take zone (NTZ))	composition and structure of parasite infracommunities fromNTZ different to other sites. Monoxenous parasites richer and more diverse in both fished areas, but more abundant in NTZ, richness and abundance of heteroxenous parasites higher in NTZ	Isbert *et al.* (2018)
Lithognathus mormyrus	*Anilocra physodes* (Isopoda)	Alboran Sea (Western Mediterranean)	three sites outside MPA and three inside MPA	prevalence significantly lower inside the MPA	Navarro-Barranco *et al.* (2019)
Percophis brasiliensis	long-lived parasites' community	Northern Argentine Sea	one and 13 years after implementation of MPA	significant differences in structure and composition of parasite assemblages. Increased loads of several parasite species	Braicovich *et al.* (2021)

could be detected, isolated and described, and with the increasing focus on fish production seen during the past century, important parasitic pathogens have been the subject of increasing interest and research efforts. In the early 20th century, Hofer (1904) and later Plehn (1924) published their treatises on parasitic diseases in fish. In the following years, a wide series of publications, research papers and textbooks emerged and now constitute a valuable basis for the control of parasitic diseases in aquaculture.

The number of parasites in wild fish is extremely high, which is a consequence of the vast number of fish species (33,000) described. The high specificity of fish parasites will result in a correspondingly high number of parasites. In contrast, there are 369 species of aquacultured fish (Food and Agriculture Organization of the United Nations, 2022), meaning that the number of parasite species is correspondingly lower. This is reflected in the publications on fish parasites published over the past century. Papers on wild fish issues are concerned with a wide diversity of parasites, whereas papers on aquaculture parasites target a limited number of species. On the other hand, the number of publications on the individual aquaculture parasite species may be extreme due to the massive problems caused by individual species such as *Ichthyophthirius multifiliis* and *L. salmonis*.

Differing impacts of different parasite types

The different parasite types also differ with regard to their role as pathogens in aquaculture settings. Nematodes with complex life cycles, such as anisakids, are highly prevalent in wild fish stocks (Gay *et al.*, 2018; Mattiucci *et al.*, 2018), but are generally not found in aquacultured fish (Fioravanti *et al.*, 2021). The swim bladder nematode *Anguillicoloides crassus*, which uses copepods as intermediate hosts (and fish as transport hosts), may occur in eel cultures following the introduction of wild-caught infected elvers, because stocking is still based on wild fish. When subsequently established in fish cultures, these can have a devastating impact on productivity, but these nematodes exert their main impact on wild stocks (Lefebvre *et al.*, 2012).

Likewise, there are reports of acanthocephalans occurring in aquacultured fish, but these are primarily associated with pond cultures connected to natural waters from where intermediate hosts (amphipods and isopods) may enter the production system. Their impact on fish in the most intensive aquaculture production systems is limited, however, because the water inlet is controlled and transmission eliminated. In contrast, other parasites with less complex life cycles may flourish. Below, selected examples of protozoans and metazoans (monogeneans, cestodes and crustaceans) in aquaculture settings are presented, focusing on their development over the past century.

Problematic protozoans

Over the past century, protozoans have caused serious disease in aquacultured fish, which has fostered a vast amount of literature focused on amoebae (Nowak, 2012; Nowak *et al.*, 2014), haemoflagellates *Cryptobia* (Woo & Li, 1990), *Trypanoplasma* (Wiegertjes *et al.*, 1995), bodonid flagellates (*Ichthyobodo*) (Chettri *et al.*, 2014), diplomonadid flagellates (*Spironucleus*) (Sterud *et al.*, 1998), scuticociliates (*Philasterides*) (Lamas *et al.*, 2008) and hymenostomatid ciliates such as *Ichthyophthirius* (Dickerson *et al.*, 1993).

Finds of *I. multifiliis* in cultured fish, macroscopically visible as epidermal white spots, were detected in China as early as the Sung dynasty (starting from AD 926) (Lom & Dykova, 1992). This protozoan was scientifically described later on in France by Fouquet (1876), as it was frequently found in trout in nearby freshwater ponds. During the 20th century, the parasite was the subject of numerous investigations due to its high pathogenicity and commercial importance. It was especially interesting that fish developed a level of resistance to reinfection indicating the development of an immune response (Buschkiel, 1910), as this could imply that immunoprophylaxis, including vaccination, would be a possible control strategy. Russian fish parasitologists investigated this in more depth and noted that the antiparasitic response was positively correlated to the size of the primary infection (Bauer, 1953). It was later shown that carp activated a series of humoral and cellular immune factors while infected (Hines & Spira, 1973, 1974), and these authors could confirm a protective response established in the fish host. The accumulation of host lymphocytes, macrophages and neutrophils around the feeding stage of the parasite (the trophont) in the host epidermis was further characterized by Cross & Matthews (1993). The lymphocytes surrounding the trophonts were later demonstrated to stain positively for B-cell and T-cell markers (Olsen *et al.*, 2011). The humoral reactions were shown to include antibodies with high specificity in some cases (Dickerson *et al.*, 1993; Clark *et al.*, 1996; Sigh & Buchmann, 2001; Alishahi & Buchmann, 2006) and complementary factors (Gonzales *et al.*, 2007).

Following the development of new immunological tools, it was shown that not only did the fish host produce immunoglobulin M (IgM) (Dickerson *et al.*, 1993; Sigh & Buchmann, 2001), but also another immunoglobulin class that was recently detected and termed immunoglobulin T (IgT). These antibodies were secreted both systemically and locally on mucosal surfaces against the invading parasite (Jørgensen *et al.*, 2011; Olsen *et al.*, 2011; Xu *et al.*, 2013). Whereas genes encoding immunoglobulin classes IgM and IgT are found upregulated during the course of infection, a third class, immunoglobulin D was downregulated (Jaafar *et al.*, 2020). Furthermore, transcriptomic data subsequently indicated that the number of genes involved in the rainbow trout response towards *I. multifiliis* infection counted more than 1796 up-regulated and 1556 down-regulated gene sequences (Syahputra *et al.*, 2019). Despite the well documented development of an adaptive immune response in fish towards *I. multifiliis*, and several attempts to produce vaccines against the infection, experimental vaccines (based on proteins or DNA) (Jørgensen *et al.*, 2012, 2017) have only exhibited a partial protection, and commercial vaccines are still not available at present.

Investigations conducted over the past century have described various ways to control the infection by use of chemotherapeutants and medicines. The organic dye malachite green was applied for years in facilities producing both ornamental and production fish (Alderman, 1985). Its toxicity and carcinogenicity, and subsequent ban of its usage (European Food Safety Authority, 2016), prompted farmers to search for alternatives (Rintamäki-Kinnunen *et al.*, 2005; Picon-Camacho *et al.*, 2012). Biocides used in water baths – such as formalin, hydrogen peroxide (Rach *et al.*, 2000), peracetic acid (Meinelt *et al.*, 2009; Mathiessen *et al.*, 2021b), sodium percarbonate (Heinecke & Buchmann, 2009), copper sulphate (Straus, 1993) and potassium permanganate (Straus & Griffin, 2001) – were then investigated for a description of their efficacy and environmental impact. The biocides releasing hydrogen peroxide generally induce an inflammatory response in the skin of the fish host (Mathiessen *et al.*, 2021b), but are considered relatively safe from an environmental point of view, because the reaction products from the interaction with organic material are carbon dioxide, oxygen and water. These oxidizing agents are being applied in increasing amounts, but the search for alternative products is still ongoing. Herbal extracts have exhibited strong effects on different stages of the parasite (Lin *et al.*, 2016; Mathiessen *et al.*, 2021a), but before licensing, marketing and possible application at farm level, further investigations into the environmental impact, toxicity towards the host and any effect on human health are needed. Correspondingly, a lipopeptide (surfactant) isolated from the bacterium *Pseudomonas* H6 has lethal effects on the theronts, tomonts and tomocysts of *Ichthyophthirius* (Al-Jubury *et al.*, 2018; Li *et al.*, 2022). Subsequent studies of this microbial compound demonstrated a low level of host effects (skin inflammation in rainbow trout) (Mathiessen *et al.*, 2021b) and limited adverse effects on cyanobacteria, green algae, *Daphnia* and zebrafish (Korbut *et al.*, 2022). These initial ecotoxicological steps suggest a potential future use of the compound in aquaculture enterprises, but the road to licensing must be completed before its usage. This will include future research into the toxicological and environmental effects.

Due to the questionable use of chemotherapy, research efforts targeting alternative methods have been increasingly prominent. One approach has highlighted the use of ultraviolet irradiation (Gratzek *et al.*, 1983), and another the application of mechanical control techniques by removing key life-cycle stages. Continuous filtration of water to remove tomonts, thus preventing tomocyst formation with the release of infective stages, was demonstrated by Heinecke & Buchmann (2009). In line with this approach, Shinn *et al.* (2009) launched a strategy for removal of tomocysts by coating fish tanks with a material to prevent tomocyst attachment. This enabled the loose parasite stages to be removed by a modified vacuum-cleaning technique.

A more recent approach to *Ichthyophthirius* control in fish farms is based on the observed differential susceptibility of fish to infection, which suggests that it is possible to breed fish with a higher natural resistance to infection. When exposing an outbred population of rainbow trout to infection, using infective theronts, a serious infection develops but with a different time span from disease to death (Jaafar *et al.*, 2020). By genotyping individual fish, both susceptible fish and those that stay healthy, it was possible to identify genetic markers (single nucleotide polymorphisms (SNPs)) in the host genome associated with relative resistance. This information was then applied by the breeder to select spawners carrying the beneficial SNPs. By using these selected fish as parent fish to produce the next generation, it is possible to establish strains with improved resistance (Buchmann *et al.*, 2022).

Problematic myxozoans

Over the past century, myxozoan biology research has expanded markedly. The number of described species in both wild and cultured fish populations has increased dramatically, but for aquaculturists the main target was to develop control methods. The impact of *Myxobolus cerebralis*, eliciting whirling disease in trout cultures, attracted the interest of various research groups. With the, at the time, surprising results by Wolf & Markiw (1984), showing that oligochaetes were obligate elements of the life cycle, a brand-new stage for biological and life-cycle studies opened up in the field of myxozoan biology. The past four decades have seen prominent research and the surprising impact of myxozoans on aquaculture production (Sitjà-Bobadilla *et al.*, 2007). The elevated exposure of this specific field has paved the way for numerous descriptions of life cycles (Székely *et al.*, 2014) and new insights into immune responses in the host towards myxozoans (Bartholomew *et al.*, 2003; Sitjà-Bobadilla *et al.*, 2007; Holzer *et al.*, 2021).

Problematic monogeneans

Monogeneans have a direct life cycle and pathogenic potential, which is illustrated by events occurring in both natural waters and aquaculture settings. A series of fish-parasitizing monogeneans were already described by Müller (1776), among these, large species such as the capsalid *Entobdella hippoglossi* from halibut, which in aquacultural settings may suffer from infection (Bergh *et al.*, 2001). In the same era, the monogeneans *Nitschia sturionis* from the sturgeon and *Axine belones*, from the garfish *Belone belone*, were described by Abildgaard (1794a, b). The latter monogenean was later shown to be highly pathogenic to *Acipenser nudiventris*, an endemic sturgeon species in the Aral Sea. The different susceptibility of different sturgeon species became evident following the anthropogenic introduction of the parasite with *Acipenser stellatus* from the Caspian Sea. The latter host species seemed to support a balanced relationship with the parasite in its original habitat (the Caspian Sea). However, when *N. sturionis* was introduced to a new location, the parasite spread to the endemic sturgeon species, which appeared highly susceptible. Consequently, the introduced monogenean caused an epidemic resulting in mass mortality among the local sturgeon population (Petrushevski & Shulman, 1961). The interest in monogeneans and their peculiarities emerged in the 20th century, and Russian (Bychowky, 1957), Pacific (Yamaguti, 1968; Ogawa, 2012; Whittington, 2012), European (Llewellyn, 1965; Justine, 1993) and American (Kritsky & Boeger, 2002) schools laid the groundwork for extensive, global monogenean research. However, the description of the genus *Gyrodactylus* by Nordmann (1832) had already initiated the description of several hundred species within this genus, many of which showed high pathogenic potential. A classic case is the epidemic caused by *Gyrodactylus salaris*, which spread through more than fifty salmon rivers in Norway. The parasite species was originally isolated and described by Malmberg (1957). The specimens were obtained from Atlantic salmon (*Salmo salar*) in a Swedish salmon hatchery producing juvenile fish from a local strain of Baltic salmon. The species was subsequently introduced in Norway during the 1970s with infected salmon smolts (Mo, 2020). In Baltic rivers (draining Swedish, Finnish and Russian catchment areas), the infection level was generally low due to a well-documented lower susceptibility/higher resistance in the strains of Baltic salmon compared to the east Atlantic salmon stocks. These Atlantic strains, occurring in Norway, Scotland and Denmark, all showed a high susceptibility and vulnerability to *G. salaris* infection (Bakke *et al.*, 1990; Dalgaard *et al.*, 2003; Lindenstrøm *et al.*, 2006). This encouraged genetic research to determine genetic markers for resistance against infection in the Atlantic salmon genome (Gilbey *et al.*, 2006), suggesting that breeding could improve the survival rate of exposed fish.

Severe disease is often associated with monogeneans infecting fish hosts in confined environments, such as public aquaria. This was documented by Jahn & Kuhn (1932) and Nigrelli & Breder (1934), both of which described massive infections by *Neobenedenia melleni* across a broad spectrum of host fishes. In the same period, freshwater aquaculture became increasingly popular, and particular attention was given to monogeneans recognized as pathogens in cyprinid aquaculture. The fish were suffering from monogenean infections comprising species within the genera *Dactylogyrus* and *Gyrodactylus*. Common carp cultures were found to be infected with *Dactylogyrus vastator*, *Dactylogyrus anchoratus* and *Dactylogyrus extensus* (Wunder, 1929; Prost, 1963; Paperna, 1964; Buchmann *et al.*, 1993) and tench cultures with *Gyrodactylus macracanthus* (Wilde, 1937). The extensive introduction of cyprinid species from East Asia to Europe further stimulated the research into parasites of aquacultured species. Thus, Molnar (1984) could add several introduced dactylogyrids, including *Dactylogyrus lamellatus* imported with grass carp *Ctenopharyngodon idella*, to the list of new species in Europe. Various chemicals and drugs have been used for treatment, and one of the anthelmintics, praziquantel, showed an effect (Schmahl & Mehlhorn, 1985). The farming of Japanese eels has a long history in the Far East including Japan, but recirculating aquaculture systems were constructed in the 1970s and stocked with glass-eels caught in natural waters. The congeneric species *Pseudodactylogyrus anguillae* and *Pseudodactylogyrus bini*, originally described in China and Japan, respectively, were thereby introduced into European farms and showed a tremendous ability to propagate under these confined conditions (Buchmann, 2012). The anthelmintic mebendazole was shown to eliminate the parasites (Szekely & Molnar, 1987), which initiated the frequent use of the compound at farm level. However, reduced sensitivity to the drug was documented in the monogeneans after repeated treatments (Buchmann *et al.*, 1992), supporting previous reports outlining the risk of anthelmintic resistance in monogeneans (Goven *et al.*, 1980).

With the development of mariculture facilities, introducing a range of new species with a high market value, the natural parasites of the new production species demonstrated their pathogenic potential. One of the maricultured species, *Seriola quinqueradiata*, carries the monogenean *Benedenia seriolae*, a large capsalid that colonizes the head, flanks, eyes and fins of the fish. The continuous browsing of epidermal tissue will cause skin erosion and require treatment (Whittington, 2012). Evidence points to the potential for breeding strains with a higher natural resistance to infection. Thus, quantitative trait loci for resistance were determined through a genome-wide analysis (Ozaki *et al.*, 2013), which paves the way for future breeding programmes. Puffer fish (*Takifugu rubripes*) are a major commodity in Japanese aquaculture, and the monogenean *Heterobothrium okamotoi*, occupying the branchial cavity of the fish, has proved a major pathogen (Ogawa, 2012). It is haematophagous, and severe infection levels cause anaemia in the host, which has made control methods a major research target (Ogawa & Yokoyama, 1998; Kimura *et al.*, 2009). The maricultured rockfish *Sebastes schlegeli* is infected with *Microcotyle sebastis*, creating corresponding pathological challenges due to the haematophagous feeding habit of the parasite. Research pointed to anthelmintic treatments using praziquantel as the most promising method (Kim & Cho, 2000). A corresponding polyopisthocotylean monogenean *Sparicotyle chrysophrii*, causing similar problems in Mediterranean mariculture of gilthead seabream, may be controlled by this anthelmintic as well (Sitjà-Bobadilla *et al.*, 2006). The possibility of taking an immunoprophylactic approach (vaccination) to reduce the impact of parasitism was presented by Kim *et al.* (2000).

Problematic cestodes

Some species of cestodes, such as the so-called Asian tapeworm *Bothriocephalus acheilognathi*, play a role in some fish productions. The parasite is associated with cyprinid production, and over the past century, reports have shown that carp fry in particular suffer due to high loads of cestodes (Scholz & Di Cave, 1993; Scholz *et al.*, 2012). As Asian carp production dominates global aquaculture (Food and Agriculture Organization of the United Nations, 2022), the overall impact of this cestode should not be disregarded. Another bothriocephalidean cestode *Eubothrium crassum* occurs in the pyloric caeca of salmonids and may decrease the growth rate in mariculture at certain sites (Saksvik *et al.*, 2001). As fish also may serve as intermediate hosts of certain cestodes with a human pathogenic potential, such as *Dibothriocephalus* (syn. *Diphyllobothrium)* *latum* and *Dibothriocephalus dendriticum*, a series of studies in this field has been published over the past century.

Problematic digeneans

Most digenean life cycles depend on an intermediate molluscan host. Various snail species have shown to be able to colonize aquaculture ponds if these are connected to natural aquatic systems. Over the past century, numerous studies have documented how these molluscs play this key role in the transmission of digeneans to aquacultured fish. Several of these digeneans have demonstrated their pathogenic potential in fish. A classic example is the group of eye flukes using birds as a final host, snails as the initial intermediate hosts and the fish host as an intermediate host harbouring metacercariae in their eyes (Karvonen & Marcogliese, 2020). Representative genera are *Diplostomum* and *Tylodelphys*, parasites occupying the lens and *corpus vitreum* of the fish host, respectively. These eye flukes may severely affect vision (Duan *et al.*, 2021), whereas other species reach maturity in mammals including humans and are thus regarded as serious zoonotic pathogens. Classic examples are *Clonorchis*, *Opisthorchis*, *Metagonimus*, *Haplorchis*, *Centrocestus* and *Pseudamphistomum* where the most effective control methods established rely on snail control in ponds and the control of infective stages in inlet water (Skov *et al.*, 2008, 2009; Madsen *et al.*, 2022). A prominent digenean group are blood flukes with a non-molluscan host, a polychaete, as the intermediate host. These parasites infect tuna in their natural environment but due to the practice of stocking wild juvenile tuna in net pens, these blood worms have become aquacultural parasites (Power *et al.*, 2021).

Problematic parasitic crustaceans

Crustacean parasites comprise a richness of species, and the literature encompassing species descriptions, life cycles and general biology has expanded over the past century (Kabata, 1979). With the advent of new aquaculture, species-specific interest has been concentrated on those exhibiting pathogenic potential. This applies to branchiurans (Møller, 2012), isopods such as *Cerathotoa* in gilthead seabream farming (Mladineo *et al.*, 2020), copepods such as lernaeids (Avenant-Oldewage, 2012) and, not least, caligids (*L. salmonis* and *C. rogercrosseyi*) (Burka *et al.*, 2012). Mariculture based on net pens stocked with salmonids developed during the 1960s (Gjedrem, 1986). With an increasing number of fish in confined environments exposed to natural environmental parameters, including various pathogens, parasitic problems rapidly emerged. Lepeophtheirus *salmonis* showed the potential to propagate rapidly in mariculture settings, and it is now considered the main parasitic problem in the net-pen based production of salmonids (Torrissen *et al.*, 2013). This causative pathogen has been known about for centuries from observations of wild Atlantic salmon returning from their sea migration. Berland & Margolis (1983) found written evidence that the bishop Erik L. Pontoppidan (1698–1764) observed Atlantic salmon (*S. salar*) with heavy infestations of lice, probably salmon lice, when they returned to the rivers of Western Norway. The first scientific description was done by Krøyer (1838), who reported that this crustacean parasite was common in Danish salmon in summer. Krøyer termed the species *Caligus salmonis*, but its lack of lunules places it in the genus *Lepeophtheirus* erected by Nordmann (1832). In high-intensity occurrences, the parasite may cause massive damage to the host's skin. Erosion of the epidermis and dermis may expose underlying muscle layers, which was also described in wild Atlantic salmon returning from sea migration to the Moser river in Nova Scotia decades before mariculture was established (White, 1940). Since the early reports of salmon lice problems in mariculture during the 1970s, the interest in research has increased exponentially. The number of peer reviewed scientific publications about *L. salmonis* found at SCI (Science Citation Index, Web of Science) has reached 1469 in mid-2022 and close to 100 papers on salmon lice are being published annually. Accordingly, the total number of citations may exceed 5000 per year. Due to the marked disease problem caused by the lice, a main part of the publications has been concerned with control methods, including chemical and medical treatments. A series of compounds and drugs have been tested and various drugs and compounds such as hydrogen peroxide (Helgesen *et al.*, 2015), organophosphates (Kaur *et al.*, 2016), pyrethroids (Bakke *et al.*, 2018), emamectin benzoate (Stone *et al.*, 2002; Lees *et al.*, 2008; Poley *et al.*, 2013) and chitin synthesis inhibitors (Harðardottir *et al.*, 2019) have been investigated and subsequently used. However, due to the rapid development of resistance to treatment (Helgesen *et al.*, 2015; Kaur *et al.*, 2016; Bakke *et al.*, 2018), researchers have been looking for other control strategies. These may include the use of cleaner fish (labrids and lumpfish) (Bjordal, 1991; Groner *et al.*, 2013; Imsland *et al.*, 2014). Removal of infective larvae using filtration by bivalves was shown to work experimentally (Bartsch *et al.*, 2013). Direct high-tech combatting of lice on salmon by radiating the lice with laser beams was tested, but found less effective (Bui *et al.*, 2020). Mechanical removal by freshwater flushing has been widely implemented in the industry (Østevik *et al.*, 2022) and may, despite its adverse effects on the host, lead to a reduction of the lice count. More intricate farm constructions have used the knowledge about host-finding behaviour by the infective salmon louse copepodids. These seek the upper layers of water when attaching to the host, an observation that was exploited by Geitung *et al.* (2019) when constructing snorkel cages to prevent copepodids from attacking salmon kept at lower water depths. Still other ideas were developed that included the use of herbal repellents to jam the parasite's host finding (O'Shea *et al.*, 2016). Genetic markers for susceptibility have been identified (Gharbi *et al.*, 2009), and quantitative trait loci for resistance in salmon have been described (Robledo *et al.*, 2019), which may lead to development of breeding programmes to obtain salmon with a higher natural resistance to infection. Several research groups have focused on the immune response in fish against lice infestations (Dalvin *et al.*, 2020) and have documented the responses. This has encouraged others to invest in the development of vaccines to control the salmon lice problem at salmon farms, and recently Tartor *et al.* (2022) reported a partial reduction of infection in Atlantic salmon vaccinated with a recombinant louse gut protein. Although the research efforts in this field must be characterized as impressive and extensive, they have yet to result in a control of the problem, but serve as a sound basis for future research.

Future perspectives

According to the United Nations, it is estimated that nearly eleven billion people will inhabit the Earth by the end of the 21st century (Adam, 2021), and the global food-producing sector, including fisheries and aquaculture, faces the challenge of increasing its levels of production to ensure food and nutrition for this growing population. Marine fish stocks, however, are in decline in many parts of the oceans due to overfishing and climate change (Sumaila & Tai, 2020), and their assessment and the basis for management are preferably achieved through integrated analysis (or integrated population modelling) methods, including the use of parasites and other biological markers (Punt *et al.*, 2020).

For such purposes, parasitologists must provide reliable tools that can be integrated into multidisciplinary studies. Therefore, further research is required to clarify the selection criteria for biological indicators, adjusting them to each kind of study, host–parasite system and environment. The role of different host traits on parasite populations must be also determined and their effects controlled in order to achieve reliable comparisons. Finally, the use of molecular studies of parasites – both to increase the taxonomic resolution of quantitative studies and to use the parasite population structure as an additional tool for fish stock assessment – is one of the most promising avenues for new research on parasite tags.

The studies on parasites in aquaculture settings have increased exponentially over the past century due to the massive development of the aquaculture business and the need to safeguard the health of production fish suffering from parasitic infections. The potential for further expanding the industry is high (Gentry *et al.*, 2017) and may surpass the expected continued expansion of aquaculture productions in coming decades (Food and Agriculture Organization of the United Nations, 2022), which will further emphasize the need for parasitological research. As the massive investment, due to the economic importance of aquaculture, already seen in parasitological research has resulted in an enormous expansion of the overall knowledge about fish parasites and their biology, it is likely that we will enjoy a further development of the literature in the field of aquaculture parasites in the years ahead.

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