

Ecology and effects of metazoan parasites of fish in transitional waters

Luisa Giari ^{1*}, Giuseppe Castaldelli ¹ and Juan Tomás Timi ²

¹ Department of Environment and Prevention Sciences, University of Ferrara, St. L. Borsari 46, 44121 Ferrara, Italy and ² 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

* **Author for correspondence:** Luisa Giari, E-mail: luisa.giari@unife.it

Abstract

Given the abundance, heterogeneity and ubiquity of parasitic organisms, understanding how they influence biodiversity, evolution, health and ecosystem functionality is crucial, especially at present when anthropogenic pressures are altering host-parasite balances. This review describes the features, roles and impacts of metazoan parasites of fish occurring in transitional waters (TW). These aquatic ecosystems are highly productive and widespread around the globe and most represent favourable theatres for parasitism given the availability of hosts (invertebrates, fishes and birds) and an increased probability of parasite transmission, especially of those having complex life cycles. Fascinating examples of how parasitism can influence different hierarchical levels of biological systems, from host individuals and populations to entire aquatic communities, through effects on food webs come from this kind of ecosystem. Edible fish of commercial value found in TW can harbour some parasite species, significantly reducing host health, marketability and food safety, with possible economic and public health consequences. Many TW are historically exploited by humans as sources of relevant ecosystem services, including fisheries and aquaculture, and they are highly vulnerable ecosystems. Alteration of TW can be revealed through the study of parasite communities, contributing, as bioindicators, to assessing environmental changes, health and restoration. Fish parasites can provide much information about TW, but this potential appears to be not fully exploited. More studies are necessary to quantify the ecological, economic and medical impacts fish parasites can have in these important ecosystems.

Key words: metazoan parasites, estuaries, lagoons, brackish waters, bioindicators, zoonoses

Introduction

Peculiarities of transitional waters and their fish fauna

Transitional waters (TW) are defined as those “bodies of surface water in the vicinity of river mouths that are partially saline in character as a result of their proximity to coastal waters but which are substantially influenced by freshwater flows” (European Communities, 2000). They include different kinds of estuaries (Elliot and McLusky, 2002) among other physiographic forms of brackish waters, with variable influences of tides and freshwater inputs (McLusky and Elliott, 2007).

The main feature of these ecotones between freshwater, marine and terrestrial ecosystems, characterized by morphological and dynamic changes between them, is the instability of physicochemical parameters, particularly the saline concentration (Cognetti and Maltagliati, 2000; Basset *et al.*, 2006). These ecotonal habitats are under the effect of marine waters, which regulate water temperature, ion balance and oxygenation; there, the lower hydrodynamism is far lower than in the shore area, and as a result, sedimentation of both terrestrial and marine materials is accentuated (Cognetti and Maltagliati, 2000), thus fuelling phytoplankton and macroalgal growth as well as benthic primary production (Douglas *et al.*, 2019).

As a consequence of these characteristics, many transitional environments harbour remarkable biodiversity levels due to high primary productivity, the occurrence of multiple habitats along gradients of abiotic variables and the contribution of terrestrial, marine and freshwater biota. Thus, these environments are considered biodiversity hotspots, including a wide range of migratory and endemic species (Martínez-Megías and Rico, 2022). Nevertheless, they are characterized by a relatively low ichthyofaunal diversity, although with a high abundance of individual taxa, and most exhibit wide tolerance limits to variable environmental conditions (Whitfield, 1996) and usually belong to only a few taxonomic groups (Yáñez-Arancibia *et al.*, 1994). Fishes occurring in lagoons and estuarine habitats vary latitudinally,

with species richness decreasing from the equator to the poles. The main families encountered in TW include numerous species of faunistic and/or commercial importance (Yáñez-Arancibia *et al.*, 1994).

Estuarine fish communities are composed of species with differential halotolerance capabilities (Schultz and McCormick, 2012), including freshwater and marine fishes that occasionally enter brackish water as adults for feeding, truly estuarine species that spend their entire lives in estuaries, those that use estuaries and lagoons primarily as nursery grounds, and diadromous species in transit during migrations (Yáñez-Arancibia *et al.*, 1994; Ray, 2005; Lowe *et al.*, 2015).

Transitional environments provide key ecosystem goods and services, not only of biological value but also of economic, societal, heritage, aesthetic and scientific relevance (Newton *et al.*, 2014). Examples of the services provided by lagoons include food provisioning, especially fish and shellfish, which support fisheries and aquaculture sectors, climate regulation, flood protection, water purification, recreation and ecotourism, resulting in a valuable contribution to human welfare (Cataudella *et al.*, 2015; Newton *et al.*, 2018). Such a wide array of living and nonliving resources has prompted human settlement and activity, with adverse effects on water quality due to, for example, the discharge of wastewater from industrial and urban sources or the application of agricultural fertilizers and manure (Arienzo *et al.*, 2020), among many other anthropogenic stressors. Due to their great biological and environmental variability and the presence of different gradients, TW environments are very fragile and easily subject to dystrophic crises (Arienzo *et al.*, 2020). Consequently, estuaries are among the most degraded aquatic habitats worldwide, as they comprise the first and often ultimate receiving environment for pollution from surrounding lands (Syvitski *et al.*, 2005). In addition, estuaries and coastal lagoons are increasingly recognized as gateways for bioinvasions, one of the main agents of global change, even in the absence of international

shipping (Wasson *et al.*, 2001; Wonham and Carlton, 2005; Newton *et al.*, 2014).

Importance of parasitism in transitional waters

Parasitism is among the most successful and widespread modes of life in nature (Poulin, 2011; Weisten and Kuris, 2016), with parasites being ubiquitous components of biological systems, where they may achieve considerable abundance, biomass and productivity (Kuris *et al.*, 2008; Hechinger *et al.*, 2011).

Host-parasite coevolution has led to tight reciprocal adaptations that allow parasites to exploit specific characteristics of their hosts, thus ensuring their transmission, survival and maintenance of viable populations (Timi and Poulin, 2020). On the other hand, they may affect different aspects of host biology. Indeed, parasites can have variable effects on host morphology, fecundity, reproduction, behaviour and survival (Marcogliese, 2004), indirectly extending their impact to host populations, communities and even ecosystems. Therefore, parasites may regulate host populations (Hudson *et al.*, 1998), affect the structure of free-living communities (Mouritsen and Poulin, 2002; Hudson *et al.*, 2006; Lafferty *et al.*, 2006a, 2008; Dunne *et al.*, 2013) and alter the functioning of ecosystems (Thomas *et al.*, 1999; Hatcher *et al.*, 2012; Preston *et al.*, 2016; Frainer *et al.*, 2018). Thus, the multiplicity of lifestyles and strategies displayed by parasites, along with their interdependence with and influence on their hosts, make them interesting organisms for biological studies but also potential sources of biological, ecological and evolutionary information on their hosts and environments.

Because parasites with complex life cycles are favoured in transitional environments, where high predation levels and a great density of organisms increase their probability of transmission, it is not surprising that parasitologists have focused on studying such environments (Thomas *et al.*, 1997; Bartoli and Boudouresque, 2007). There, they have economic and medical impacts for humans but also ecological and evolutionary influences on

the biota. Consequently, parasitic organisms provide a plethora of tools to detect and understand biological patterns and processes in transitional environments.

The characteristics of natural stress in estuaries are similar to those for anthropogenic stress, making the detection of the latter more difficult, a difficulty known as the estuarine quality paradox (Elliot and Quintino, 2007). Therefore, parasite populations and communities have become excellent models as indicators of the effects and consequences of the main challenges to biodiversity, such as the loss and degradation of habitat, pollution (Sures *et al.*, 2017), climate change (Marcogliese, 2001, 2016), increased disease risks (Harvell *et al.*, 2002; Lafferty *et al.*, 2004; Paull *et al.*, 2012), and invasive species (Torchin *et al.*, 2002; Goedknecht *et al.*, 2016), among others.

This review includes those features of metazoan parasites of fish inhabiting TW that make them peculiar in comparison to other ecosystems, those factors influencing parasitism and their use as indicators for detecting and interpreting natural patterns and processes as well as disturbances of anthropogenic origin, and finally, the economic and medical impact of parasitism in these environments.

FEATURES OF METAZOAN PARASITES OF FISH FROM TRANSITIONAL WATERS

Parasite communities of fish are driven, in part, by host characteristics such as size, age, trophic level, density, habitat, feeding habits, immunological responses (Timi, 2007; Timi *et al.*, 2010, 2011), and estuarine fish are not an exception. However, their spatial distributions, particularly those of marine parasites, are mainly determined by temperature-salinity profiles and their association with specific masses of water (Esch and Fernández, 1993; Cantatore and Timi, 2015). In TW, fish inhabit different biotopes with features of marine, freshwater and brackish waters, therefore composing a variety of amphihaline, euryhaline and true estuarine fish

assemblages (Ray, 2005; Lowe *et al.*, 2015). Such high variability is mostly determined by the recruitment of species from the sea and/or from rivers, given the relatively small number of truly estuarine fish species (Snigirov *et al.*, 2019). This set of assemblages with differential halotolerance capabilities (Schultz and McCormick, 2012) and modes of response to natural and anthropogenic factors are expected to harbour an equivalent variety of parasite assemblages with marine, estuarine and freshwater lineages.

Indeed, and given the ecotonal nature of TW, where gradients dominate the dynamics of biotopes, a high species richness is expected due to an “edge effect” (Odum, 1959), defined as the “tendency for increased population species richness and density in the junction zone between communities”. This occurs because an ecotone contains representatives of species characteristic of adjacent communities. Indeed, parasite assemblages in ecotonal regions where, for example, convergent masses of water supply their own infective stages, also display ecotonal structure and composition (Lanfranchi *et al.*, 2016).

Interesting examples about the effects of environmental features on the composition of parasite assemblages in TW have focused on the influence of hydrological characteristics (Kesting *et al.*, 1996; Landsberg *et al.*, 1998; Snigirov *et al.*, 2019), mainly of salinity profiles (Zander *et al.*, 1984; Zander, 1998; Blonar *et al.*, 2011; Rashnavadi *et al.*, 2014), whose gradients determine concomitant variations in parasite burdens depending on the parasite guilds. Indeed, ectoparasites, which are generally monoxenous and live in direct contact with the surrounding water, are more sensitive to changes in salinity but also to other factors, such as temperature and dissolved oxygen, e.g., parasitic copepods are recognized as highly stenohaline (Cavaleiro and Santos, 2009). On the other hand, heteroxenous parasites depend largely on the availability of other hosts involved in their life cycles (Landsberg *et al.*, 1998). Ectoparasites, in general, as well as trophically transmitted gastrointestinal parasites, face drastic changes in the physical characteristics of habitats when their hosts migrate to estuarine

waters. For example, the skate *Symperigia bonapartii* harbours parasite communities that are significantly different between estuarine and marine waters after performing reproductive migrations in the Argentine coast when ectoparasites and gastrointestinal helminths are included in the analyses, but no differences are observed when only larval parasites from the body cavity or other tissues are considered (Irigoitia *et al.*, 2017). These later guilds, represented mostly by long-lived larval helminths, can persist for long periods, generally encysted or encapsulated in fish tissues and body cavities (Braicovich *et al.*, 2016), and should be able to survive under different conditions when diadromous fish alternate between marine, transitional and freshwater habitats. Thus, for instance, consecutive infections of the "sea" perch *Perca fluviatilis* with freshwater parasites can take place during seasonal reproductive migrations to lakes (Wierzbicka *et al.*, 2005).

The freshwater, estuarine or marine origin of fish, and therefore the proportion of each lineage in the host community, are further relevant determinants of the structure of parasite assemblages. A study of six estuarine-dependent marine fish species caught in the Mar Chiquita coastal lagoon, Argentina, showed that five of them harboured parasite faunas of predominantly marine origin, with only one species, the mullet *Mugil platanus*, with parasite communities dominated by true estuarine parasites (Alarcos and Etchegoin, 2010). The authors attributed such differences to the longer residence time of mullets in the coastal lagoon. A broader study, including 22 species of marine, brackish water and freshwater fishes, carried out in the Celestun coastal lagoon, Mexico, also showed the dominance of the marine euryhaline fishes that apparently enter the lagoon already infected with typical marine parasites (Sosa-Medina *et al.*, 2015). In contrast, in northeastern Bothnian Bay, Baltic Sea, a minor proportion of parasites (8 out of 63) found in 31 sympatric fish species were marine (Valtonen *et al.*, 2001). The authors argued that due to ecological factors acting over short time scales, rather than evolutionary ones, marine parasite species are able to utilize both freshwater and

marine fish species as intermediate or final hosts, and marine fish can harbour freshwater parasite species. Given the relatively recent origins of the Baltic Sea and Bothnian Bay, the establishment of marine parasites in the bay has probably depended on the immediate presence of suitable intermediate and definitive hosts (Valtonen *et al.*, 2001).

Beyond the results of ecological mechanisms, the physical variability of TW is thought to promote evolutionary processes by selecting generalist genotypes to adapt to a wide range of conditions, therefore preadapting them to colonize new habitats (Bamber and Henderson, 1988). As an example, living cystacanths of acanthocephalans of the genus *Profilicollis*, characterized by using marine/estuarine decapod crustaceans as their unique intermediate hosts (Nickol *et al.*, 1999, 2002), were found parasitizing the body cavity of a freshwater fish host, *Oligosarcus jenynsii*, for the first time in the freshwater section of the Mar Chiquita coastal lagoon, Argentina (Levy *et al.*, 2020). These findings were interpreted as a possible case of incipient paratenicity for *Profilicollis* and a colonization event of freshwater habitats, probably promoted by the highly variable conditions typical of estuarine environments.

Thus, in addition to ecological mechanisms, eco-evolutionary mechanisms can be identified as drivers of the composition and structure of fish parasite communities in TW. For instance, in the same coastal lagoon, a euryhaline marine silverside, *Odontesthes argentinensis*, is commonly reported. It shows substantial genetic differences with conspecifics from adjacent marine coasts, despite no geographic barriers separating them, and is considered an example of a marine to freshwater incipient speciation event (Gonzalez-Castro *et al.*, 2019). A comparative parasitological study of estuarine and marine samples demonstrated enough qualitative and quantitative differences to be strong support for the ongoing speciation process proposed for the host in the lagoon (Levy *et al.*, 2021). Beyond a few individual exclusively marine parasites found in estuarine waters and *vice versa*, some marine parasites seem to have coinvasioned the lagoon. Indeed, the nematodes *Cucullanus marplatensis* and *Huffmanella*

moraveci, both specific to silversides and of marine origin, are commonly reported in marine congeners but not in freshwater ones. Both species are found at high burdens in the estuary, indicating that they have coestablished estuarine populations.

ANTHROPOGENIC FACTORS INFLUENCING METAZOAN PARASITES IN TRANSITIONAL WATERS

In addition to host characteristics and natural abiotic and biotic features of the environment, parasites are influenced by anthropogenic factors, among which climate change, pollution and biological invasion are examined below. Because parasites, similar to free-living organisms, are impacted by habitat modification, they can reveal environmental changes (Hudson *et al.*, 2006). The study of parasite community composition and of the variations in time and space of population parameters could provide useful information on anthropogenic alterations affecting parasites themselves, the hosts and/or the ecosystem (Lafferty, 1997). Parasites may respond to environmental perturbations in different ways (i.e., increasing or decreasing richness and/or abundance) depending on their condition of ecto- or endo-parasites, their direct or indirect life cycle, and their host specificity (Marcogliese, 2004), and this crucial issue should be considered when using them as sentinels.

Climate change \

Climate change is undoubtedly one of the major challenges leading to an irreversible transformation of the planet. Anthropogenic activities have unequivocally warmed the atmosphere, ocean, and land by increasing greenhouse gas concentrations (IPCC, 2021). Increases in temperature but also changes in the amount of solar radiation, sea level, precipitation, circulation patterns, ocean acidification and salinity are expected, with variable effects on many ecological networks and biological systems, such as changes in community

structure and species interactions, including parasitism (Marcogliese, 2004; Widmann, 2013). Relatively small changes in environmental variables may alter the metabolism and physiology of any organism, with consequences for growth, fecundity, feeding behaviour, distribution, migration, and abundance (Marcogliese, 2008). Such ecological perturbations may, therefore, cause geographical and phenological shifts and alter the dynamics of parasite transmission, increasing life cycle completion rates and the potential for host switching, even permitting the emergence of parasites and diseases without evolutionary changes in their capacity for host utilization (Brooks and Hoberg, 2007; Macnab and Barber, 2012). Consequently, the distribution and abundance of parasites are affected not only directly by global warming but also indirectly through effects on the distribution range and abundance of their hosts (Marcogliese, 2001). Indeed, many of these factors have been postulated to be responsible for disease outbreaks in marine life (Lafferty *et al.*, 2004), and among metazoan parasites, the increase in the emergence output of trematode cercariae from molluscs with rising temperature is a well-documented phenomenon (Poulin, 2006; Berkhout *et al.*, 2014). However, the negative impacts of climate change on parasite diversity remain largely undocumented (Carlson *et al.*, 2017).

Estuarine environments are probably some of the most susceptible habitats to temperature swings, since water temperature is most affected in shallow areas, along with other factors of global change, such as salinity, hypoxia, salinity, and acidity (Byers, 2020). However, despite the relevance of parasitism in TW, few studies have focused on the effects of global change on host-parasite systems in general and on fish hosts in particular. Nevertheless, some factors related to increasing temperatures and decreasing water levels, such as eutrophication and anoxia (Marcogliese, 2001), have resulted in a reduction in invertebrate populations, affecting the completion of parasitic life cycles in fjords of the Baltic Sea (Kesting *et al.*, 1996; Zander, 1998).

Despite the scarcity of studies on the effects of global change on estuarine parasite dynamics, extreme weather events have provided evidence of possible changes under novel conditions mimicking future climate change (Marcogliese, 2016). For instance, after Hurricane Katrina, which affected the northern Gulf of Mexico in August 2005, a notable absence of or reduction in fish parasites was observed as well as a variability of time for parasite re-establishment according to its life cycle and habitat (Overstreet, 2007). Similarly, it took several years for snail and trematode populations from a coastal lagoon to recover after Hurricane Isidore devastated the Yucatán Peninsula in September 2002 (Aguirre-Macedo *et al.*, 2011). Thus, transitional environments and their parasite fauna offer excellent models for the study of the effects of climate change and its causative agents and on its possible synergistic or antagonistic combination with other anthropogenic stressors, such as pollutants, habitat loss and species introductions, which can mitigate or exacerbate negative effects on biological systems.

Pollution

The myriad of ecological roles that parasites play in ecosystems and their ubiquity and sensitivity to environmental disturbances make many parasite taxa useful indicators of chemical contamination (Sures and Nachev, 2015). Environmental parasitology thus addresses the interactions between parasites and pollutants in the environment (Nachev and Sures, 2016).

During recent decades, there has been an increasing number of successful studies using parasites as indicators of environmental impact, most of which focus on the effects of pollution (e.g., eutrophication, pulp-mill effluent, thermal effluent, oil, acid precipitation, sewage and heavy metals) on fish parasites (Lafferty, 1997; Blonar *et al.*, 2009; Sures *et al.*, 2017). Three main fields of environmental parasitology have been recognized as the most relevant, namely, parasites as accumulation indicators for selected pollutants, parasites as effect indicators, and

the role of parasites interacting with established bioindicators (Sures *et al.*, 2017).

A large amount of research has been published on these topics, especially in aquatic environments, showing variable and sometimes disparate responses of individual taxa and functional groups to specific contaminants (Blanar *et al.*, 2009; Sures *et al.*, 2017). Blanar *et al.* (2009) quantitatively assessed the sizes of the effects of parasite responses to specific contaminants and compared them between freshwater and marine habitats. Unfortunately, brackish and estuarine habitats were pooled with marine habitats, and no specific characteristics of TW were analysed in relation to the effects of contamination. The authors found differences in the sizes of the effect between freshwater and marine habitats, which were attributed to the differential toxicity of pollutants in each environment and, more likely, to a higher complexity in marine environments due to tides, spatial variation in water parameters such as salinity and temperature, large-scale currents, the fugacity of host species, and the open nature of the ecosystem, which may reduce impacts (Blanar *et al.*, 2009). On the other hand, in freshwater environments, sources of contamination and other human activities are readily identified and localized in a more geographically constrained area, which render more consistent results on the effects of contaminants (Blanar *et al.*, 2009).

By definition, transitional environments combine several features typical of both marine and freshwater habitats (European Communities, 2000). Because estuaries are prone to increasing the intensity of human perturbations, parasites can be useful tools for a more complete understanding of how interacting physical, chemical and biological processes can be affected by anthropogenic stressors. This is confirmed by a number of studies showing different effects on parasitism by a variety of stressors in estuaries, such as the degree of urbanization (Machut and Limburg, 2008), eutrophication via municipal sewage combined with salinity gradients (Blanar *et al.*, 2011), contamination by chlorinated hydrocarbons and heavy metals (Broeg *et al.*, 1999; Pech *et al.*, 2009), industrial sewage (Fajer-Ávila *et al.*, 2006),

eutrophication and anoxia in sediments (Kesting and Zander, 2000) or different combinations of these factors (Overstreet and Howse, 1977; Landsberg *et al.*, 1998).

The responsiveness of parasitic organisms to environmental stress, to which they appear to be more sensitive than the fish themselves (Landsberg *et al.*, 1998), makes them valuable tools for detecting different patterns and processes related to pollution and habitat degradation as well as for monitoring protection measures implemented to promote the recovery of transitional environments.

Biological invasions

Biological invasions are one of the major global environmental problems due to their strong impacts on native species and invaded environments (Chalkowski *et al.*, 2018). Over time, freshwater, marine and estuarine organisms have dispersed at increasing and accelerated rates around the globe through human-mediated transport (Cohen and Carlton, 1998), especially in recent times (Seebens *et al.*, 2017), resulting in ecological alterations that range from competitive exclusions to extinctions (Chalkowski *et al.*, 2018), and they are the second leading cause of the extinction of fish species worldwide (Clavero and García-Berthou, 2005).

One of the hypotheses for the success of introduced species relative to where they are native, known as the “enemy release hypothesis”, is the paucity of predators and parasites in the colonized habitat because they normally are not cointroduced or, if they were, often fail to invade the new habitat (Torchin *et al.*, 2002, 2003; Goedknecht *et al.*, 2016). Additionally, parasitism can have a paramount role in determining invasion outcomes by transmitting parasites from invading to native species in two ways: transmitting exotic, coinvasive parasites (“parasite spillover”) or being competent hosts for native parasites, increasing disease impacts in native hosts (“parasite spillback”). Both processes aid the invasion process. Finally, native parasites may negatively affect exotic hosts, or the abundance of their infective stages can be

diluted if the nonindigenous species is a competent host, with the opposite effect on the success of the invasion (Prenter *et al.* 2004; Kelly *et al.*, 2009*a,b*; Poulin, 2017; Chalkowski *et al.*, 2018).

Beyond the effect on individual hosts, exotic parasites have also marked effects on ecological systems (Chalkowski *et al.*, 2018), modifying structural features of recipient ecological networks, such as the connectance or modularity of food webs, therefore representing additional aspects of global change with undesirable consequences on multiple trophic levels (Britton, 2013; Médoc *et al.*, 2017).

Estuaries are among the most common sites of invasions, accumulating from tens to hundreds of nonindigenous species of all major taxonomic and trophic groups that have changed estuarine communities globally (Ruiz *et al.*, 1997). However, despite the relevance of parasitism in these environments, few studies have dealt with biological invasions relating to fish and parasites, focusing on species of particular importance, such as the endangered European eel *Anguilla anguilla* (Lefebvre and Crivelli, 2004; Morozińska-Gogol, 2009; Giari *et al.*, 2021). On the other hand, the role of parasites in biological invasions of estuaries, either as invaders or as deleterious agents for invaders, has been mostly investigated for invertebrates, mainly molluscs and crustaceans (Aguirre-Macedo and Kennedy, 1999; Byers and Goldwasser, 2001; MacNeil *et al.*, 2003; Lafferty and Kuris, 2009; Troost, 2010; Chapmann *et al.*, 2012; O'Shaughnessy, 2014; Blakeslee *et al.*, 2015), including research aiming to reveal the impact of biological invaders on estuarine food webs (Lafferty and Kuris, 2009).

Specific research on fish-parasite relationships in the context of biological invasions is scarcely available for TW, with variable effects of such invasions on fish hosts being recorded (Giari *et al.*, 2021). It is expected, however, that strong impacts could take place after an invasion of estuaries by either exotic fish, parasites or both, such as occurs for other animal groups and for many receiving ecosystems. Indeed, there is strong evidence from freshwater

environments where fish populations have been dramatically affected as a consequence of invasion by exotic pathogenic parasites, such as the copepod *Lernaea cyprinacea* and the nematode *Anguillicola crassus* (Kirk, 2003; Maceda-Veiga *et al.*, 2019), and even human parasites have been introduced to naive populations, such as the fish tapeworm *Dibothriocephalus latus* (Kuchta *et al.*, 2019). Otherwise, it has been documented that introduced fish can have a dilution effect, reducing the rate of encounters between native fish and parasites through different mechanisms, such as acting as sinks that remove infective stages from the environment, competing with native fish as prey in food webs or predated other intermediate hosts, consequently decreasing parasite transmission to definitive hosts (Kelly, 2009b; Gendron and Marcogliese, 2017).

In summary, knowledge of the role of parasites in biological invasions to estuaries and their effect on fish hosts requires further analysis at the level of both host species and communities. Although other host-parasite-environment systems have provided a conceptual frame to the intersections of parasitology and invasion biology, the peculiarities of transitional environments as well as of their parasite faunas due to their fragility, diversity and variability can provide valuable evidence to gain a better understanding of biological invasions and their consequences.

ECOLOGICAL ROLE AND IMPACT OF METAZOAN PARASITES OF FISH IN TRANSITIONAL WATERS

It is implied in the definition of parasitism that parasites are detrimental to their hosts, showing more or less adverse effects at the individual and population levels (Combes, 2001). Parasites may also affect and regulate the community and the ecosystem in which they occur and not necessarily with negative outcomes (Marcogliese, 2004; Wood and Johnson, 2015). The role of parasites at these higher levels of biological organization is difficult to understand and

quantify, and perhaps for this reason, it has often been overlooked by ecologists (Marcogliese and Cone, 1997; Bartoli and Boudouresque, 2007). Moreover, such roles can vary depending on parasite pathogenicity, the position in the food webs and the condition of generalist or specialist (Hudson, 2005).

Information on the ecosystem effects of parasites, especially on food web processes and energy flow, is mainly derived from long-term studies in estuaries from southern California (Lafferty and Morris 1996; Lafferty *et al.*, 2006*a,b*, 2008; Lafferty, 2008; Kuris *et al.*, 2008). Although parasite biomass often appears negligible, especially when compared with that of free-living organisms, in Carpinteria Salt Marsh, parasites represent a relevant amount of biomass and an important food source (Lafferty, 2008). Indeed, cumulatively, parasite biomass (i.e., all parasites counted and weighed together) ranges from 6 to 12 kg ha⁻¹ and constitutes one-third of the standing stock of fish biomass and 0.2-1.3% of the free-living animals (Kuris *et al.*, 2008). Although parasitic organisms are generally considered only as consumers, they can also be important prey, being ingested with their hosts by their predators or directly eaten as ecto-parasites or in free-living stages (Kaplan *et al.*, 2009; Johnson *et al.*, 2010; Thieltges *et al.*, 2013). For instance, small fish of different species can rely on digenean cercariae for nutrition, partially deviating the energy flow in estuarine ecosystems (Kuris *et al.*, 2008; Lafferty, 2008).

Many heteroxenous parasites, such as cestodes, digeneans and acanthocephalans, having indirect life cycles with two or more hosts exploit trophic relationships for transmission, participating in most links of aquatic food webs, particularly those involving fishes, and even dominating them (Lafferty *et al.* 2006*a*; Lafferty, 2008). There is growing evidence that parasites are important in food-web topology and improve the nestedness, connectivity and stability of the community (Lafferty, 2008; Hatcher *et al.*, 2012). The alteration of predator–prey interactions is a typical way by which parasites may affect trophic webs. Given the

energetic cost of parasitism, infected hosts are often weakened and then more vulnerable to predation. Additionally, behavioural or morphological/physiological alterations imposed by parasites determine an increased susceptibility to the predation of hosts by reducing their ability to avoid predators and/or to escape from them (Thomas *et al.*, 1997). As a result, parasites are facilitated to reach their final host and successfully complete their life cycle, predator species often benefit from enhanced food accessibility, and trophic links are influenced by an increase in predation rates. The manipulative capacity of some parasites to change fish behaviour (for example, foraging activity, habitat selection, competition, predator–prey interactions, swimming ability, and sexual and mate behaviour) is well documented (Barber *et al.*, 2000). There are interesting examples of altered behaviour in TW, with evident ecological consequences, sometimes dramatic ones, especially when fishes serve as intermediate hosts (Lafferty, 2008). For instance, California killifish *Fundulus parvipinnis*, the most common fish species in Carpinteria Salt Marsh, shows a very high prevalence and intensity of infection by the trematode *Euhaplorchis californiensis*, which has birds as final hosts. Infected killifish with encysted larvae in the brain exhibit a conspicuous behaviour that makes them up to 30 times more susceptible to bird catch (Lafferty and Morris, 1996). Other examples of altered behaviour in TW fish are available in the literature. The shoaling behaviour in parasitized *Fundulus diaphanus* is modified, exposing the fish to a higher predation risk by piscivorous birds (Krause and Godin, 1994). Predators may also be facilitated by parasites that damage eyes (Kinne, 1984), obtrude vision (Stumbo and Poulin, 2016) or impair fin mobility in fish hosts, as in the case of *Gobius* infected by the trematode *Cainocreadium labracis* (Maillard, 1976). Parasites can increase food and oxygen demand in their fish hosts that, by spending more time close to the water surface or engaged in food acquisition, are consequently easier to prey upon (Curio, 1988).

In addition to influencing predation rates, other impacts of parasites on their fish hosts

have been documented in TW, for example, on sexual selection, with male pipefish avoiding females infected by a trematode (Rosenqvist and Johansson, 1995) and on modifications of movement with consequences for population and ecosystem processes such as migration and dispersal (Binning *et al.*, 2017). For example, infection with a copepod inhibits the migration to the sea of *Gadus merlangius*, which remains “trapped” in estuarine waters (Sproston and Hartley, 1941). Similarly, the nematode *Anguillicola crassus*, a haematophagous parasite infecting the swim bladder of eel, can limit swimming performance and speed, and some authors argue that this specialist pathogen has contributed to the decline of European eel *Anguilla anguilla* (Kennedy, 2007; Palstra *et al.*, 2007). Among the possible population effects of anguillicolosis are the selective capture of infected eels and impairment of the migratory capacity to the Sargasso Sea for spawning and mortality when the infection acts in combination with other environmental stressors (Molnar *et al.*, 1991; Kennedy, 2007; Palstra *et al.*, 2007). The severity of the impact on eel health depends on the prevalence and intensity of *A. crassus*, which vary greatly in freshwater and brackish water sites (Dezfuli *et al.*, 2014; Giari *et al.*, 2021; Sayyaf Dezfuli *et al.*, 2021) in relation to salinity, which tends to inhibit *A. crassus*, as it is considered a freshwater parasite (Lefebvre and Crivelli, 2012; Giari *et al.*, 2021). Thus, an abiotic parameter, along with other factors, could determine the degree of adverse effects of anguillicolosis in different TW and is a promising tool to control the disease (Lefebvre and Crivelli, 2012).

METAZOAN PARASITES AS BIOINDICATORS OF ENVIRONMENTAL HEALTH IN TRANSITIONAL WATERS

Parasites can be useful and sensitive indicators of aquatic health (Lafferty, 2008). There are both advantages and disadvantages in using parasites as health bioindicators in transitional ecosystems. Among the former, some parasites are easier to monitor than their hosts and

provide integrated information on the presence, trophic position and abundance of all their hosts over a given period of time (Hechinger and Lafferty, 2005; Marcogliese, 2005). This is especially true for parasites with complex life cycles. Among the disadvantages arises the high degree of temporal variability (both seasonal and interannual) in the parasite levels due to the changes in environmental conditions, which typically and naturally occur in brackish waters (Costa *et al.*, 2012).

There is contrasting evidence on the impact of habitat degradation on aquatic parasites (Sures *et al.*, 2017). Indeed, stressful conditions tend to reduce heteroxenous endoparasites and have variable effects on monoxenous ectoparasites that could be favoured by a compromised immune response of the hosts or damaged by direct exposure to environmental alterations (Marcogliese, 2004). A recent study comparing the community of gill parasites in fishes of two estuaries in Brazil showed that parasite species richness and mean abundance of the most prevalent monogeneans are lower where there is significant anthropogenic pressure than inside a protected area (Falkenberg *et al.*, 2019). The relation found between parasitological indices and water quality parameters supports the use of ectoparasites as environmental bioindicators (Falkenberg *et al.*, 2019). Cunha *et al.* (2021) confirmed monogeneans as sentinels of water quality, but their research in Amazon estuaries indicated a higher parasite abundance in the impacted area than in the reference area. Urbanization, measured through landscape and physicochemical factors, has been proven to influence parasite communities in the estuarine fish *Fundulus heteroclitus*, with the most significant effects detected in indirect life-cycle parasites (Alfieri and Anderson, 2019). The health of a brackish lagoon in Indonesia has been successfully measured by Palm and Rückert (2009), applying a selection of three parasitological parameters (i.e., the prevalence of trichodinid ciliates, the ecto/endoparasite ratio and the endoparasite diversity), and this method is suggested to monitor tropical ecosystems characterized by high parasite biodiversity.

The use of fish parasites as bioecological indicators of ecosystem biodiversity and trophic complexity is growing in estuaries and lagoons (Huspeni *et al.*, 2005; Culurgioni *et al.*, 2015). The high richness and abundance of helminth parasites, which require several host species and rely on predator–prey interactions for transmission, are indicative of favourable environmental conditions not only for the parasites themselves but also for all the hosts involved in their life cycles (Culurgioni *et al.*, 2015). In the same way, the disappearance or decreased occurrence of a parasite in an ecosystem could suggest a decline in the density of a host due to environmental changes (Giari *et al.*, 2020, 2021). A rich parasite community, especially if it includes specialist species, is associated with a diverse and abundant community of hosts; thus, parasites might represent biodiversity indicators in line with the hypothesis that a healthy ecosystem is rich in parasites (Hudson *et al.*, 2006; Hatcher *et al.*, 2012). Helminth larval stages are especially sensitive to abiotic factors (Huspeni *et al.*, 2005) and thus have been proposed to assess the environmental status in brackish systems in combination with standard techniques (Culurgioni *et al.*, 2015).

Approximately 50% of global wetland areas have been lost due to anthropogenic impacts, and thus, restoration projects have been developed to recover the health and sustainability of these vulnerable ecosystems (Meli *et al.*, 2014; Morales-Serna *et al.*, 2019). Among other ecological variables (i.e., organic content, water parameters, abundance and diversity of plants and free-living animals) (Zhao *et al.*, 2016), parasites might also be candidates to evaluate the efficacy of the restoration processes in TW.

The abundance of trematodes, which is low in degraded estuarine habitats, has been shown to increase following habitat restoration that attracts birds (Lafferty, 1997). In the Terminos Lagoon, one of the most relevant in the Yucatan Peninsula, a parasitological analysis of the fish *Poecilia velifera* has been performed 5 years after the beginning of a restoration programme (Morales-Serna *et al.*, 2019). Because no differences have been found between

degraded and conserved sites in terms of parasite community and populations, the diagnostic value of parasites in assessing ecosystem health and progress in restoration appears limited in this case (Morales-Serna *et al.*, 2019).

In conclusion, can the analysis of parasite fauna be applied as a metric of the status of TW? Some studies say yes (Alfieri and Anderson, 2019; Falkenberg *et al.*, 2019), while others say no (Costa *et al.*, 2012; Morales-Serna *et al.*, 2019). The main reason for the conflicting responses and the lack of a standardized method is that host-parasite interactions are hardly predictable and not necessarily the same across all ecosystems, but parasites undoubtedly have enormous potential to provide information on environmental health.

Transitional waters are still understudied in this aspect and deserve particular attention due to their peculiarities (Falkenberg *et al.*, 2019). The open challenge in the use of parasites as bioindicators is selecting the best abiotic variables and the most promising parasite group/species or parasitological parameters that describe the ecological status of a specific transitional environment and its possible changes. This implies a detailed knowledge of the features and functioning of the site, including the parasites present and their life cycles, the biology of hosts and the temporal variations in the parasite level, which should all be taken into account to properly design this kind of study.

IMPACT OF METAZOAN PARASITES OF FISH IN TRANSITIONAL WATERS ON HUMAN HEALTH

Fish occurring in TW may be infected by some parasite species that are potentially harmful to humans and a risk to public health. The high demand for fish as a source of animal proteins, the change in dietary habits with a growing consumption of exotic and raw dishes, and the global trade of foodstuffs have contributed in recent decades to the increase and geographical spread of fish-borne zoonoses. The most relevant among these emerging diseases are

anisakidosis, gnathostomiasis and capillariasis caused by nematodes and heterophyiasis caused by trematodes (McCarthy and Moore, 2000; Broglia and Kapel, 2011). The parasites responsible for the abovementioned diseases use marine, brackish water or freshwater fish as intermediate or transport hosts, and human infection occurs through the consumption of raw or undercooked fish containing larval stages in muscle (filet), body cavity or visceral organs (Broglia and Kapel, 2011; Buchmann and Mehrdana, 2016; Shamsi, 2019).

While in the past eating raw or lightly cooked fish was common only in countries with specific traditions (for example Japan), cosmopolitan and globalized food habits and the increase in international travel have recently led to a worldwide occurrence of cases of some fish-borne diseases, especially anisakidosis (Buchmann and Mehrdana, 2016; Shamsi, 2019). In addition to Asian dishes, such as sushi and sashimi, which today are highly consumed in Western countries, traditional fish specialities from Europe (salted or smoked herring, marinated anchovies, and fermented salmon) and Latin America (“ceviche” in Peru, Chile and Mexico and smoked fish in Brazil) may, if not adequately treated, be at risk of transmitting anisakid infection (Laffon-Leal *et al.*, 2000; Mercado *et al.*, 2001; EFSA, 2010).

Reports from transitional waters of the main fish-borne parasites of public health relevance belonging to the genera *Anisakis*, *Pseudoterranova*, *Contracaecum*, *Gnathostoma*, *Capillaria*, and *Heterophyes* are listed in Supplementary Table 1 with indication of the fish host and of the locality where they have been found. Members of *Anisakis*, *Pseudoterranova* and *Contracaecum* nematodes, all belonging to the family Anisakidae, show low specificity for their fish hosts and a high adaptability to environmental conditions, allowing the widespread occurrence in teleost populations and a worldwide distribution (Ángeles-Hernández *et al.*, 2020). The complex life cycle involving several hosts is illustrated by Buchmann and Mehrdana (2016) for these three genera that contain species of particular clinical importance for human health. Whereas adults of several species of *Contracaecum* infect piscivorous birds

in any aquatic environment, some congeneric species, together with representatives of most *Anisakis* and all *Pseudoterranova* species, are parasites of marine mammals, consequently having marine life cycles (Mattiucci and Nascetti, 2008). The presence of these species in estuarine fishes, where they can persist over time, is surely due to fish movements from or to the sea to feed on intermediate hosts or because infected intermediate hosts entered the estuary with tides.

In some geographic areas, the recent recovery of populations of marine mammals serving as final hosts (for example seals) seems to be linked to increasing infection levels in fish products (Mehrdana *et al.*, 2014). Anisakid larvae ingested with raw fish by humans invade the alimentary canal and may induce the formation of eosinophilic granulomas, gastrointestinal symptoms and allergic reactions, including anaphylaxis (Broglia and Kapel, 2011). Not only alive larvae but also dead larvae can elicit allergic responses through parasite heat-resistant molecules, making anisakids particularly insidious and prevalent hidden allergens of public health concern (Audicana *et al.*, 2002; Rahmati *et al.*, 2020). A recent systematic review explored the relationship between fish infection and human allergic anisakiasis and indicated the highest rate of allergic cases in Portugal and Norway (Rahmati *et al.*, 2020). It is estimated that the number of human anisakid infections is underreported due to frequent misdiagnosis and will increase in the future (Shamsi, 2019).

Several nematode species of *Gnathostoma* (including *G. binucleatum*, *G. spinigerum*, and *G. turgidum*) could cause disease, although most human cases are due to *G. spinigerum* being reported in Asia, Thailand and Japan and over the last 30 years also in Latin America from Mexico, Argentina, Peru, and Ecuador (Nawa, 1991; Ogata *et al.*, 1998). In Mexico, gnathostomiasis represents an emerging public health problem (Rojas-Sánchez *et al.*, 2014). *Gnathostoma* parasites move in the body of infected people, causing fever, lack of appetite, nausea, vomiting, diarrhoea, abdominal pain, and symptoms associated with their presence

under the skin (Shamsi, 2019). Recently, the possibility of human infections by *Echinocephalus* misdiagnosed as gnathostomiasis due to its morphological similarity to *Gnathostomum* has been reported in Australia by the consumption of freshwater fish (Jeremiah *et al.*, 2011; Shamsi *et al.*, 2021).

Although human infections are generally assumed to result from eating raw freshwater fish (Ogata *et al.*, 1998), saltwater fish are known intermediate hosts in some regions (Waikagul and Diaz Chamacho, 2007). For example, in some states of Mexico, where human gnathostomiasis is one of the most important public health issues (Alvarez Guerrero and Alba-Hurtado, 2007), estuarine fish are not only commonly reported intermediate hosts for these parasites but also the most consumed and, consequently, the first suspects of being the main sources of human infection (Alvarez Guerrero and Alba-Hurtado, 2007; Díaz- Camacho *et al.*, 2008).

Capillariasis is a food-borne zoonosis recently discovered in the second half of the last century after an epidemic episode resulted in the death of infected people (Cross, 1992). This intestinal disease is caused by the nematode *Capillaria philippinensis*, which is endemic in the Philippines, where the first cases were described, and Thailand but has also widened to other countries outside Asia (McCarthy and Moore, 2000). In the human intestine, female parasites produce embryonated eggs, causing autoinfection and faecal contamination of water (Shamsi, 2019). The clinical signs are alteration of gastrointestinal functions, diarrhoea and vomiting, which can lead to chronic malabsorption and protein and electrolyte loss, with possible fatal outcomes (Cross, 1992). Through experimental infection, several lagoon fish species have been proven to be natural intermediate hosts (Cross and Basaca-Sevilla, 1991).

Heterophyid trematodes are minute flukes infecting animals and humans. Human heterophyiasis is derived from the consumption of improperly cooked freshwater or brackish water fish, especially mullets and gobies, having metacercariae of the genus *Heterophyes*

encysted in their muscle, and is considered a dangerous endemic disease in Mediterranean countries (Chai, 2014; Attia *et al.*, 2021). *Heterophyes heterophyes* is transmitted in lagoons where euryhaline first (i.e., snails) and second intermediate hosts (Mugilidae) are abundant, and humans become easily infected after eating raw fish (Taraschewski, 1984). Infections occur in Africa (Sudan, Egypt, Tunisia) and are common in the Nile Delta, South Europe (Greece, Italy) and the Middle East (Saudi Arabia, Iran, Iraq, United Arab Emirates, Kuwait, Yemen), with an estimated 30 million people parasitized (Chai, 2014; Tandon *et al.*, 2015). The main symptoms elicited by the trematodes in the small intestine are inflammation, diarrhoea, abdominal pain, and weight loss (Chai and Jung, 2017).

Most of the reports of human cases dealt in general with seafood- or freshwater-borne parasitic diseases, while data on fish-borne zoonoses specifically referring to aquatic transitional ecosystems are limited. Thus, it is difficult to quantify the risk deriving from TW compared to coastal and marine waters. Specific projects and studies on risk assessment in TW are needed at the local, national and international levels. However, the analysis of available literature suggests that some fish, such as mugilids, that are typical, widespread and abundant in many TW and may harbour parasites of medical importance could constitute a zoonotic threat (Chai and Jung, 2017). This holds true especially in ill-developed communities where lagoons and estuaries often support important fisheries and aquaculture activities and represent a crucial food source in the absence of tools for control (Harrison, 1995; Froese and Pauly, 2004; Fajer-Avila *et al.*, 2006). More information about the environmental factors that can influence the parasite prevalence, movements of the fish hosts or their preference for specific zones (more or less saline) determining seasonal trends or the spatial distribution of infection (Rolbiecki and Rokicki, 2002) could help to assess and reduce the sanitary risk in TW.

A “one-health” approach integrating medical aspects with consumer, aquatic animal, and environmental/ecological aspects is the way to tackle fish-borne parasitic diseases and find

potential solutions (Shamsi, 2019).

ECONOMIC IMPACT OF METAZOAN PARASITES OF FISH FROM TRANSITIONAL WATERS

Brackish waters, especially coastal lagoons, are historically exploited for fish harvesting and production (Cataudella *et al.*, 2015). Edible fish of commercial importance harbour numerous parasite species, and some of them could affect fisheries and the market value of fish (Lafferty, 2008). On the other hand, fishing, especially if intensive, could reduce parasitism, as suggested by the application of mathematical models and the analysis of literature data (Wood *et al.*, 2010). In contrast, fish farming offers ideal conditions for high pathogen transmission and abundance, especially for parasites with direct life cycles (i.e., Monogenea and Crustacea), and often suffers from significant economic losses due to parasitic outbreaks (Shinn *et al.*, 2015). The economic impact of parasites is more evident for farmers than for fishers (Lafferty *et al.*, 2015). Therefore, it is not surprising that most of the analyses of the costs associated with parasitic diseases focus on fish farms (Abolofia *et al.*, 2017; Tavares-Dias and Martins, 2017; Peterman and Posadas, 2019; Radwan, 2022; Fernández Sánchez *et al.*, 2022). Regardless, in both situations (i.e., activity with wild and farmed fish), the multiple factors that influence infection make it difficult to calculate the economic damage effectively attributable to parasites, and a precise estimation of the costs would require information on morbidity and mortality, which is not always available or known (Shinn *et al.*, 2015; Tavares-Dias and Martins, 2017). However, some examples are available, such as losses up to 12–15% in profit margin per ton of fish caused by ectoparasites (especially monogeneans) in farms, based on the price of Nile tilapia in Mexico (Paredes-Trujillo *et al.*, 2021).

From an economic point of view, parasitic diseases can be detrimental by reducing biological productivity due to increased mortality, slower growth or limited reproduction, with

the consequent decrease of potential catch and/or by impairing meat quality, appearance or security with consequent reduction of appeal for consumers, commercial value and marketability (Lafferty *et al.*, 2015).

Digenetic trematodes have been reported to produce economic losses in aquaculture in terms of reducing fish growth/weight and increasing mortality (Crotti, 2013). Additionally, ectoparasites, such as Monogenea and Crustacea, frequently cause localized epizootics and serious damage to the aquaculture industry (Cone, 1995) and sometimes reduce the production of economically important fish in coastal lagoons (Aladetohun *et al.*, 2013). However, ectoparasite occurrence in wild fishes of TW does not necessarily have severe or lethal outcomes, as supported by several examples. In the estuary of Patos Lagoon (Brazil), whitemouth croaker, *Micropogonias furnieri*, harbours four parasite species, *Gauchergasilus euripedesi* (Copepoda), *Myzobdella uruguayensis* (Hirudinea), *Neomacrovalvitrema argentinensis* and *Neopteriotrematoides avaginata* (Monogenea), but the absence of correlation between parasite abundance and host health indices suggests that the found parasite levels are tolerable (Velloso and Pereira, 2010). Mullet, *Mugil liza*, a commercially important fish exploited by fishermen in an estuary system on the northern coast of Rio Grande do Sul (Brazil), was infected by several species of ectoparasites without clinical signs of disease and had the same length-weight relationship as uninfected specimens (Mentz *et al.*, 2016). A gill parasitic isopod affecting approximately 40% of sand smelt *Atherina boyeri* in two Greek lagoons does not constitute a significant threat to fish survival (Leonardos and Trilles, 2003). A study comparing the infection levels in sea bream, *Sparus aurata*, and sea bass, *Dicentrarchus labrax*, sampled from two different cage farms and from a lagoon in Greece showed a higher prevalence of ectoparasites but lower intensity and pathogenicity in the latter (Vagianou *et al.*, 2006). This result was probably linked to the lower fish density and stress level in the lagoon than in the semi-intensive systems.

As seen in the section dedicated to medical impact, *Anisakis* worms, which infect many marine edible fishes, pose a risk for human health, and their appearance in muscle or viscera can cause rejection by purchasers (Bao *et al.*, 2019). European Union regulations and international guidelines from FAO and WHO require that the fishery production chain monitors and ensures food safety (for example, performing the visual inspection of fish), but the limits and low efficiency of the control procedures have been pointed out (Levsen and Lunestad, 2010; Llarena-Reino *et al.*, 2012). The distrust of consumers towards fishery products due to *Anisakis*, confirmed by a study investigating the opinions of Spanish consumers, may thus negatively impact the seafood business (Bao *et al.*, 2018). Additionally, *Pseudoterranova decipiens* larvae can devalue fish (cod, herring, pollock), causing cosmetic problems to flesh in addition to concern for consumer health (McClelland, 2002).

To our knowledge, only a very few estimates of economic losses due to fish parasites have been made at TW sites and are provided by Shinn *et al.* (2015), who examined the major marine and brackish aquaculture industries worldwide. For instance, the economic costs of the protozoan *Trichodina* sp. and the digenean *Furnestinia echeneis* infections from Bardawil Lagoon (Israel) were calculated (see Shinn *et al.*, 2015) according to the mortality data (approximately 40-50% of the stock) of *Sparus aurata* fingerlings reported by Paperna *et al.* (1977). No economic studies are available for wild populations where the estimate of impact is certainly more difficult and the losses lower than for cultured fish.

Conclusions

Although attention to parasites from an ecological point of view has increased in recent decades, the observation made by Hudson (2005) appears valid today: more investigations are needed if we want to truly and fully appreciate the multiple roles of parasites and to control the threat of parasitic diseases. Parasite-host systems are incredibly diverse and full of

nonlinearities, and thus, their considerations are far from generalizable. Knowledge of parasite diversity (i.e., species community composition), factors driving host-parasite relationships, and risks and benefits derived from parasites are necessary to effectively manage transitional ecosystems and deserve further research efforts. More quantitative data, especially from long-term studies and field studies, appear pivotal for a better understanding of the complex role and impact of parasites in a changing world.

Attention to the public health significance of food-borne diseases caused by helminths and their links to several factors, such as poverty, cultural traditions, and environmental degradation, is increasing (World Health Organization, 2004). Nevertheless, there is a lack of studies on zoonotic risk assessment specifically focused on TW that should be bridged due to the crucial importance of these ecosystems. Additionally, the quantification of the economic impact of fish parasites in TW is ignored, although parasitism may affect some of their ecosystem services.

Transitional environments are excellent habitats for parasites and, therefore, for parasitological studies and are also among the most degraded environments. Thus, parasites could provide excellent information as indicators of anthropogenic impact; nevertheless, these advantages have not yet been fully exploited by the scientific community.

Supplementary material

The supplementary material for this article can be found at <https://www.cambridge.org/core/journals/parasitology>

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Author Contributions

Conceptualization: LG and JTT; resources: LG, GC and JTT; writing – original draft preparation: LG and JTT; writing – review and editing, LG, GC and JTT. All authors read and approved the final manuscript.

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Conflicts of Interest

The authors declare that there are no conflicts of interest.

Ethical Standards

Not applicable - the study did not involve research on live animals.

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