Ecology and effects of metazoan parasites of fish in transitional waters

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Abstract

Given the abundance, heterogeneity and ubiquity of parasitic organisms, understanding how they influence biodiversity, evolution, health and ecosystem functionality is crucial, especially currently 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 represent most 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, for 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 on these important ecosystems.

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 (Elliott 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; here, the lower hydrodynamism is far lower than that 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 hot spots, 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 comprise 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 non-living 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 TW

Parasitism is among the most successful and widespread modes of life in nature (Poulin, 2011; Weinstein 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, makes 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). Here, they have not only 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 (Elliott 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; Goedknegt et al., 2016), among others.

This review includes those features of metazoan parasites of fish inhabiting TW that make them peculiar in comparison with 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 TW

Parasite communities of fish are driven, in part, by host characteristics such as size, age, trophic level, density, habitat, feeding habits and 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; Blanar 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 not only 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 Sympterygia 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 6 estuarine-dependent marine fish species caught in the Mar Chiquita coastal lagoon, Argentina, showed that 5 of them harboured parasite faunas of predominantly marine origin, with only 1 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 was 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 (González-Castro et al., 2019). A comparative parasitological study of estuarine and marine samples demonstrated enough qualitative and quantitative differences to be a 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 coinvaded the lagoon. Indeed, the nematodes Cucullanus marplatensis and Huffmanela 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 TW

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). Besides increases in temperature, there are also changes in the amount of solar radiation, sea level, precipitation, circulation patterns, ocean acidification and salinity that 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, as water temperature is most affected in shallow areas, along with other factors of global change, such as salinity, hypoxia, 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; Blanar 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; Goedknegt et al., 2016). Additionally, parasitism can have a paramount role in determining invasion outcomes by transmitting parasites from invading to native species in 2 ways: transmitting exotic, coinvading 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 non-indigenous species is a competent host, with the opposite effect on the success of the invasion (Prenter et al., 2004; Kelly et al., 2009a, 2009b; 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 at multiple trophic levels (Britton, 2013; Médoc et al., 2017).

Estuaries are among the most common sites of invasions, accumulating from tens to hundreds of non-indigenous 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; Chapman et al., 2012; O'Shaughnessy et al., 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 predating other intermediate hosts, consequently decreasing parasite transmission to definitive hosts (Kelly et al., 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 TW

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., 2006a, 2006b, 2008; Kuris et al., 2008; Lafferty, 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 ectoparasites 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 2 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., 2006a; 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 (e.g. 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 merlangus*, which remains

'trapped' in estuarine waters (Sproston and Hartley, 1941). Similarly, the nematode *A. 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 *A. 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 TW

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 2 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 that 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 3 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 to be 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.

TW 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 TW 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 (e.g. 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 TW 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 3 genera that contain species of particular clinical importance for human health. Although 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 (e.g. 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 live 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 Gnathostoma binucleatum, Gnathostoma spinigerum and Gnathostoma 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 Gnathostoma 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 widespread to other countries outside Asia (McCarthy and Moore, 2000). In the human intestine, female parasites produce embryonated eggs, causing autoinfection and fecal 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-Ávila *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 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 TW

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; Fernández Sánchez *et al.*, 2022; Radwan, 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 tonne 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 in 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 4 parasite species, *Gauchergasilus euripedesi* (Copepoda), *Myzobdella uruguayensis* (Hirudinea), *Neomacrovalvitrema argentinensis* and

Neopterinotrematoides 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 ~40% of sand smelt *Atherina boyeri* in 2 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 2 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 (e.g. 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 carried out 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 (~40–50% of the stock) of *S. 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.

References

Abolofia J, Asche F and Wilen JE (2017) The cost of lice: quantifying the impacts of parasitic sea lice on farmed salmon. *Marine Resource Economics* **32**, 3.

Aguirre-Macedo ML and Kennedy CR (1999) Diversity of metazoan parasites of the introduced oyster species *Crassostrea gigas* in the Exe estuary. *Journal of the Marine Biological Association of the United Kingdom* **79**, 57–63.

Aguirre-Macedo ML, Vidal-Martínez VM and Lafferty KD (2011) Trematode communities in snails can indicate impact and recovery from hurricanes in a tropical coastal lagoon. *International Journal for Parasitology* **41**, 1403–1408.

Aladetohun NF, Sakiti NG and Babatunde EE (2013) Copepoda parasites in economically important fish, Mugilidae (*Mugil cephalus* and *Liza falcipinnis* from Lac Nokoue lagoon in Republic of Benin, West Africa. *African Journal of Environmental Science and Technology* **7**, 8.

Alarcos AJ and Etchegoin JA (2010) Parasite assemblages of estuarine-dependent marine fishes from Mar Chiquita coastal lagoon (Buenos Aires Province, Argentina). *Parasitology Research* **107**, 1083–1091.

Alfieri JM and Anderson TK (2019) Life-cycle mediated effects of urbanization on parasite communities in the estuarine fish, *Fundulus heteroclitus*. *PLoS One* **14**, e0225896.

Alvarez-Guerrero C and Alba-Hurtado F (2007) Estuarine fish and turtles as intermediate and paratenic hosts of *Gnathostoma binucleatum* in Nayarit, México. *Parasitology Research* **102**, 117–122.

Ángeles-Hernández JC, Gómez-de Anda FR, Reyes-Rodríguez NE, Vega-Sánchez V, García-Reyna PB, Campos-Montiel RG, Calderón-Apodaca NL, Salgado-Miranda C and Zepeda-Velázquez AP (2020) Genera and species of the Anisakidae family and their geographical distribution. *Animals* **10**, 2374.

Arienzo M, Bolinesi F, Aiello G, Barra D, Donadio C, Stanislao C, Ferrara L, Mangoni O, Toscanesi M, Giara A and Trifuoggi M (2020) The environmental assessment of an estuarine transitional environment, southern Italy. *Journal of Marine Science and Engineering* **8**, 628.

Attia MM, Elgendy M, Abdelsalam M, Hassan A, Prince A, Salaeh NMK and Younis NA (2021) Morpho-molecular identification of *Heterophyes*

heterophyes encysted metacercariae and its immunological and histopathological effects on farmed *Mugil cephalus* in Egypt. *Aquaculture International* **29**, 1393–1407.

Audicana MT, Ansotegui IJ, Fernandez de Corres L and Kennedy MW (2002) *Anisakis simplex*: dangerous – dead and alive? *Trends in Parasitology* **18**, 20–25.

Bamber RN and Henderson PA (1988) Pre-adaptive plasticity in atherinids and the estuarine seat of teleost evolution. *Journal of Fish Biology* **33**, 17–23.

Bao M, Pierce GJ, Strachan NJC, Martínez C, Fernández R and Theodossiou I (2018) Consumers' attitudes and willingness to pay for Anisakis-free fish in Spain. *Fisheries Research* **202**, 149–160.

Bao M, Pierce GJ, Strachan NJC, Pascual S, González-Muñoz M and Levsen A (2019) Human health, legislative and socioeconomic issues caused by the fish-borne zoonotic parasite Anisakis: challenges in risk assessment. *Trends in Food Science & Technology* **86**, 298–310.

Barber I, Hoare D and Krause J (2000) Effects of parasites on fish behaviour: a review and evolutionary perspective. *Reviews in Fish Biology and Fisheries* **10**, 131–165.

Bartoli P and Boudouresque CF (2007) Effect of the digenean parasites of fish on the fauna of Mediterranean lagoons. *Parassitologia* **49**, 111–117.

Basset A, Sabetta L, Fonnesu A, Mouillot D, Do Chi T, Viaroli P, Giordani G, Reizopoulou S, Abbiati M and Carrada GC (2006) Typology in Mediterranean transitional waters: new challenges and perspectives. *Aquatic Conservation: Marine and Freshwater Ecosystems* **16**, 441–455.

Berkhout BW, Lloyd MM, Poulin R and Studer A (2014) Variation among genotypes in responses to increasing temperature in a marine parasite: evolutionary potential in the face of global warming? *International Journal for Parasitology* **44**, 1019–1027.

Binning SA, Shaw AK and Roche DG (2017) Parasites and host performance: incorporating infection into our understanding of animal movement. *Integrative and Comparative Biology* **57**, 267–280.

Blakeslee AM, Keogh CL, Fowler AE and Griffen BD (2015) Assessing the effects of trematode infection on invasive green crabs in eastern North America. *PLoS One* **10**, e0128674.

Blanar CA, Munkittrick KR, Houlahan J, MacLatchy DL and Marcogliese DJ (2009) Pollution and parasitism in aquatic animals: a meta-analysis of effect size. *Aquatic Toxicology* **93**, 18–28.

Blanar CA, Marcogliese DJ and Couillard CM (2011) Natural and anthropogenic factors shape metazoan parasite community structure in mummichog (*Fundulus heteroclitus*) from two estuaries in New Brunswick, Canada. *Folia Parasitologica* **58**, 240–2488.

Braicovich PE, Ieno EN, Sáez M, Despos J and Timi JT (2016) Assessing the role of host traits as drivers of the abundance of long-lived parasites in fish stock assessment studies. *Journal of Fish Biology* **89**, 2419–2433.

Britton JR (2013) Introduced parasites in food webs: new species, shifting structures? *Trends in Ecology & Evolution* **28**, 93–99.

Broeg K, Zander S, Diamant A, Körting W, Krüner G, Paperna I and Westernhagen HV (1999) The use of fish metabolic, pathological and parasitological indices in pollution monitoring. *Helgoland Marine Research* **53**, 171–194.

Broglia A and Kapel C (2011) Changing dietary habits in a changing world: emerging drivers for the transmission of foodborne parasitic zoonoses. *Veterinary Parasitology* **182**, 2–13.

Brooks DR and Hoberg EP (2007) How will global climate change affect parasite–host assemblages? *Trends in Parasitology* **23**, 571–574.

Buchmann K and Mehrdana F (2016) Effects of anisakid nematodes *Anisakis simplex* (s.l.), *Pseudoterranova decipiens* (s.l.) and *Contracaecum osculatum* (s.l.) on fish and consumer health. *Food and Waterborne Parasitology* **4**, 13–22.

Byers JE (2020) Effects of climate change on parasites and disease in estuarine and nearshore environments. *PLoS Biology* **18**, e3000743.

Byers JE and Goldwasser L (2001) Exposing the mechanism and timing of impact of nonindigenous species on native species. *Ecology* **82**, 1330–1343.

Cantatore DMP and Timi JT (2015) Marine parasites as biological tags in South American Atlantic waters, current status and perspectives. *Parasitology* **142**, 5–24.

Carlson CJ, Burgio KR, Dougherty ER, Phillips AJ, Bueno VM, Clements CF, Castaldo G, Dallas TA, Cizauskas CA, Cumming GS, Doña J, Harris NC, Jovani R, Mironov S, Muellerklein OC, Proctor HC and Getz WM (2017) Parasite biodiversity faces extinction and redistribution in a changing climate. *Science Advances* **3**, e1602422.

Cataudella S, Crosetti D and Massa F (eds) (2015) *Mediterranean Coastal Lagoons: Sustainable Management and Interactions among Aquaculture,*

Capture Fisheries and the Environment Studies and Reviews. General Fisheries Commission for the Mediterranean. No. 95. Rome: FAO.

Cavaleiro FI and Santos MJ (2009) Seasonality of metazoan ectoparasites in marine European flounder *Platichthys flesus* (Teleostei: Pleuronectidae). *Parasitology* **136**, 855–865.

Chai JY (2014) *Heterophyes heterophyes*. In Motarjemi Y, Moy GG and Todd CD (eds), *Encyclopedia of Food Safety*, Vol. **2**. Amsterdam, Boston, Heidelberg, London, New York, Oxford, Paris, San Diego, San Francisco, Singapore, Sydney, Tokyo: Academic Press, pp. 158–163.

Chai JY and Jung BK (2017) Fishborne zoonotic heterophyid infections: an update. *Food and Waterborne Parasitology* **8–9**, 33–63.

Chalkowski K, Lepczyk CA and Zohdy S (2018) Parasite ecology of invasive species: conceptual framework and new hypotheses. *Trends in Parasitology* **34**, 655–663.

Chapman JW, Dumbauld BR, Itani G and Markham JC (2012) An introduced Asian parasite threatens northeastern Pacific estuarine ecosystems. *Biological Invasions* **14**, 1221–1236.

Clavero M and Garcia-Berthou E (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution* **20**, 110.

Cognetti G and Maltagliati F (2000) Biodiversity and adaptive mechanisms in brackish water fauna. *Marine Pollution Bulletin* **40**, 7–14.

Cohen AN and Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. *Science (New York, N.Y.)* **279**, 555–558.

Combes C (2001) *Parasitism: The Ecology and Evolution of Intimate Interactions*. Chicago, IL: University of Chicago Press.

Cone DK (1995) Monogenea (Phylum Platyhelminthes). In Woo PTK (ed.), *Fish Diseases and Disorders, Vol. 1, Protozoan and Metazoan Infections*. Wallingford: CABI Publishing, pp. 289–327.

Costa JL, Marques JF, Alves J, Gamito R, Fonseca VF, Goncalves CI, Cabral HN and Costa MJ (2012) Is parasitism in fish a good metric to assess ecological water quality in transitional waters? What can be learned from two estuarine resident species? *Ecological Indicators* **19**, 154–160.

Cross JH (1992) Intestinal capillariasis. *Clinical Microbiology Reviews* **5**, 120–129.

Cross JH and Basaca-Sevilla V (1991) *Capillariasis philippinensis*: a fishborne parasitic zoonosis. *The Southeast Asian Journal of Tropical Medicine and Public Health* **22**(suppl), 153–157.

Crotti M (2013) Digenetic trematodes: an existence as parasites. Brief general overview. *Microbiologia Medica* **28**, 97–101.

Culurgioni J, Figus V, Cabiddu S, De Murtas R, Cau A and Sabatini A (2015) Larval helminth parasites of fishes and shellfishes from Santa Gilla lagoon (Sardinia, Western Mediterranean), and their use as bioecological indicators. *Estuaries and Coasts* **38**, 1505–1519.

Cunha KN, Domingues MV, Cunha LDS and Nunes ZMP (2021) Parasitic monogenoideans of *Sciades herzbergii* as bioindicators of environmental quality in Amazonian estuarines ecosystems. *Brazilian Journal of Veterinary Parasitology* **30**, e024220.

Curio E (1988) Behavior and parasitism. In Mehlhorn H (ed.), *Parasitology in Focus*. New York: Springer-Verlag, pp. 149–160.

Dezfuli BS, Giari L, Castaldelli G, Lanzoni M, Rossi R, Lorenzoni M and Kennedy CR (2014) Temporal and spatial changes in the composition and structure of helminth component communities in European eels *Anguilla anguilla* in an Adriatic coastal lagoon and some freshwaters in Italy. *Parasitology Research* **113**, 113–120.

Díaz Camacho SP, de la Cruz-Otero M, Zazueta-Ramos ML, Bojórquez-Contreras A, Sicairos-Félix J, Campista-León S, Guzmán-Loreto R, Delgado-Vargas F, León-Règagnon V and Nawa Y (2008) Identification of estuarine fish *Dormitator latifrons* as an intermediate host and *Eleotris picta* as a paratenic host for *Gnathostoma binucleatum* in Sinaloa, Mexico. *Parasitology Research* **103**, 1421–1425.

Douglas EJ, Lohrer AM and Pilditch CA (2019) Biodiversity breakpoints along stress gradients in estuaries and associated shifts in ecosystem interactions. *Scientific Reports* **9**, 17567.

Dunne JA, Lafferty KD, Dobson AP, Hechinger RF, Kuris AM, Martínez ND, McLaughlinm JP, Muritsen KN, Poulin R, Reises K, Stouffer DB, Thieltges DW, Williams RJ and Zander CD (2013) Parasites affect food web structure primarily through increased diversity and complexity. *PLoS Biology* **11**, e1001579.

EFSA (2010) Scientific opinion of the panel on biological hazards on risk assessment of parasites in fishery products. *EFSA Journal* **8**, 91.

Elliott M and McLusky DS (2002) The need for definitions in understanding estuaries. *Estuarine, Coastal and Shelf Science* **55**, 815–827.

Elliott M and Quintino V (2007) The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Marine Pollution Bulletin* **54**, 640–645.

Esch GW and Fernández JC (1993) *A Functional Biology of Parasitism*, 1st Edn. London, UK: Chapman & Hall.

European Communities (2000) Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for community action in the field of water policy. *Official Journal of the European Communities* **43**, 1–72.

Fajer-Ávila EJ, García-Vásquez A, Plascencia-González H, Ríos-Sicairos J, Parra LM and Betancourt-Lozano M (2006) Copepods and larvae of nematodes parasitizing the white mullet *Mugil curema* (Valenciennes, 1836): indicators of anthropogenic impacts in tropical coastal lagoons? *Environmental Monitoring and Assessment* **122**, 221–237.

Falkenberg JM, Golzio JESA, Pessanha A, Patrício J, Vendel AL and Lacerda ACF (2019) Gill parasites of fish and their relation to host and environmental factors in two estuaries in northeastern Brazil. *Aquatic Ecology* **53**, 109–118.

Fernández Sánchez JL, Le Breton A, Brun E, Vendramin N, Spiliopoulos G, Furones D and Basurco B (2022) Assessing the economic impact of diseases in Mediterranean grow-out farms culturing European sea bass. *Aquaculture* **547**, 737530.

Frainer A, McKie BG, Amundsen PA, Knudsen R and Lafferty KD (2018) Parasitism and the biodiversity–functioning relationship. *Trends in Ecology & Evolution* **33**, 260–268.

Froese R and Pauly D (2004) FishBase, World Wide Web electronic publication, version (12/2004). Available at www.fishbase.org.

Gendron AD and Marcogliese DJ (2017) Enigmatic decline of a common fish parasite (*Diplostomum* spp.) in the St. Lawrence river: evidence for a dilution effect induced by the invasive round goby. *International Journal for Parasitology: Parasites and Wildlife* **6**, 402–411.

Giari L, Ruehle B, Fano EA, Castaldelli G and Poulin R (2020) Temporal dynamics of species associations in the parasite community of European eels, *Anguilla anguilla*, from a coastal lagoon. *International Journal for Parasitology: Parasites and Wildlife* **12**, 67–75.

Giari L, Castaldelli G, Gavioli A, Lanzoni M and Fano EA (2021) Long-term ecological analysis of *Anguillicola crassus* occurrence and impact on the European eel population in a Mediterranean lagoon (North Italy). *Estuarine, Coastal and Shelf Science* **249**, 107117.

Goedknegt MA, Feis ME, Wegner KM, Luttikhuizen PC, Buschbaum C, Camphuysen KC, van der Meer J and Thieltges DW (2016) Parasites and marine invasions: ecological and evolutionary perspectives. *Journal of Sea Research* **113**, 11–27.

González-Castro M, Rosso JJ, Delpiani SM, Mabragaña E and Diaz de Astarloa JM (2019) Inferring boundaries among fish species of the new world silversides (Atherinopsidae; genus *Odontesthes*): new evidences of incipient speciation between marine and brackish populations of *Odontesthes argentinensis*. *Genetica* **147**, 217–229.

Harrison IJ (1995) Mugilidae. Lisas. In Fischer W, Krupp F, Schneider W, Sommer C, Carpenter KE and Niem V (eds), *Guia FAO para Identification de Especies para lo Fines de la Pesca. Pacifico Centro-Oriental*. Rome: FAO, pp. 1293–1298.

Harvell CD, Mitchell CE, Ward JR, Altizer S, Dobson AP, Ostfeld RS and Samuel MD (2002) Climate warming and disease risks for terrestrial and marine biota. *Science (New York, N.Y.)* **296**, 2158–2162.

Hatcher MJ, Dick JTA and Dunn AM (2012) Diverse effects of parasites in ecosystems: linking interdependent processes. *Frontiers in Ecology and the Environment* **10**, 186–194.

Hechinger RF and Lafferty KD (2005) Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. *Proceedings of the Royal Society of London B: Biological Sciences* **272**, 1059–1066.

Hechinger RF, Lafferty KD, Dobson AP, Brown JH and Kuris AM (2011) A common scaling rule for abundance, energetics, and production of parasitic and free-living species. *Science (New York, N.Y.)* **333**, 445–448.

Hudson P (2005) Introduction – Parasites, diversity, and the ecosystem. In Thomas F, Renaud F and Guegan J-F (eds), *Parasitisms & Ecosystems*. Oxford, UK: Oxford University Press, pp. 1–12.

Hudson PJ, Dobson AP and Newborn P (1998) Prevention of population cycles by parasite removal. *Science (New York, N.Y.)* **282**, 2256–2258.

Hudson PJ, Dobson AP and Lafferty KD (2006) Is a healthy ecosystem one that is rich in parasites? *Trends in Ecology & Evolution* **21**, 381–385.

Huspeni TC, Hechinger RF and Lafferty KD (2005) Trematode parasites as estuarine indicators: opportunities, applications and comparisons with conventional community approaches. In Bortone S (ed.), *Estuarine Indicators*. Boca Raton: CRC, pp. 297–314.

IPCC (2021) Summary for policymakers. In Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, Caud N, Chen Y, Goldfarb L, Gomis MI, Huang M, Leitzell K, Lonnoy E, Matthews JBR, Maycock TK, Waterfield T, Yelekçi O, Yu R and Zhou B (eds), *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK and New York, NY, USA: Cambridge University Press, pp. 3–32. Available at doi: 10.1017/9781009157896.001.

Irigoitia MM, Incorvaia IS and Timi JT (2017) Evaluating the usefulness of natural tags for host population structure in chondrichthyans: parasite assemblages of *Sympterygia bonapartii* (Rajiformes: Arhynchobatidae) in the Southwestern Atlantic. *Fisheries Research* **195**, 80–90.

Jeremiah CJ, Harangozo CS and Fuller AJ (2011) Gnathostomiasis in remote northern Western Australia: the first confirmed cases acquired in Australia. *Medical Journal of Australia* **195**, 42–44.

Johnson PT, Dobson A, Lafferty KD, Marcogliese DJ, Memmott J, Orlofske SA, Poulin R and Thieltges DW (2010) When parasites become prey: ecological and epidemiological significance of eating parasites. *Trends in Ecology & Evolution* **25**, 362–371.

Kaplan AT, Rebhal S, Lafferty KD and Kuris AM (2009) Small estuarine fishes feed on large trematode cercariae: lab and field investigations. *Journal of Parasitology* **95**, 477–480.

Kelly DW, Paterson RA, Townsend CR, Poulin R and Tompkins DM (2009*a*) Parasite spillback: a neglected concept in invasion ecology? *Ecology* **90**, 2047–2056.

Kelly DW, Paterson RA, Townsend CR, Poulin R and Tompkins DM (2009*b*) Has the introduction of brown trout altered disease patterns in native New Zealand fish? *Freshwater Biology* **54**, 1805–1818.

Kennedy CR (2007) The pathogenic helminth parasites of eels. *Journal of Fish Diseases* **30**, 319–334.

Kesting V and Zander CD (2000) Alteration of the metazoan parasite faunas in the brackish Schlei fjord (Northern Germany, Baltic Sea). *International Review of Hydrobiology* **85**, 325–340.

Kesting V, Gollasch S and Zander CD (1996) Parasite communities of the Schlei fjord (Baltic coast of northern Germany). *Helgoländer Meeresuntersuchungen* **50**, 477–496.

Kinne O (1984) *Diseases of Marine Animals*. Hamburg, Germany: Biologische Anstalt Helgoland.

Kirk RS (2003) The impact of *Anguillicola crassus* on European eels. *Fisheries Management and Ecology* **10**, 385–394.

Krause J and Godin JGJ (1994) Influence of parasitism on the shoaling behaviour of banded killifish, *Fundulus diaphanus*. *Canadian Journal of Zoology* **72**, 1775–1177.

Kuchta R, Radačovská A, Bazsalovicsová E, Viozzi G, Semenas L, Arbetman M and Scholz T (2019) Host switching of zoonotic broad fish tapeworm (*Dibothriocephalus latus*) to salmonids, Patagonia. *Emerging Infectious Diseases* **25**, 2156.

Kuris AM, Hechinger RF, Shaw JC, Whitney KL, Aguirre-Macedo L, Boch CA, Dobson AP, Dunham EJ, Fredensborg BL, Huspeni TC, Lorda J, Mababa L, Mancini FT, Mora B, Pickering M, Talhouk NL, Torchin ME and Lafferty KD (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* **454**, 515–518.

Lafferty KD (1997) Environmental parasitology: what can parasites tell us about human impacts on the environment? *Parasitology Today* **13**, 251–255.

Lafferty KD (2008) Ecosystem consequences of fish parasites. *Journal of Fish Biology* **73**, 2083–2093.

Lafferty KD and Kuris AM (2009) Parasites reduce food web robustness because they are sensitive to secondary extinction as illustrated by an invasive estuarine snail. *Philosophical Transactions of the Royal Society B* **364**, 1659–1663.

Lafferty KD and Morris AK (1996) Altered behavior of parasitized killifish increases susceptibility to predation by bird final hosts. *Ecology* **77**, 1390–1397.

Lafferty KD, Porter JW and Ford SE (2004) Are diseases increasing in the ocean? *Annual Review of Ecology, Evolution, and Systematics* **35**, 31–54.

Lafferty KD, Dobson AP and Kuris AM (2006*a*) Parasites dominate food web links. *Proceedings of the National Academy of Sciences* **103**, 11211–11216.

Lafferty KD, Hechinger RF, Shaw JC, Whitney KL and Kuris AM (2006*b*) Food webs and parasites in a salt marsh ecosystem. In Collinge S and Ray C (eds), *Disease Ecology: Community Structure and Pathogen Dynamics*. Oxford: Oxford University Press, pp. 119–134.

Lafferty KD, Allesina S, Arim M, Briggs CJ, De Leo G, Dobson AP, Dunne JA, Johnson PTJ, Kuris AM, Marcogliese DJ, Martinez ND, Memmott J, Marquet PA, McLaughlin JP, Mordecai EA, Pascual M, Poulin R and Thieltges DW (2008) Parasites in food webs: the ultimate missing links. *Ecology Letters* **11**, 533–546.

Lafferty KD, Harvell CD, Conrad JM, Friedman CS, Kent ML, Kuris AM, Powell EN, Rondeau D and Saksida SM (2015) Infectious diseases affect marine fisheries and aquaculture economics. *Annual Review of Marine Science* **7**, 471–496.

Laffon-Leal SM, Vidal-Martinez VM and Arjona-Torres G (2000) 'Cebiche' – a potential source of human anisakiasis in Mexico? *Journal of Helminthology* **74**, 151–154.

Landsberg JH, Blakesley BA, Reese RO, McRae G and Forstchen PR (1998) Parasites of fish as indicators of environmental stress. *Environmental Monitoring and Assessment* **51**, 211–232.

Lanfranchi AL, Braicovich PE, Cantatore DM, Alarcos AJ, Luque JL and Timi JT (2016) Ecotonal marine regions–ecotonal parasite communities: helminth assemblages in the convergence of masses of water in the Southwestern Atlantic Ocean. *International Journal for Parasitology* **46**, 809–818.

Lefebvre F and Crivelli AJ (2004) Anguillicolosis: dynamics of the infection over two decades. *Diseases of Aquatic Organisms* **62**, 227–232.

Lefebvre F and Crivelli AJ (2012) Salinity effects on anguillicolosis in Atlantic eels: a natural tool for disease control. *Marine Ecology Progress Series* **471**, 193–202.

Leonardos I and Trilles JP (2003) Host–parasite relationships: occurrence and effect of the parasitic isopod *Mothocya epimerica* on sand smelt *Atherina boyeri* in the Mesolongi and Etolikon lagoons (W. Greece). *Diseases of Aquatic Organisms* **54**, 243–251.

Levsen A and Lunestad BT (2010) *Anisakis simplex* third stage larvae in Norwegian spring spawning herring (*Clupea harengus* L.), with emphasis on larval distribution in the flesh. *Veterinary Parasitology* **171**, 247–253.

Levy E, Rossin MA, Braicovich PE and Timi JT (2020) *Profilicollis chasmagnathi* (Acanthocephala) parasitizing freshwater fishes: paratenicity and an exception to the phylogenetic conservatism of the genus? *Parasitology Research* **119**, 3957–3966.

Levy E, Canel D, Rossin MA, González-Castro M and Timi JT (2021) Parasite assemblages as indicators of an incipient speciation process of *Odontesthes argentinensis* in an estuarine environment. *Estuarine, Coastal and Shelf Science* **250**, 107168.

Llarena-Reino M, González ÁF, Vello C, Outeiriño L and Pascual S (2012) The accuracy of visual inspection for preventing risk of *Anisakis* spp. infection in unprocessed fish. *Food Control* **23**, 54–58.

Lowe ML, Morrison MA and Taylor RB (2015) Harmful effects of sediment-induced turbidity on juvenile fish in estuaries. *Marine Ecology Progress Series* **539**, 241–254.

Maceda-Veiga A, Mac Nally R, Green AJ, Poulin R and de Sostoa A (2019) Major determinants of the occurrence of a globally invasive parasite in riverine fish over large-scale environmental gradients. *International Journal for Parasitology* **49**, 625–634.

Machut LS and Limburg KE (2008) *Anguillicola crassus* infection in *Anguilla rostrata* from small tributaries of the Hudson river watershed, New York, USA. *Diseases of Aquatic Organisms* **79**, 37–45.

Macnab V and Barber I (2012) Some (worms) like it hot: fish parasites grow faster in warmer water, and alter host thermal preferences. *Global Change Biology* **18**, 1540–1548.

MacNeil C, Dick JT, Hatcher MJ, Terry RS, Smith JE and Dunn AM (2003) Parasite-mediated predation between native and invasive amphipods. *Proceedings of the Royal Society of London B: Biological Sciences* **270**, 1309–1314.

Maillard C (1976) *Distomatoses de poissons en milieu lagunaire* (PhD thesis). University of Montpellier, Montpellier, France.

Marcogliese DJ (2001) Implications of climate change for parasitism of animals in the aquatic environment. *Canadian Journal of Zoology* **79**, 1331–1352.

Marcogliese DJ (2004) Parasites: small players with crucial roles in the ecological theatre. *EcoHealth* **1**, 151–164.

Marcogliese DJ (2005) Parasites of the superorganism: are they indicators of ecosystem health? *International Journal for Parasitology* **35**, 705–716.

Marcogliese DJ (2008) The impact of climate change on the parasites and infectious diseases of aquatic animals. *Revue scientifique et technique* 27, 467–484.

Marcogliese DJ (2016) The distribution and abundance of parasites in aquatic ecosystems in a changing climate: more than just temperature. *Integrative and Comparative Biology* 56, 611–619.

Marcogliese DJ and Cone DK (1997) Parasite communities as indicators of ecosystem stress. *Parassitologia* 39, 227–232.

Martínez-Megías C and Rico A (2022) Biodiversity impacts by multiple anthropogenic stressors in Mediterranean coastal wetlands. *Science of the Total Environment* 818, 151712.

Mattiucci S and Nascetti G (2008) Advances and trends in the molecular systematics of anisakid nematodes, with implications for their evolutionary ecology and host–parasite co-evolutionary processes. *Advances in Parasitology* 66, 47–148.

McCarthy J and Moore T (2000) Emerging helminth zoonoses. *International Journal for Parasitology* 30, 1351–1360.

McClelland G (2002) The trouble with sealworms (*Pseudoterranova decipiens* species complex, Nematoda): a review. *Parasitology* 124, S183–S203.

McLusky DS and Elliott M (2007) Transitional waters: a new approach, semantics or just muddying the waters? *Estuarine, Coastal and Shelf Science* 71, 359–363.

Médoc V, Firmat C, Sheath DJ, Pegg J, Andreou D and Britton JR (2017) Parasites and biological invasions: predicting ecological alterations at levels from individual hosts to whole networks. *Advances in Ecological Research* 57, 1–54.

Mehrdana F, Bahlool QZ, Skov J, Marana MH, Sindberg D, Mundeling M, Overgaard BC, Korbut R, Strøm SB, Kania PW and Buchmann K (2014) Occurrence of zoonotic nematodes *Pseudoterranova decipiens*, *Contracaecum osculatum* and *Anisakis simplex* in cod (*Gadus morhua*) from the Baltic Sea. *Veterinary Parasitology* 205, 581–587.

Meli P, Rey Benayas JM, Balvanera P and Martínez Ramos M (2014) Restoration enhances wetland biodiversity and ecosystem service supply, but results are context-dependent: a meta-analysis. *PLoS One* 9, e93507.

Mentz MB, Lanner M, Fagundes N, Sauter IP and Marques LS (2016) Ectoparasites on *Mugil liza* (Osteichthyes: Mugilidae) from the Tramandai-Armazém lagoon system, Southern Brazil. *Pan-American Journal of Aquatic Sciences* 11, 130–134.

Mercado R, Torres P, Munoz V and Apt W (2001) Human infection by *Pseudoterranova decipiens* (Nematoda Anisakidae) in Chile: report of seven cases. *Memórias do Instituto Oswaldo Cruz* 96, 653–655.

Molnar K, Szekely C and Baska F (1991) Mass mortality of eel in lake Balaton due to *Anguillicola crassus* infection. *Bulletin of the European Association of Fish Pathologists* 11, 211–212.

Morales-Serna FN, Rodríguez-Santiago MA, Gelabert R and Flores-Morales LM (2019) Parasites of fish *Poecilia velifera* and their potential as bioindicators of wetland restoration progress. *Helgoland Marine Research* 73, 1.

Morozińska-Gogol J (2009) Alien species of fish parasites in the coastal lakes and lagoons of the southern Baltic. *Oceanologia* 51, 105–115.

Mouritsen KN and Poulin R (2002) Parasitism, community structure and biodiversity in intertidal ecosystems. *Parasitology* 124, S101–S117.

Nachev M and Sures B (2016) Environmental parasitology: parasites as accumulation bioindicators in the marine environment. *Journal of Sea Research* 113, 45–50.

Nawa Y (1991) Historical review and current status of gnathostomiasis in Asia. *The Southeast Asian Journal of Tropical Medicine and Public Health* 22 (suppl), 217–219.

Newton A, Icely J, Cristina S, Brito A, Cardoso AC, Colijn F, Riva SD, Gertz F, Hansen JW, Holmer M, Ivanova K, Leppäkoski E, Canu DM, Mocenni C, Mudge S, Murray N, Pejrup M, Razinkovas A, Reizopoulou S, Pérez-Ruzafa A, Schernewski G, Schubert H, Carr L, Solidoro C, Viaroli P and Zaldívar JM (2014) An overview of ecological status, vulnerability and future perspectives of European large shallow, semi-enclosed coastal systems, lagoons and transitional waters. *Estuarine, Coastal and Shelf Science* 140, 95–122.

Newton A, Brito AC, Icely JD, Derolez V, Inês C, Angus S, Schernewski G, Inácio M, Lillebø AI, Sousa AI, Béjaoui B, Solidoro C, Tosic M, Cañedo-Argüelles M, Yamamuro M, Reizopoulou S, Tseng H-C, Canu D, Roselli L, Maanan M, Cristina S, Ruiz-Fernández AC, de Lima RF, Kjerfve B, Rubio-Cisneros N, Pérez-Ruzafa A, Marcos C, Pastres R, Pranovi F, Snoussi M, Turpie J, Tuchkovenko Y, Dyack B, Brookes J, Povilanskas R and Khokhlov V (2018) Assessing, quantifying and valuing the ecosystem services of coastal lagoons. *Journal for Nature Conservation* 44, 50–65.

Nickol BB, Crompton DWT and Searle DW (1999) Reintroduction of *Profilicollis* Meyer, 1931, as a genus in Acanthocephala: significance of the intermediate host. *Journal of Parasitology* 85, 716–718.

Nickol BB, Heard RW and Smith NF (2002) Acanthocephalans from crabs in the southeastern US, with the first intermediate hosts known for *Arhythmorhynchus frassoni* and *Hexaglandula corynosoma*. *Journal of Parasitology* 88, 79–83.

Odum EP (1959) *Fundamentals of Ecology*, 2nd Edn. Philadelphia, USA: Saunders.

Ogata K, Nawa Y, Akahane H, Diaz Camacho SP, Lamothe-Argumedo R and Cruz-Reyes A (1998) Short report: gnathostomiasis in Mexico. *The American Journal of Tropical Medicine and Hygiene* 58, 316–318.

O'Shaughnessy KA, Harding JM and Burge EJ (2014) Ecological effects of the invasive parasite *Loxothylacus panopaei* on the flatback mud crab *Eurypanopeus depressus* with implications for estuarine communities. *Bulletin of Marine Science* 90, 611–621.

Overstreet RM (2007) Effects of a hurricane on fish parasites. *Parassitologia* 49, 161–198.

Overstreet RM and Howse HD (1977) Some parasites and diseases of estuarine fishes in polluted habitats of Mississippi. *Annals of the New York Academy of Sciences* 298, 427–462.

Palm HW and Rückert S (2009) A new approach to visualize ecosystem health by using parasites. *Parasitology Research* 105, 539–553.

Palstra AP, Heppener DFM, van Ginneken VJT, Szekely C and van den Thillart GEEJM (2007) Swimming performance of silver eels is severely impaired by the swim-bladder parasite *Anguillicola crassus*. *Journal of Experimental Marine Biology and Ecology* 352, 244–256.

Paperna I, Colorni A, Gordin H and Kissil GW (1977) Diseases of *Sparus aurata* in marine culture at Elat. *Aquaculture* 10, 195–213.

Paredes-Trujillo A, Velázquez-Abunader I, Papiol V, Rodolfo E and Vidal-Martínez VM (2021) Negative effect of ectoparasite burdens on the condition factor from farmed tilapia *Oreochromis niloticus* in the Yucatan, Mexico. *Veterinary Parasitology* 292, 109393.

Paull SH, LaFonte BE and Johnson PT (2012) Temperature-driven shifts in a host-parasite interaction drive nonlinear changes in disease risk. *Global Change Biology* 18, 3558–3567.

Pech D, Vidal-Martínez VM, Aguirre-Macedo ML, Gold-Bouchot G, Herrera-Silveira J, Zapata-Pérez O and Marcogliese DJ (2009) The checkered puffer (*Spheroides testudineus*) and its helminths as bioindicators of chemical pollution in Yucatan coastal lagoons. *Science of the Total Environment* 407, 2315–2324.

Peterman MA and Posadas BC (2019) Direct economic impact of fish diseases on the east Mississippi catfish industry. *North American Journal of Aquaculture* 81, 222–229.

Poulin R (2006) Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. *Parasitology* 132, 143–151.

Poulin R (2011) The many roads to parasitism: a tale of convergence. *Advances in Parasitology* 74, 1–40.

Poulin R (2017) Invasion ecology meets parasitology: advances and challenges. *International Journal for Parasitology: Parasites and Wildlife* 6, 361–363.

Prenter J, MacNeil C, Dick JT and Dunn AM (2004) Roles of parasites in animal invasions. *Trends in Ecology & Evolution* 19, 385–390.

Preston DL, Mischler JA, Townsend AR and Johnson PT (2016) Disease ecology meets ecosystem science. *Ecosystems* 19, 737–748.

Radwan M (2022) Vital economic threat of predatory birds and parasites to cultivated fishes in Egypt. *Aquaculture* 548, 737666.

Rahmati AR, Kiani B, Afshari A, Moghaddas E, Williams M and Shamsi S (2020) World-wide prevalence of Anisakis larvae in fish and its relationship to human allergic anisakiasis: a systematic review. *Parasitology Research* 119, 3585–3594.

Rashnavadi M, Lymbery AJ, Beatty SJ and Morgan DL (2014) Ecological response of an estuarine atherinid to secondary salinisation in south-western Australia. *Journal of the Royal Society of Western Australia* 97, 343–353.

Ray GC (2005) Connectivities of estuarine fishes to the coastal realm. *Estuarine, Coastal and Shelf Science* 64, 18–32.

Rojas-Sánchez A, Lamothe-Argumedo MR and García-Prieto L (2014) Parasitosis transmitidas por el consumo de peces en México. *Ciencia* 65, 83–87.

Rolbiecki J and Rokicki J (2002) III-stage *Anisakis simplex* (Rudolphi, 1809) (Nematoda; Anisakidae) larvae in herring caught in autumn from the Polish part of the Vistula Lagoon. *Acta Scientiarum Polonorum* 1, 105–110.

Rosenqvist G and Johansson K (1995) Male avoidance of parasitized females explained by direct benefits in a pipefish. *Animal Behaviour* 49, 1039–1045.

Ruiz GM, Carlton JT, Grosholz ED and Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *American Zoologist* 37, 621–632.

Sayyaf Dezfuli B, Maestri C, Lorenzoni M, Carosi A, Maynard BJ and Bosi G (2021) The impact of *Anguillicoloides crassus* (Nematoda) on European eel swimbladder: histopathology and relationship between neuroendocrine and immune cells. *Parasitology* 148, 612–622.

Schultz ET and McCormick SD (2012) Euryhalinity in an evolutionary context. *Fish Physiology* 32, 477–533.

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšec P, Winter M, Arianoustou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker B, Weigelt P, Yamanaka T and Essl F (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8, 14435.

Shamsi S (2019) Seafood-borne parasitic diseases: a 'one-health' approach is needed. *Fishes* 4, 9.

Shamsi S, Steller E and Zhu X (2021) The occurrence and clinical importance of infectious stage of *Echinocephalus* (Nematoda: Gnathostomidae) larvae in selected Australian edible fish. *Parasitology International* 83, 102333.

Shinn AP, Pratoomyot J, Bron JE, Paladini G, Brooker EE and Brooker AJ (2015) Economic costs of protistan and metazoan parasites to global mariculture. *Parasitology* 142, 196–270.

Snigirov S, Kvach Y, Goncharov O, Sizo R and Sylantyev S (2019) Hydrology and parasites: what divides the fish community of the lower Dniester and Dniester estuary into three? *Estuarine, Coastal and Shelf Science* 217, 120–131.

Sosa-Medina T, Vidal-Martinez VM and Aguirre-Macedo ML (2015) Metazoan parasites of fishes from the Celestun coastal lagoon, Yucatan, Mexico. *Zootaxa* 4007, 529–544.

Sproston NG and Hartley PHT (1941) The ecology of some parasitic copepods of gadoids and other fishes. *Journal of the Marine Biological Association of the United Kingdom* 25, 361–392.

Stumbo AD and Poulin R (2016) Possible mechanism of host manipulation resulting from a diel behaviour pattern of eye-dwelling parasites? *Parasitology* 143, 1261–1267.

Sures B and Nachev M (2015) Environmental parasitology. In Mehlhorn H (ed.), *Encyclopedia of Parasitology*. Berlin, Heidelberg: Springer-Verlag, pp. 1–4. Available at doi: 10.1007/978-3-642-27769-6_1076-2.

Sures B, Nachev M, Selbach C and Marcogliese DJ (2017) Parasite responses to pollution: what we know and where we go in 'environmental parasitology'. *Parasites & Vectors* 10, 1–19.

Syvitski JPM, Vörösmarty CJ, Kettner AJ and Green P (2005) Impact of humans on the flux of terrestrial sediment to the global coastal ocean. *Science (New York, N.Y.)* 308, 376–380.

Tandon V, Shylla JA, Ghatani S, Athokpam VD and Sahu R (2015) Neglected tropical diseases: trematodiases – the Indian scenario. *Proceedings of the National Academy of Sciences, India Section B: Biological Sciences* 85, 901–907.

Taraschewski H (1984) Heterophyiasis, an intestinal fluke infection of man and vertebrates transmitted by euryhaline gastropods and fish. *Helgolander Meeresunters* 37, 463–478.

Tavares-Dias M and Martins ML (2017) An overall estimation of losses caused by diseases in the Brazilian fish farms. *Journal of Parasitic Diseases* 41, 913–918.

Thieltges DW, Amundsen P-A, Hechinger RF, Johnson PTJ, Lafferty KD, Mouritsen KN, Preston DL, Reise K, Zander CD and Poulin R (2013) Parasites as prey in aquatic food webs: implications for predator infection and parasite transmission. *Oikos* 122, 1473–1482.

Thomas F, Cezilly F, De Meeüs T, Crivelli A and Renaud F (1997) Parasitism and ecology of wetlands: a review. *Estuaries* 20, 646–654.

Thomas F, Poulin R, de Meeüs T, Guégan J-F and Renaud F (1999) Parasites and ecosystem engineering: what roles could they play? *Oikos* 84, 167–171.

Timi JT (2007) Parasites as biological tags for stock discrimination in marine fish from South American Atlantic waters. *Journal of Helminthology* 81, 107–111.

Timi JT and Poulin R (2020) Why ignoring parasites in fish ecology is a mistake. *International Journal for Parasitology* 50, 755–761.

Timi JT, Luque JL and Poulin R (2010) Host ontogeny and the temporal decay of similarity in parasite communities of marine fish. *International Journal for Parasitology* 40, 963–968.

Timi JT, Rossin MA, Alarcos AJ, Braicovich PE, Cantatore DMP and Lanfranchi AL (2011) Fish trophic level and the similarity of larval parasite assemblages. *International Journal for Parasitology* 41, 309–316.

Torchin ME, Lafferty KD and Kuris AM (2002) Parasites and marine invasions. *Parasitology* 124, 137–151.

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ and Kuris AM (2003) Introduced species and their missing parasites. *Nature* 421, 628–630.

Troost K (2010) Causes and effects of a highly successful marine invasion: case-study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. *Journal of Sea Research* 64, 145–165.

Vagianou S, Athanassopoulou F, Ragias V, Di Cave D, Leontides L and Golomazou E (2006) Prevalence and pathology of ectoparasites of Mediterranean sea bream and sea bass reared under different environmental and aquaculture conditions. *The Israeli Journal of Aquaculture – Bamidgeh* 58, 78–88.

Valtonen ET, Pulkkinen K, Poulin R and Julkunen M (2001) The structure of parasite component communities in brackish water fishes of the northeastern Baltic Sea. *Parasitology* 122, 471–481.

Velloso AL and Pereira J (2010) Influence of ectoparasitism on the welfare of *Micropogonias furnieri*. *Aquaculture* 310, 43–46.

Waikagul J and Diaz Chamacho SP (2007) Gnathostomiasis. In Darwin KD (ed.), *Food-Borne Parasitic Zoonoses, Fish and Plant-Borne Parasites, World Class Parasites*. Berlin: Springer, p. 235.

Wasson K, Zabin CJ, Bedinger L, Diaz MC and Pearse JS (2001) Biological invasions of estuaries without international shipping: the importance of intraregional transport. *Biological Conservation* 102, 143–153.

Weinstein SB and Kuris AM (2016) Independent origins of parasitism in Animalia. *Biology Letters* 12, 20160324.

Whitfield AK (1996) A review of factors influencing fish utilization of South African estuaries. *Transactions of the Royal Society of South Africa* 51, 115–137.

Widmann M (2013) Impact of large-scale environmental features changes on host–parasite interaction in marine and freshwater ecosystems. *BioSciences Master Reviews* 1, 1–9.

Wierzbicka J, Wierzbicki K, Piasecki W and Smietana P (2005) A comparative study on the parasite fauna of perch, *Perca fluviatilis* L., collected from a freshwater coastal lake brackish-water Baltic Sea and the interconnecting canal. *Wiadomości Parazytologiczne* 51, 295–302.

Wonham MJ and Carlton JT (2005) Trends in marine biological invasions at local and regional scales: the Northeast Pacific Ocean as a model system. *Biological Invasions* 7, 369–392.

Wood CL and Johnson PT (2015) A world without parasites: exploring the hidden ecology of infection. *Frontiers in Ecology and the Environment* 13, 425–434.

Wood CL, Lafferty KD and Micheli F (2010) Fishing out marine parasites? Impacts of fishing on rates of parasitism in the ocean. *Ecology Letters* 13, 761–775.

World Health Organization (2004) Report of Joint WHO/FAO Workshop on Food-Borne Trematode Infections in Asia, Ha Noi, Vietnam, 26–28 November, 2002. Geneva, Switzerland: World Health.

Yáñez-Arancibia A, Domínguez ALL and Pauly D (1994) Chapter 12. Coastal lagoons as fish habitats. *Elsevier Oceanography Series* 60, 363–376.

Zander CD (1998) Ecology of host parasite relationships in the Baltic Sea. *Naturwissenschaften* 85, 426–436.

Zander CD, Kollra HG, Antholz B, Meyer W and Westphal D (1984) Small-sized euryhaline fish as intermediate hosts of the digenetic trematode *Cryptocotyle concavum*. *Helgoländer Meeresuntersuchungen* 37, 433–443.

Zhao Q, Bai J, Huang L, Gu B, Lu Q and Gao Z (2016) A review of methodologies and success indicators for coastal wetland restoration. *Ecological Indicators* 60, 442–452.