



Review Paper

# From ecological functions to ecosystem services: linking coastal lagoons biodiversity with human well-being

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**Abstract** In this review we highlight the relevance of biodiversity that inhabit coastal lagoons, emphasizing how species functions foster processes and services associated with this ecosystem. We identified 26 ecosystem services underpinned by ecological functions performed by bacteria and other microbial organisms, zooplankton, polychaetae worms, mollusks, macro-crustaceans, fishes, birds, and aquatic mammals. These groups present high functional redundancy but perform complementary functions that result in distinct ecosystem processes.

Because coastal lagoons are located in the interface between freshwater, marine and terrestrial ecosystems, the ecosystem services provided by the biodiversity surpass the lagoon itself and benefit society in a wider spatial and historical context. The species loss in coastal lagoons due to multiple human-driven impacts affects the ecosystem functioning, influencing negatively the provision of all categories of services (i.e., supporting, regulating, provisioning and cultural). Because animals' assemblages have unequal spatial and temporal distribution in coastal lagoons, it is necessary to adopt ecosystem-level management plans to protect habitat heterogeneity and its biodiversity, ensuring the provision of services for human well-being to multi-actors in the coastal zone.

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## Introduction

Coastal lagoons are inland water bodies isolated from the ocean by a physical barrier, which may be intermittently connected to the sea by one or more restricted inlets (Kjerfve, 1994). These estuarine ecosystems are widely distributed across world's coastlines (Barnes, 1980), usually in human densely populated areas (Gönenç & Wolflin, 2004; El Mahrad et al., 2020). The proximity with urban areas accounts for a variety of non-natural stressors on coastal lagoons, such as eutrophication, input of contaminants, introduction of non-indigenous species and fishery overexploitation (Esteves et al., 2008; Zaldívar et al., 2008; Munaron et al., 2012). Consequently, coastal lagoons are one of the most threatened ecosystems in the world (Newton et al., 2018) and may become more vulnerable with the increasing pressures derived from climate change (Beer & Joyce, 2012).

Although multiple stressors threat coastal lagoons, these ecosystems still underpin human welfare and livelihoods (Newton et al., 2014), providing several ecosystem services, which are functions and products that benefit humans, or yield welfare to society (MEA, 2005). Dozens of provisioning (e.g., food and raw material), regulating (e.g., carbon sequestration and water regulation), supporting (e.g., habitat for species and nutrient cycling) and cultural (e.g., aesthetic and educational values) services are directly

associated with these ecosystems (Newton et al., 2018; Pérez-Ruzafa et al., 2019). The importance of services provided by coastal lagoons is clear to experts worldwide (Newton et al., 2018) and has been increasingly recognized by distinct stakeholders (Sy et al., 2018). Broad recognition of services provided by coastal lagoons is crucial to enhance good management practices through ecosystem approaches, such as the Millennium Ecosystem Assessment (MEA, 2005) and the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES, 2019).

Besides the practical progress in ecosystem services science, the theoretical foundations that guide our understanding about how ecosystem functioning provides ecosystem services must be thoroughly discussed and acknowledged, especially the links between biodiversity and ecosystem services (Haines-Young & Potschin, 2010; Mace et al., 2012). In this context, it is essential to understand the term 'species function', here defined as the role that each biotic component plays in the environment that surrounds it (biotic and abiotic), so that it can refer to the interactions between two objects by cause within an ecological system (Calow, 1987; Fu et al., 2013). Also, it is important to understand the mechanism in which multiple and interactive species functions generate ecosystem processes (Mace et al., 2012), driving to the provision of ecosystem services (Bennett, 2017; Rullens et al., 2019).

For instance, in coastal lagoons, high biodiversity is driven by the remarkable patterns of spatial-temporal variations (Meerhoff et al., 2013; Bellino et al., 2019) derived from the variability of abiotic factors (Basset et al., 2013) in a mosaic of heterogeneous

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habitats (e.g., salt marshes, seagrass meadows, and mangroves; see Bloomfield & Gillanders, 2005). Such high biodiversity in coastal lagoons (Newton et al., 2018) may yield different ecosystem functions (Loreau, 2000; Mace et al., 2012) that may influence the ecosystem structure and processes (Tilman, 2001; Petchey & Gaston, 2006; Rullens et al., 2019), and can explain the vast array of services provided by ecosystems (Balvanera et al., 2006; Pérez-Ruzafa et al., 2019). However, even though well-grounded in theory, understanding the relationships between biodiversity, ecological functions and services in coastal lagoons is incipient since efforts in this direction are scarce (see: Danovaro & Pusceddu, 2007).

This non-systematic review highlights the main characteristics and ecological functions of the aquatic taxon that inhabit coastal lagoons. We cover the following groups: bacteria and other microbial organisms, zooplankton, polychaete worms, mollusks, macro-crustaceans, fishes, birds, and aquatic mammals. By preference, we extracted information from peer reviewed papers with international scope. In the absence of this possibility, we selected reports, books, and book's chapters with international scope. To highlight the role of each group (i.e., their species function), we reviewed species/taxon behavioural (i.e., movements, burrowing, feeding, foraging and migration) and population/group processes (i.e., growth=biomass production, excretion, and recruitment). Then, we related their species functions with ecosystem processes and services in coastal lagoons through cause-effects relationships (Jax, 2005). The designations of the ecosystem services follow the United Nations Millennium Ecosystem Assessment (MEA, 2005). To avoid double-counting in MEA's classification, we highlight how a given species functions might through a causal relationship provide an intermediate (i.e., supporting and regulating) or instead a final ecosystem service (i.e., provision or cultural), considering that the outputs of the former flow indirectly to humans and underpin other final services, which provides direct values and benefits to citizens (DeWitt et al., 2020). From this approach, we emphasized how species functions foster ecosystem processes and services associated with coastal lagoons (Table 1; Fig. 1).

Furthermore, we reviewed how multiple threats impact biodiversity and how this reverberates in the provision of ecosystem services. This review does

not intend to address the whole aquatic biodiversity in coastal lagoons nor to exhaust the ecological functions and their interaction with ecosystem services. Instead, we intend to advance on the understanding of the ecosystem functioning and on the mechanisms that generates the provision of ecosystem services by biodiversity of coastal lagoons.

## Bacteria and other microbial organisms

Prokaryotic communities in coastal lagoons occupy different habitats (i.e., water column, sediments, biofilms on different biotic and abiotic substrates) with varying abundance and diversity (Alonso et al., 2009, 2013; Mohit et al., 2014). They show distinct life strategies in coastal lagoons such that communities that live attached to particles are consistently more diverse than their free-living counterparts in the water column (LaMontagne & Holden, 2003; Mohit et al., 2014).

Microbial communities are crucial elements of the food web because they consume and decompose organic matter and foster the *nutrient cycling*, an important intermediary service to coastal lagoon functioning. Both species functions are performed by a variety of microorganisms, mainly heterotrophic prokaryotes (Amaral et al., 2016). Fungi, for example, can decompose recalcitrant molecules, *i.e.* lignin and cellulose from leaves and branches (Ortega-Arbulú et al., 2019) and assist with the supply of nutrients otherwise unavailable for other organisms. Microbial communities are also integrated into food webs as resources to many consumers (i.e., grazing and filtering invertebrates), ultimately subsidizing the biomass production of organisms in upper trophic levels (e.g., enabling the provision and cultural services by other taxa; see the following sections). Apart from their small size, viruses are so abundant in the water column and sediment and can also provide organic matter for consumers through viral-induced cell lysis (Weitz et al., 2015).

Microbial communities not only supply mineralized and organic matter to the food webs, but also assist with incorporation of inorganic nutrients from the sediment and water column into the aquatic food web (Mulholland et al., 2009). In particular, the N and S cycles are strongly driven by different prokaryotic functional groups as Nitrogen fixers, Ammonia

**Table 1** Ecosystem services provided by biodiversity of coastal lagoons (according to the Millennium Ecosystem Assessment Report, 2003, 2005)

Biodiversity component	Taxon/Group	Ecological function	Mechanism	Ecosystem processes	Ecosystem service category	Ecosystem service
Microbes	Heterotrophic prokaryotes and Fungi	Feeding	Pollutants degradation	Decomposition/ Secondary production	Regulating	Water purification
	Heterotrophic prokaryotes	Feeding	Toxin degradation	Decomposition/ Secondary production	Regulating	Water purification
	Eukaryotic and prokaryotic predators	Feeding	Predation on pathogenic species	Ecological interactions	Regulating	Disease regulation
	Photo and chemo- autotrophic microbes and heterotrophic microbes	Biomass production	Emission or sequestration of greenhouse gases (CO <sub>2</sub> , CH <sub>4</sub> , N <sub>2</sub> ) through Photo/chemosynthesis	Biogeochemical cycles/ Primary/ Secondary production	Regulating	Climate regulation
	Bacterivorous protists	Feeding	Predation and Competition	Ecological interactions	Regulating	Biological control
	Heterotrophic prokaryotes, fungi, viruses	Feeding	Organic matter degradation	Decomposition/Secondary production	Supporting	Nutrient cycling
	Denitrifying bacteria, archaea and protists, Sulfur-oxidizing bacteria and archaea, Sulfide-oxidizing bacteria, Sulfate-reducing bacteria and archaea, DMSP producers and consumers	Feeding	Inorganic nutrient recycling (e.g., nitrogen and sulfur)	Biogeochemical Cycles	Supporting	Nutrient cycling
	Photo- and chemo- autotrophic prokaryotes and Photoautotrophic protists	Biomass production	Oxygenic and Anoxygenic Photosynthesis/ Chemoautotrophy	Primary production	Supporting	Primary production

**Table 1** (continued)

Biodiversity component	Taxon/Group	Ecological function	Mechanism	Ecosystem processes	Ecosystem service category	Ecosystem service
Zooplankton	Zooplankton species	Respiration/Excretion	Vertical distribution of carbon through the system	Biogeochemical Cycles	Supporting	Nutrient cycling
	Marine zooplankton species	Feeding/Excretion	Detritus from zooplanktons as carbon input to bottom habitats	Biogeochemical Cycles	Regulating	Climate regulation
	Rotifera, cladocera and copepoda species	Biomass production	Fossil record in coastal sedimentary layers	Biogeochemical Cycles	Cultural	Formal knowledge system; educational values
	Dormant zooplankton species	Recruitment	Re-suspension or re-emerging of dormant stages to restore communities	Secondary production/ Evolutionary processes	Provisioning	Genetic resources
	Zooplankton species	Feeding	Recovering energy from protist sink	Biogeochemical Cycles/ Secondary production	Supporting	Nutrient cycling
	Zooplankton species (e.g., copepods)	Biomass production	Biomass/abundance of prey availability in foraging habitats to pelagic fishes	Secondary production/ Ecological interactions	Supporting	Provisioning of habitat
	Grazing zooplanktons (e.g., <i>Daphnia</i> spp.)	Feeding	Grazing activity over autotrophs	Biogeochemical Cycles/ Ecological interactions	Regulating	Water purification
	<i>Daphnia</i> spp., <i>Acartia</i> cf. <i>fancetti</i> <i>Brachionus plicatilis</i> , <i>Cyclophora</i> sp. and <i>Scrippsiella</i> sp.	Biomass production	Biomass/abundance availability of bioindicator species	Secondary production	Cultural	Formal knowledge system

Table 1 (continued)

Biodiversity component	Taxon/Group	Ecological function	Mechanism	Ecosystem processes	Ecosystem service category	Ecosystem service
Polychaeta	Polychaeta species	Biomass production	Detrital material converted into biomass	Biogeochemical Cycles/ Secondary production	Supporting	Nutrient cycling
	Polychaeta species	Biomass production	Biomass/abundance prey availability in foraging habitats to macrobenthic fishes	Secondary production/ Ecological interactions	Supporting	Provisioning of habitat
	Polychaeta species	Movement (habitat use)	Bioturbation enhancing oxygen penetration in sediment	Biogeochemical cycle/ Decomposition	Supporting	Sediment formation
	Polychaeta species	Movement (habitat use)	Bioturbation releasing nutrients to the water column	Biogeochemical Cycles	Supporting	Nutrient cycling
Mollusks	Polychaeta species	Biomass production	Biomass/abundance availability of bioindicator species	Secondary production	Cultural	Formal knowledge system
	Arenicolidae, Glyceridae, Lumbrineridae, Nereididae, Nephthyidae, Onuphidae and Eunicidae species	Biomass production	Biomass/abundance availability as fishing baits	Secondary production	Cultural	Sense of place, Social relationships, Recreational values and Cultural heritage values
	Deposit-feeders (e.g., <i>A. ovata</i> )	Feeding	Sediment reworking from feeding activity enhancing oxygen penetration and bacterial growth in benthic habitats	Biogeochemical cycle / Decomposition	Supporting	Nutrient cycling, Sediment formation
	Deposit-feeders (e.g., <i>A. ovata</i> )	Feeding	Sediment oxygenation fostering bacterial activity in the water column	Decomposition/ Secondary production	Regulating	Water purification

**Table 1** (continued)

Biodiversity component	Taxon/Group	Ecological function	Mechanism	Ecosystem processes	Ecosystem service category	Ecosystem service
Mollusks	Grazing gastropods (e.g., <i>Strombus gigas</i> ; <i>M. modiolus</i> )	Feeding	Feeding activities enhancing photosynthetic rates in seagrass and its carbon sequestration	Ecological interactions/ Primary production	Regulating	Climate regulating
	Suspension feeder bivalves (e.g. <i>A. tuberculosa</i> ; <i>P. rugosa</i> )	Feeding	Feeding activities removing phytoplankton and controlling eutrophication	Ecological interactions/ Primary production	Regulating	Water purification
	Suspension feeder bivalves (e.g. <i>A. tuberculosa</i> ; <i>P. rugosa</i> )	Feeding	Feeding activities removing other particles in suspension and influencing on carbon cycling	Biogeochemical Cycles	Supporting	Nutrient cycling
	<i>Erodoma macroides</i> Bosc, 1801 and other mollusks	Biomass production	Prey biomass/abundance availability in nursery area to decapoda species	Secondary production/ Ecological interactions	Supporting	Provisioning of habitat
Mollusk's fishery resource	Biomass production	Biomass/abundance availability supporting fishing activity	Secondary production/ Ecological interactions	Provisioning	Food	
Mollusk's fishery resource	Biomass production	Biomass/abundance availability supporting fishing activity	Secondary production/ Ecological interactions	Cultural	Sense of place, Social relationships, Recreational values and Cultural heritage values	
Mollusk species	Biomass (shell) production	External shell formation as carbon long-term sink	Secondary production/ Biogeochemical cycle	Regulating	Climate regulating	

Table 1 (continued)

Biodiversity component	Taxon/Group	Ecological function	Mechanism	Ecosystem processes	Ecosystem service category	Ecosystem service
Mollusks	Mollusk species	Biomass (shell) production	Shells used to craft decoration artefacts or jewels	Secondary production/ Biogeochemical cycle	Cultural	Aesthetic, inspirational values
	Mollusk species	Biomass production	Mollusk's species used to classical studies	Secondary production	Cultural	Educational, cultural heritage
	<i>Anomalocardia</i> spp; <i>Phacoides</i> spp	Biomass production	Mollusks used as food and to build "Sam-baquis"	Secondary production	Cultural	Formal and traditional knowledge system, educational, inspirational, cultural heritage, and recreational and touristic values
Macro-crustaceans	Gastropods species	Biomass (shell) production	Shells (named "Búzios") used in spiritual ceremonies	Secondary production	Cultural	Spiritual
	Isopods; Amphipods species	Biomass production	Prey biomass/abundance availability in nursery area to fish species	Secondary production/ Ecological interactions	Supporting	Provisioning of habitat
	Grapsid crabs; Thalassinidean shrimps; <i>Callinectes</i> spp	Burrowing behaviour	Bioturbation releasing nutrients (e.g. phosphorous; nitrogen) to water column	Biogeochemical cycles	Supporting	Nutrient cycling
	Grapsid crabs; Thalassinidean shrimps; <i>Callinectes</i> spp.	Burrowing behaviour	Nutrients from bioturbation enhancing primary producers	Primary production	Supporting	Primary production
	Grapsid crabs; Thalassinidean shrimps; <i>Callinectes</i> spp.	Burrowing behaviour	Bioturbation enhancing oxygen penetration and bacterial growth in sediment	Decomposition/ Biogeochemical cycle	Supporting	Sediment formation



**Table 1** (continued)

Biodiversity component	Taxon/Group	Ecological function	Mechanism	Ecosystem processes	Ecosystem service category	Ecosystem service
Macro-crustaceans	Grapsid crabs; Thalassinidean shrimps; <i>Callinectes</i> spp	Burrowing behaviour	Bioturbation enhancing oxygen penetration in sediment (habitat quality to benthic communities)	Sediment formation/Bio-geochemical cycle	Supporting	Provisioning of habitat
	Penaeids shrimps (and others)	Biomass production	Biomass/abundance availability supporting fishing activity	Secondary production	Provisioning	Food
	Crustacean’s fisheries resource	Biomass production	Chitin biomass availability	Secondary production	Provisioning	Biochemical material provision
	Crustacean’s fisheries resource	Biomass production	Biomass/abundance availability supporting fishing activity	Secondary production	Cultural	Sense of place, social relationships, Recreational values; Cultural heritage values
Fish	Bottom-dwelling fish (e.g., Pleuronectiformes)	Feeding	Bioturbation releasing nutrients to the water column	Biogeochemical cycles	Supporting	Nutrient cycling
	Bottom-dwelling fish (e.g., Pleuronectiformes)	Feeding	Nutrients from bioturbation fostering primary producers	Primary Production	Supporting	Primary production
	Fish (all groups)	Excretion	Excretion of mineralized nutrients	Biogeochemical cycles	Supporting	Nutrient cycling
	Burrower fish (e.g., Pleuronectiformes)	Burrowing behaviour	Bioturbation releasing nutrients to water column	Biogeochemical cycles	Supporting	Nutrient cycling
	Burrower fish (e.g., Pleuronectiformes)	Burrowing behaviour	Nutrients from bioturbation fostering primary producers	Primary Production	Supporting	Primary production
	Zooplanktivorous fish	Feeding	Predation on zooplankton in the water column influencing growth of phytoplankton and reducing carbon sequestration	Ecological interactions/Primary production	Regulating	Climate regulation

Table 1 (continued)

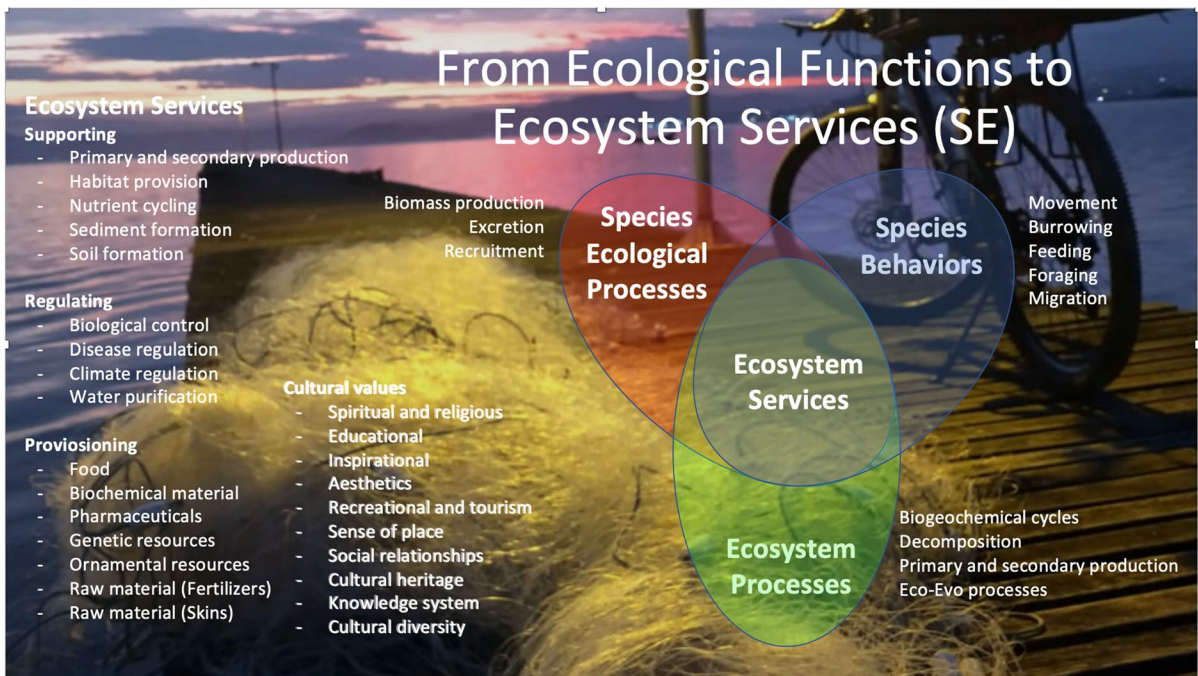
Biodiversity component	Taxon/Group	Ecological function	Mechanism	Ecosystem processes	Ecosystem service category	Ecosystem service
Fish	Phytoplanktivorous fish	Feeding	Grazing of algae and cyanobacteria controlling eutrophication	Ecological interactions/ Primary production	Regulating	Water purification
	Piscivorous fish	Feeding	Predation on zooplanktivorous fishes, growth of zooplankton that consumes phytoplankton (releasing of carbon)	Ecological interactions/ Secondary production	Regulating	Climate regulation
	Diadromous fish (e.g., <i>G. genidens</i> , <i>P. marinus</i> )	Excretion/migration	Excretion of mineralized nutrients and movement connecting freshwater and marine systems	Biogeochemical cycles	Supporting	Nutrient cycling
	Larvivorous fish (e.g., <i>G. affinis</i> )	Feeding	Predation on mosquito larvae	Ecological interactions/ Secondary production	Regulating	Biological control, Disease regulation *
	Fish (all groups)	Biomass production	Mutation and natural recombination	Ecological interactions/ Evolutionary processes	Provisioning	Genetic resources
	Fish (e.g., mullet, sea lamprey)	Biomass production	Increase of biomass and abundance of fish	Secondary production	Provisioning	Food
	Fish (e.g., Tilapia species)	Biomass production	Increase of biomass and abundance of fish	Secondary production	Provisioning	Biochemicals, natural medicines and pharmaceuticals
	Fish (e.g., <i>N. notopterus</i> and <i>O. gachua</i> )	Biomass production	Increase of biomass and abundance of fish	Secondary production	Provisioning	Ornamental resources
	Fish (all groups)	Biomass production	Fish markets underpin relationships among social actors	Secondary production	Cultural	Cultural diversity, social relations

Table 1 (continued)

Biodiversity component	Taxon/Group	Ecological function	Mechanism	Ecosystem processes	Ecosystem service category	Ecosystem service
Fish	Fish (e.g., seahorse as amulet)	Biomass production	Availability of biomass and abundance of fish	Secondary production	Cultural	Spiritual and religious values
	Fish (e.g., sensitive species such as <i>L. saltiens</i> , or tolerant species such as <i>P. marmoratus</i> )	Biomass production	Death (or behavior alteration) of sensitive species. Endurance of tolerant species (with dominance in the system)	Secondary production/ Ecological interactions	Cultural	Knowledge systems
	Fish (all groups)	Biomass production	Biomass/abundance availability supporting fishing and social activities	Ecological interactions/ Secondary production	Cultural	Educational, inspirational, aesthetic, cultural heritage, recreational and ecotourism values
	Predator birds ( <i>N. brasilianus</i> ; diving ducks)	Feeding	Biological control of pests, dominant or exotic species populations	Ecological interactions/ Secondary production	Regulating	Biological control, Disease regulation
	Cormorants, Terns and Gulls	Excretion	Guano and eggshells deposition on land	Biogeochemical cycles	Provisioning	Raw material (Fertilizer) provision
	Cormorants, Terns and Gulls	Excretion/movement	Guano deposition and nutrient enrichment connecting terrestrial and aquatic habitats	Biogeochemical cycles	Supporting	Soil Formation
	Cormorants, Terns and Gulls	Excretion	Guano deposition on water influencing nutrients cycling and enhance primary production	Biogeochemical cycles/ Primary production	Supporting	Nutrient cycling, Primary production

Table 1 (continued)

Biodiversity component	Taxon/Group	Ecological function	Mechanism	Ecosystem processes	Ecosystem service category	Ecosystem service
Birds	Bird species, Flamingos <i>P. roseus</i> , rare and migrating species	Biomass production	Bird diversity promoting recreational activities, as birdwatching	Ecological interactions/ Secondary production	Cultural	Formal and informal knowledge system, educational, aesthetics, social relations and recreation and tourism values
	Geese, Swans and Ducks	Biomass production	Bird diversity promote the creation of conservation actions	Ecological interactions/ Secondary production	Cultural	Educational values, social relations, sense of place
	Flamingos <i>P. roseus</i> ; Sacred Ibis <i>T. aethiopicus</i>	Biomass production	Bird species as cultural values to ancient societies	Ecological interactions/ Secondary production	Cultural	Inspirational, formal and traditional knowledge systems, spiritual, cultural heritage
Aquatic mammals	Aquatic and semi-aquatic species	Excretion/movementation	Mammal's releasing faecal plumes in their foraging habitats	Biogeochemical cycles/ Primary production	Supporting	Nutrient cycling, Primary production
	Aquatic and semi-aquatic species	Biomass production	Mammal's body as carbon sink, and mammal's carcass as carbon source	Secondary production/ Biogeochemical cycle	Regulating	Climate regulating
	<i>Beluga D. leucas</i> ; Harbor seal <i>P. vitulina</i>	Biomass production	Biomass/abundance availability supporting hunting activities	Secondary production/ Ecological interactions	Provisioning	Food
	<i>Beluga D. leucas</i> ; Harbor seal <i>P. vitulina</i>	Biomass production	Mammal's skin and other raw materials used for clothing, equipment, and ornamental	Secondary production/ Ecological interactions	Provisioning	Raw material (Skin)
	Irrawaddy dolphin <i>O. brevirostris</i> ; Lahille's Bottlenose dolphin <i>T. truncatus</i> <i>gephyreus</i>	Foraging behaviour	Mammals' species supporting fishing activity	Ecological interactions	Cultural	Recreational, sense of place, social relations, aesthetics, cultural heritage, formal, traditional knowledge, cultural, diversity values



**Fig. 1** Interactions among species functions (i.e., species processes and behaviors), ecosystem processes and ecosystem services in coastal lagoons. Eco-Evo=Ecological and Evolutionary processes

oxidizing bacteria and archaea, Nitrite-oxidizing bacteria, Comammox bacteria, Denitrifying bacteria, archaea and protists, Sulfur-oxidizing bacteria and archaea, Sulfide-oxidizing bacteria, Sulfate-reducing bacteria and archaea, DMSP producers and consumers (Madigan et al., 2008). Prokaryotic and eukaryotic microbial communities also incorporate nutrients, playing an important role in *primary production* in coastal lagoons (Fontes et al., 2011).

Microbial communities are key players in Regulating Services. Members of diverse taxonomic groups frequently encountered in coastal lagoons—such as the bacterial genera *Acinetobacter*, *Alcaligenes*, *Burkholderia*, *Flavobacterium*, *Pseudomonas*, and *Sphingomonas*, and the fungal genera *Candida*, *Geotrichum* and *Rhodotorula*—are known to degrade anthropogenic pollutants, and thus provide *water purification service* (Leahy & Colwell, 1990; Aislabie & Lloyd-Jones, 1995; Seo et al., 2009). Water quality is also maintained by microbial degradation of cyanobacterial toxins by bacterial genera *Arthrobacter*, *Burkholderia*, *Brevibacterium*, *Rhodococcus*, *Sphingomonas*, and *Sphingosinicella* (Donovan et al., 2008; Lemes et al., 2008; Kormas & Lymeropoulou,

2013). Bacterivorous protists control microbial pathogens that reach the coastal lagoons through predation (i.e., mainly Ciliates, Mast, 1947) (Staley et al., 2014; Balzano et al., 2015) and competition with the native bacterial community (Korajkic et al., 2013), providing the *biological control service*. Because microbial communities perform aerobic and anaerobic respiration, aside from nitrogen fixation (i.e., methanogenic *Archaea* and *Cyanobacteria*, and autotrophic N fixing prokaryotes), they assist with *climate regulation* through the production and consumption of greenhouse gases, such as CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O (Hirota et al., 2007; Muduli et al., 2012). Also, changes in carbon availability and DOM quality linked to hydrology strongly affects the activity of different bacterial exoenzymes (Conan et al., 2017), the extent of dissolved organic matter biodegradation and its resulting quality (Alonso et al., 2013; Amaral et al., 2016). Such effects lead to strong spatiotemporal variations in the CO<sub>2</sub> emissions (Muduli et al., 2012), and might assist the *regulation of carbon exchange* in local and regional scales.

As microorganisms occupy the basis of the food web, their functions are integrated within processes

that generate intermediary supporting and regulating services. Nonetheless, they are important to subsidize final ecosystem services provided by other organisms from the coastal lagoons.

## Zooplankton

Zooplankton pertain to the animal or animal-like heterotrophic organisms comprising the plankton group, a diverse community limited by the water-column interfaces with adjacent aquatic habitats e.g., littoral and sediment zones (Hutchinson, 1959; Margalef, 1983). In high productive and intermittently disturbed environments such as coastal lagoons, zooplankton can show enormous functional complexity (Santangelo et al., 2007). The shallow water columns of coastal lagoons congregate species that spend their entire lives in the pelagic environment (holoplankton) with several occasional planktonic taxa, such as early stages and larvae of shrimps, insects, crabs, and temporary members of the plankton (meroplankton). Therefore, the biological dynamics and ecosystem functioning depend on these benthic–pelagic interactions, connecting higher productive epipelagic zone with bottom communities (Kiljunen et al., 2020).

The importance of zooplankton groups and their contribution in ecosystem services may be the result of the flourishing biodiversity of marine, brackish and freshwater assemblages (Santangelo et al., 2007; Branco et al., 2008; Paturej, 2009), as well as their interactions and functionalities. Due to their short life spans, ubiquity and high abundances, zooplankton can drive the aquatic biogeochemical cycles of essential elements such as carbon, phosphorus and nitrogen which is respired and converted to inorganic matter, supporting primary producers e.g., phytoplankton and macrophyte banks in coastal lagoons. These biogeochemical processes involve mainly the respiratory carbon (CO<sub>2</sub>) and particulate organic carbon (POC) through faecal pellets and detritus, not only *recycling carbon* (i.e., Supporting service), but also defining vertical distribution of carbon through the system. Furthermore, these sinking particles' movement is related with *carbon pool* formation in bottom habitats, an important regulating service for the “climate crisis”. Considering that many zooplankton species found in coastal lagoons are from the marine realm (e.g., the oceanic copepod *Calanus finmarchicus*

Gunnerus, 1770, see Jónasdóttir et al., 2015), it is possible to assume that these organisms also play a role in ocean's biological pump (Lebrato et al., 2019; Robison et al., 2005), the main process that connect atmosphere, pelagic surface layers and deep ocean through the carbon cycle. Besides both intermediary services mentioned above, the fossil record documentation of some groups, although poorly documented, may provide a final ecosystem service to human society, assisting with a formal knowledge system and educational values (cultural services), since they allow us to understand the mechanisms and processes that shape aquatic ecosystems at different time scales. For instance, the fossil record documentation of rotifers (Waggoner & Poinar, 1993), cladocerans (Van Damme & Kotov, 2016) or copepods (Selden et al., 2010) is placed in the context of major historical changes in the aquatic environment, including the appearance of predator–prey relationships and niche availability that have impacted their evolution.

The dormancy is a conspicuous feature of zooplanktonic taxa. In the littoral zone of coastal lagoons, species of certain zooplankton groups leave resting cysts banks (e.g., ephippia in cladocerans, resting eggs in rotifers and copepods and cysts in *Artemia* spp.), dormant stages that sink to the bottom sediment until they are re-suspended or the right conditions return for them to re-emerge and restore active communities seasonally (Eskinazi-Sant'Anna & Pace, 2018). The dormant stages provide important *genetic resources* (i.e., provisioning ecosystem service) for the resilience of populations after disturbances (Latta et al., 2010). The restoration of aquatic systems from cyst banks could be further developed in advance of heavily impacted coastal wetlands or coastal lagoons affected by changes in water regimes (Williams et al., 2008; Santangelo et al., 2014; Eskinazi-Sant'Anna & Pace, 2018).

Through grazing and predation, zooplankters play relevant ecological functions by actively participating in ecosystem metabolism. For instance, by grazing on bacteria and very small protists, zooplankton species recover matter and associated energy through the microbial loop that otherwise could be lost to ecosystem sinks (Feitosa et al., 2019). The zooplankton biomass generated may show quite regular patterns and strategically assure fish recruitment and presence of fish stock by acting as a hub of food webs. Copepods represent an important alternative live-feed in marine/

brackish fish production, as they improve survival, growth and development of fish larvae (Hansen, 2017). In addition, the vertical migration of microcrustaceans influences migration and consequently food availability to pelagic fishes (Perissinotto & McQuaid, 1992). Thus, this is a suitable example of how zooplankton biomass availability in foraging areas assists with the *provision of habitats*, intermediating important commercial fisheries in coastal lagoons (Lomartire et al., 2021). The application of large herbivorous zooplankton, especially calanoid copepods and *Daphnia* spp., in promoting clear-water phases due to its grazing effect on phytoplankton is well documented (Sommer et al., 1986). This has potential application in biological control actions in coastal lagoons, as regulating service to improve *water quality*.

Since the predicted effects of global climate change, including sea level rise, most likely will intensify saline intrusions into coastal lagoons (Schalenberg et al., 2003; Jeppesen et al., 2007), some zooplankton could be used as biomonitors, providing direct values to human society. The zooplankton abundance and biomass are very sensitive to changes, thus the response to the disturbance will appear in a short-time for the higher trophic level (Jeppesen et al., 2011; Mackas et al., 2012; García-Chicote et al., 2018). Their short time response, their ubiquity and their trophic relationships make them potential bioindicators for different aquatic ecosystems all over the world (Serranito et al., 2016; Kruk et al., 2021), a *cultural service* which may be framed as *formal knowledge system*. Examples of zooplankton bioindicators of extreme environmental fluctuations are *Daphnia* spp., *Acartia* cf. *fancetti* McKinnon, Kimmerer & Benzie, 1992, *Brachionus plicatilis* (Müller, 1786), *Cyclophora* sp. and *Scrippsiella* sp. (Attayde & Bozelli, 1998; Branco et al., 2000; Waterkeyn et al., 2008; Souza et al., 2011; Quintana et al., 2018).

### Polychaeta worms

Polychaeta are an abundant component in benthic communities in coastal lagoons (Day et al., 2013; Misturini & Colling, 2021). Species of the families Nereididae (e.g., *Laeonereis acuta* (Treadwell, 1923)), Capitellidae (e.g., *Heteromastus similis* Southern, 1921), Nephytidae (e.g., *Nephtys fluviatilis*

Monto, 1937) and Spionidae (e.g., *Prionospio heterobranchia* Moore, 1907) thrive in most of the habitats of coastal lagoons (Netto et al., 2018).

Polychaetes have large variability in their morphological structure, size, and life history, performing different ecological functions by borrowing into sediments, or living within tubes (Hutchings, 1998). They are common components in the estuarine food chain, acting as primary and secondary consumers, contributing to the trophic complexity of shallow bottoms, and often important in determining the structure of the infauna communities (Ambrose, 1984; Muro-Torres et al., 2019). The estuarine worms form one of the bases of the estuarine trophic web, converting part of the detrital material produced in coastal wetlands into biomass, which becomes available to organisms in other trophic levels, including invertebrates, fish, and birds (Iwamatsu et al., 2007; Caron et al., 2004; Palomo & Irbane, 2000). The benthic secondary production drives matter and energy flow along the food web (Sánchez-Moyano et al., 2017), promoting *nutrient cycling* (i.e., supporting services). Still, polychaeta biomass in coastal lagoons habitats provide a supporting service since polychaetes are key preys to macrobenthic fish predators in coastal lagoons (Vinagre et al., 2008).

Polychaeta worms are also important to the breakdown and remobilization of sediment, particulate organic and inorganic matter and metabolites due to their intense borrowing activities. Intense bioturbation, modification of sediments through particle reworking and burrow ventilation, is a crucial mediator of many geochemical processes in estuaries (Queiros et al., 2013). Filtering and bioturbator polychaetes increase the percolation of water and nutrients in the sediment, both through the pumping process and through the action of feeding, digging and excretion (Díaz-Castañeda & Reish, 2009). The capacity of polychaetes to affect biogeophysical components of the sediment and to be available as a resource to organisms of other trophic levels are dependent on their morphological and life-history traits (Wouters et al., 2018; Otegui et al., 2016). These functions performed by polychaetes assist with *sediment formation* and *nutrient cycling*, both supporting services essential to coastal lagoons.

Polychaetes are numerically dominant in macrobenthic components, and they have diverse functional traits in estuarine ecosystems (Hutchings,

1998; Martins & Barros, 2022). The relationships between structure and function of polychaete assemblages might provide a measure of the resilience of estuarine conditions (Magalhães & Barros, 2011) and might be used as *bioindicators* of environmental disturbance (Pocklington & Wells, 1992; Giangrande et al., 2005), providing an important *scientific and formal knowledge* service to monitor coastal lagoons. Furthermore, polychaete species from families such as Arenicolidae, Glyceridae, Lumbrineridae, Nereididae, Nephtyidae, Onuphidae and Eunicidae are widely captured as *fishing bait* (i.e., provision service) worldwide (see Cabral et al., 2019). These organisms are harvested from intertidal flats habitats in coastal ecosystems, such as Ria do Aveiro and Ria Formosa coastal lagoons (Cabral et al., 2019), underpinning recreational fishing and tourism. Since recreational fishing is associated with ecosystem services, such as provisioning (e.g., food) and cultural (e.g., recreation and social relations), it is notorious that the biomass from polychaete supports these goods to fishers.

## Mollusks

Gastropod and bivalve' mollusks are components of the benthic macroinfauna community (Netto et al., 2018), namely animals larger than most of the sediment particles where they inhabit (McLachlan & Defeo, 2017). In coastal lagoons, both groups are abundant in soft-bottom habitats (Warme, 1969; de Jesús-Carrillo et al., 2020) and the composition of these assemblages is heterogeneous (Morelos-Villegas et al., 2018), responding to variations in water conditions and habitat features (Montagna et al., 2008; Davis et al., 2017; Abdelhady et al., 2019).

Similar to freshwater ecosystems (Vaughn, 2018), the functions performed by mollusk in coastal lagoons may underpin processes that benefit human societies. The sediment reworking activity performed by mollusks (Rhoads & Young, 1970) may disrupt sediments and increase the depth of oxygen in benthic habitats. *Abra ovata* (Philippi, 1836) is an example of primarily surface deposit-feeders (Charles, 1993) in coastal lagoons (Gontikaki et al., 2003). From its feeding activity, *A. ovata* promotes frequent and small-scale particle displacement, fostering vertical sediment mixing (Maire et al., 2007). This ecological function can support ecosystem services in coastal

lagoons because it contributes to *nutrient cycling*, oxygen penetration and enhances bacterial decomposition (i.e., releasing carbon and nitrogen).

Furthermore, mollusk's feeding strategies strongly influence soft-bottom species composition (Hunt et al., 1987; Skilleter et al., 1994). Grazing gastropods are a dominant group in coastal lagoons (Almeida et al., 2008) and intertidal estuarine grazing gastropods as *Assiminea globulus* Connolly, 1939 shapes communities in unequal ways. Such species increases bacterial density and decreases microphytobenthos density not affecting overall meiofaunal density, but affecting meiofaunal community structure (Pillay et al., 2009). In vegetated habitats, grazers such as *Strombus gigas* (Stoner & Waite, 1991) and *Modulus modiolus* (Mook, 1977) remove epiphyte algae associated with seagrass leaves, enhancing seagrass photosynthetic rates (van Montfrans et al., 1984). In both cases, grazing functions are regulation services since they perform *biological control* in coastal lagoon. However, worth mentioning the indirectly influence of grazers on organic carbon sequestration and storage by seagrass ecosystems, contributing to climate regulation of the most efficient natural carbon sink on earth (Serrano et al., 2021).

Suspension feeder bivalves are a common component of benthic habitats in coastal lagoons (Dame, 1993; Wall et al., 2008). For instance, in Bahía Magdalena coastal lagoon (Mexico), *Anadara tuberculosa* (G. B. Sowerby I, 1833) is more abundant in habitats with silt and mangrove sediments, while *Pinna rugosa* G. B. Sowerby I, 1835 is more abundant in sand-mud benthic habitats (Jiménez-Quiroz et al., 2021). Both species (and others with similar ecological functions) play a key role in water column particles filtration, removing phytoplankton and other particles in suspension (Dame et al., 2002). As a result of this ecological function, suspension feed bivalves may play a role in eutrophication control, promote *water purification* and influence *nutrient cycling* (i.e., carbon; Officer et al., 1982; Doering et al., 1986), which can be framed as regulating and supporting ecosystem services, respectively. Also, the suspension-feeding behaviour of bivalve mollusks promote indirectly nutrients and organic matter transfer from the water column to the bottom (Smaal & Prins, 1993), enhancing macroalgae and seagrass growth (Wall et al., 2008).



The secondary production of mollusks species might be associated with several ecosystem services. Bivalves and gastropods are an important food resource for fish and crustaceans in coastal lagoons (Vega-Cendejas & Arreguín-Sánchez, 2001). For instance, *Erodoma mactroides* Bosc, 1801 is a known prey for decapods, such as *Callinectes sapidus* Rathbun, 1896, and function as a vector for the cirriped *Amphibalanus improvisus*, that lives attached to the gastropod shells (Bemvenuti, 1997). The high availability of prey in some habitats might be associated with a nursery function (Liquete et al., 2016) or with *provisioning of habitat*, a supporting service necessary to produce other ecosystem services, as the provision of fisheries resources (MEA, 2005). Not only are mollusks a food resource to the aquatic food web, but their biomass is also a valuable resource to fisheries in coastal lagoons worldwide (Pérez-Ruzafa & Marcos, 2012; Jiménez-Quiroz et al., 2021), feeding human populations (i.e., provision service).

Mollusks' secondary production in coastal lagoons generates a significant biomass of external shells. Even though gastropods and bivalves have very distinct morphologies, both groups have calcium carbonate as the main component of their external carapace (Checa, 2018). Therefore, mollusks may influence the CO<sub>2</sub> balance between surface waters and the atmosphere and store carbon in a long-term sink (i.e., *climate regulation* service). Moreover, the shell deposited adds complexity to the sediment structure in bottom habitats (i.e., *sediment formation* service), promoting an increase in animal population from epibenthic assemblages (Reise, 2002; Petersen et al., 2010).

The morphology and beauty of mollusks' shells make them a charismatic group (Morris et al., 2016). Many kinds of shells and other structures (e.g., pearls) are used to craft decoration artefacts or jewels (Haszprunar & Wanninger, 2012). These have direct values to human societies, can be framed as *cultural ecosystem services* and subcategorized as *aesthetic* and *inspiration services*. Mollusk's exploitation is an ancient activity of citizens in coastal zones. Some of them are illustrious, such as Aristotle and Hippocrates, which created classical zoological and medicine work using shellfish (Voultsiadou et al., 2010), contributing to *formal and informal education* of current human societies. Information extracted from mollusk's species provided educational services to the

mentioned ancient human societies in the past, while currently their works are a *cultural heritage* to the global population. In Latin America, there are big mounds (30 m high and hundreds of meters wide) of *Anomalocardia* and *Phacoides* (old *Lucina*) shells (Rohr, 1984) associated with lagoons' systems. For instance, in the south of Santa Catarina lagoon complex (southern Brazil) there are dozens of these cultural deposits, which are denominated as "Sambaqui" (Deblasis et al., 2007). They have distinct sizes and stratigraphy, encompassing accumulations with several functions and origins (Gaspar et al., 2008). In the Sambaquis the indigenous people buried the corpses of their peers and had other *social rituals* (Ferreira & Noelli, 2007). Nowadays, the Sambaquis provides arrays of cultural services, such as *research, education, inspiration, cultural heritage, and recreation/touristic* options. Another interesting service associated with the gastropod's shells (named as "Búzios") is their *spiritual* value in native South American and Afro-Brazilian ceremonies (Léo Neto et al., 2012).

### Macro-crustaceans

The shallow vegetated intertidal areas along coastal lagoons (e.g., mangrove, saltmarsh, seagrass bed) shelter several crustaceans, such as shrimps and crabs in post larvae and juveniles' phases (Minello et al., 2008; Nagelkerken et al., 2015), populations of adult crabs (e.g., Grapsidea, Portunidae and Xanthidae), freshwater prawns (e.g., Palaemonidea), isopods (e.g., Sphaeromatidae) and amphipods (e.g., Talitridae) (Iribarne et al., 1997; Conde & Díaz, 1989; Bloomfield & Gillanders, 2005; Khemaissia et al., 2018). For some species such as penaeids shrimps, non-vegetated areas may support higher densities (Zimmerman & Minello, 1984), while for others, like blue crabs *Callinectes sapidus* Rathbun, 1896, non-vegetated and vegetated habitats might be equivalent in terms of abundance and biomass (Rodrigues et al., 2019).

Spatiotemporal variations in environmental conditions shape the macro-crustacean assemblage in coastal lagoons (Fortes et al., 2014). For example, the swimming blue crabs *Callinectes* spp. are represented by dozens of species (see compilation in Mantelatto et al., 2014) that respond to salinity variations in estuarine ecosystems: *C. ornatus* is abundant

in high salinity, *C. danae* is a dominant species in a wide range of salinity values, while *C. exasperatus* is less frequent in high salinity locations (De Carvalho & Couto, 2011). Unequal demography in response to environmental conditions may also occur, for example, when the blue crabs' females migrate to higher salinity areas after matting, while males remain in the low salinity areas (Norse, 1977; Buchanan & Stoner, 1988).

The complex life histories of macro-crustaceans' species are related to evolutionary adaptation processes and high environmental heterogeneity, playing essential functions in energy flow and nutrient cycling in the food web (Hines, 2007). Because distinct species make different use of the estuarine habitat (Whitfield, 2017), they also contribute to nutrient exchange within the coastal lagoons and between adjacent ecosystems (i.e., freshwater, brackish and marine). Consequently, several ecosystem services provided by coastal lagoons are tied to life history processes of macro-crustacean species (Newton et al., 2018). For instance, the nursery function provided by the estuarine ecosystem (Beck et al., 2001) may be an indicator of ecosystem condition or be directly related with tangible goods that enhance human well-being (Liquete et al., 2016), such as the maintenance of fisheries stocks (Martinho et al., 2007; Barbier et al., 2011). The nursery function may be classified as a *provision of habitat*, a *supporting service* necessary for the production of other ecosystem services (MEA, 2005). One important aspect that might modulate the value of habitat as nursery ground is the prey abundance and availability (Peterson, 2003; Adams et al., 2004; Nagelkerken et al., 2015), such as isopods and amphipods species which are important resources in the estuarine food web (Pasquaud et al., 2008; Wouters & Cabral, 2009).

Burrowing behaviour in soft sediments is widespread among decapod crustaceans (Rice & Chapman, 1971), and might be classified as ecological engineering. In coastal lagoons, some species live within a cavity excavated in the substratum, such as the semiterrestrial grapsid crabs *Neohelice granulata* (or *Chasmagnathus granulatus* (Dana, 1851)), which inhabit mudflat habitats (Spivak et al., 1994) and the deep-burrowing thalassinidean shrimps, commonly named as mud shrimp or ghost shrimp, that inhabit soft substrates (Felder, 2001). Other crustaceans move into the substratum and encase

their body temporally to avoid predators (Bellwood, 2002), as can be observed with *Callinectes* spp. (Ward, 2012) and penaeid shrimps (Minello, 2017). Independently of the ecological implications to species that perform them, these behaviours are associated with sediment movement and resuspension (Bellwood, 2002). This bioturbation mechanism provides supporting ecosystem services in coastal lagoons because it contributes to *nutrient cycling* (e.g., nitrogen), which are essential to the energy flow (Forster & Graf, 1995; Webb & Eyre, 2004). Furthermore, the bioturbation mechanism supports oxygen penetration into sediment, enhancing microbial processes and nutrients transport (e.g., phosphorus and nitrogen) through the sediment–water interface (Adámek & Maršálek, 2013), processes that underpin sediment formation and provisioning of habitat (both supporting services) for benthic communities' maintenance (Rossi et al., 2008) in coastal lagoons.

The secondary production of crustacean species (Zimmerman et al., 2002) provide direct value as *food (provision service)*, sustaining the livelihood of the local human communities that live in coastal areas (García & Le Reste, 1987; Berkes & Seixas, 2005; Ikhwanuddin et al., 2017). For instance, the penaeids shrimp's species that grow in coastal lagoons (Manzano-Sarabia et al., 2007; Mosha & Gallardo, 2013) are harvested by artisanal fisheries as small juveniles and subadults (D'incao, 1991; Rivera-Velázquez et al., 2009), being an important food item to human societies (Almudi & Kalikoski, 2010). As a commercial resource, shrimps biomass underpins the fishing activity in several tropical and subtropical coastal lagoons worldwide (Pérez-Castañeda & Defeo, 2001; Macia, 2004; Suradi et al., 2017).

The secondary production of crustaceans also generates chitin, present in their exoskeleton (Jayakumar et al., 2011). Because of this, chitin is present in estuarine systems (Goody et al., 1991), although its degradation and mineralization to CO<sub>2</sub> occur rapidly in these ecosystems (Goody et al., 1991; Boyer, 1994). In areas where crustacean fisheries are intense as coastal lagoons, the waste or by-product of this activity can be hazardous for the environment, increasing risks of biological (e.g., pathogens) and chemical (e.g., oxygen demand and organic matters) pollution (Bruck et al., 2011; Morganti et al., 2011). However, this waste is a potential high value resource, and

might be transformed into chitosan (El Knidri et al., 2018), which has several applications in technological and scientific areas (Philibert et al., 2017). The production of chitin and chitosan provide *biochemicals* (i.e., provision service) even if currently it is not fully explored.

In general, crustacean fisheries in coastal lagoons have large social, economic, cultural and historical values (Pérez-Castañeda & Defeo, 2001, Sunye et al., 2014), delivering direct *cultural services* to social actors involved in this activity. As for many other small-scale fisheries activities carried out in coastal lagoons (Machado et al., 2019) as well as in other coastal ecosystems (Pellowe & Leslie, 2021), crustacean fisheries may provide several services, such as *sense of place, social relationships, recreational, and cultural heritage values*. As fisheries in coastal lagoons are widespread and target several biological groups such as prawns and crabs (Pérez-Ruzafa & Marcos, 2012), several crustacean species are potentially related to cultural services worldwide.

## Fish

Fish assemblages are composed of species (and life stages) that occupy a wide range of trophic levels in the food chain and assist with the regulation of trophic structure and ecosystem resilience in coastal lagoons (Ocana-Luna & Sanchez-Ramirez, 1998; Pérez-Ruzafa et al., 2007; Muro-Torres et al., 2019). Fish can use coastal lagoons as their primary habitat (i.e., residents, estuarine dependents), may obligatorily pass through it during some life stage (i.e., catadromous and anadromous species), or enter the lagoons to forage (i.e., amphidromous species) (Nagelkerken, 2009; Potts et al., 2014). Fish movement (use of habitat) and feeding patterns within the lagoon, and between the lagoon and freshwater or marine environments generate many ecological interactions that assist with *sediment formation* (i.e., bioturbation), *nutrient exchange* (i.e., migration) and *primary production* (i.e., excretion and carcass decomposition) (e.g., Supporting Services, according to MEA, 2005) and *connect different ecosystems* (Murillas et al., 2020). While undertaking these migrations for reproduction purposes (diadromous) and for habitat use (distinct life stages or trophic guilds), all fishes feed and interact with other organisms, generating

*regulation of food web dynamics* and other processes through organisms' consumption and trophic cascades (Bueno-Pardo et al., 2018; Muro-Torres et al., 2019; Zheng et al., 2020).

By regulating food web dynamics, fish feeding activities can assist with *carbon exchange regulation* and contribute to global carbon dynamics and climate regulation (i.e., regulating ecosystem service). For example, coastal lagoons can become sources or sinks of carbon because of the feeding activities of fishes. Lagoons with zooplanktivorous fish can become a carbon sink because zooplankton are consumed, and primary producers (carbon fixers) can be released from grazing pressure. Coastal lagoons with piscivorous fishes can become a carbon source because the piscivorous fish suppress the abundance of zooplanktivores, allowing the zooplankton community to grow. Large zooplankton are expected to grow more than small-sized zooplankton and are more efficient grazers on phytoplankton. Hence, phytoplankton abundance decrease, and primary production can be temporarily suppressed (Guariento et al., 2010, 2011).

Fish feeding activity on phytoplankton can assist with the *regulation of eutrophication* processes (i.e., water purification service) in coastal lagoons, especially because eutrophication is expected to increase due to climate change (Souza et al., 2018). Net productivity regulation in coastal lagoons from Brazil has been hypothesized to be an outcome of fish consumption of periphytic biomass (Guariento et al., 2010). In a eutrophic coastal ecosystem from Japan, *Hypomesus nipponensis* McAllister, 1963 and *Mugil cephalus* Linnaeus, 1758 consumed cyanobacteria directly (Fujibayashi et al., 2018). Although previous studies have already shown that cyanobacteria (common group during eutrophication process) are not a preferable carbon source for many aquatic consumers because of the colony formation, filament shape and toxin production (de Bernardi & Giussani, 1990), these brackish fish species can rely on them whenever available (Fujibayashi et al., 2018), providing an important service of *biological control*.

By consuming other organisms, fishes help the *recycling of nutrients* within the aquatic ecosystem because they mineralize nitrogen and phosphorus through excretion and defecation, making these nutrients available for primary production (Naiman et al., 2002; Oliveira et al., 2014). Freshwater subsidies

to estuarine fish consumers in Lagoa do Patos, a coastal lagoon from south Brazil, was attributed (among other factors) to freshwater fish dispersal during flood pulses, that contributed with fish-derived nutrients from drainage basin to the lagoon (Garcia et al., 2017). On the other way, the anadromous alewife *Alosa pseudoharengus* (Wilson, 1811) excreted an average of  $24.71 \mu\text{g N g}^{-1}$  of wet fish mass per hour during their spring spawning, and because they aggregate in high densities within small coastal streams, they contributed substantially with marine-derived nutrients to the freshwater food web (Post & Walters, 2009). Marine-derived carbon and nutrients are also delivered through the production of gametes and fish carcass decomposition, and contribute to the biomass production of algae, insect larvae, microbial decomposers, and other fishes (Boros et al., 2014). For example, the live and carcasses of salmon increased the concentration of  $\text{NH}_4^+$  and phosphorus in the water column of freshwater streams where they spawn (Janetski et al., 2009). The activities and live strategies undertaken by fish that integrate the nutrient cycling (supporting) in coastal lagoons provide important services such as biomass production (provisioning and cultural) and primary production (supporting) in both coastal ecosystems and coastal-influenced freshwaters (Janetski et al., 2009).

There is a historical belief that fish can be used as *biological control of diseases* because larvivorous fish can consume the aquatic larval stage of mosquitos (Griffin & Knight, 2012). Since some mosquitoes are vectors of diseases such as yellow fever, dengue fever (i.e., *Aedes aegypti* Linnaeus, 1762) and arboviruses (i.e., *Aedes vigilax* (Skuse)), fish feeding behaviour could then provide this ecosystem service. For example, *Aplocheilus panchax* (Hamilton, 1822), *Colisa fasciatus* (Bloch & Schneider, 1801) and *Gambusia affinis* (Baird & Girard, 1853) are all species that inhabit brackish waters and are reported as efficient biocontrollers in experimental conditions and their introduction on aquatic ecosystems are encouraged for biological control (Chandra et al., 2008). However, recent evidence has shown that, whenever other prey is available (i.e., annelids, crustacea, rotifers), larvivorous fish consumes only a small proportion of disease-mosquito larvae (Rowe et al., 2008; Kumar et al., 2015) and might even produce a “disservice” to the society because they can also deplete native aquatic fauna, increase primary production (e.g.,

eutrophication) and alter nitrogen fluxes through the food web (El-Sabaawi et al., 2016).

Since fishes are one of the most diverse assemblages in coastal lagoons, their population growth and reproduction behaviour contribute to the maintenance of *genetic variability* (Esteves et al., 2008; Gjedrem, 2012). The genetic material of fish populations serves as a source of information for aquaculture production and biological conservation (Esteves et al., 2008; Suplicy et al., 2015; Cossu et al., 2021). For example, *Salvelinus fontinalis* (Mitchill, 1814), the brook trout, was selected for increased survival to furunculosis, and over three generations survival rate increased from 2 to 69%, protecting the species (for further examples, see Gjedrem, 2012). Genetic manipulation to increase growth rates for aquaculture production has been done for striped bass in the USA, clarid catfish in Thailand and characids in Venezuela (Bartley et al., 2001). Genetic variability among fishes from brackish environments also enhances the diversity of colour patterns and morphologies that draws attention and fosters the *ornamental fishing* industry (Pouil et al., 2019).

Coastal lagoons provide habitat to immense biodiversity and sustain high abundance and biomass of fishes (Esteves et al., 2008). Because of this availability, fishes play essential *Provision Services* that benefit society. One of the most recognizable is *food provision* that can be delivered through fishing of natural populations or aquaculture. The high fish diversity found in lagoons has always represented a source of income and livelihood for human settlements (FAO, 2015). Fishes are one of the main protein sources for 3.3 billion people in the world (FAO, 2020), and for some countries like Bangladesh, Cambodia, the Gambia, Indonesia, Sierra Leone and Sri Lanka, the highest fish productivity derive from coastal lagoons (Pauly & Yáñez-Arancibia, 1994). The typical marine migrants (i.e., diadromous) species are the most important biomass to support fisheries in coastal lagoons (Pérez-Ruzafa & Marcos, 2012). The global average fisheries production in coastal lagoons is around  $109.8 (\pm 11.2 \text{ SE}) \text{ kg ha}^{-1} \text{ year}^{-1}$ . The main catches in coastal lagoons worldwide are of Mugilidae and Sparidae (Pérez-Ruzafa & Marcos, 2012, FAO 2015). *Mugil cephalus* (Linnaeus, 1758) is an important species for fisheries in the Mediterranean and Australian lagoons (Broadhurst et al., 2003), while *Mugil liza* Valenciennes, 1836, is an important

fishery resource in southern Brazil (Simões-Lopes et al., 1998). Sea lamprey, an anadromous species, supports important commercial fisheries in Portugal, Spain and France (Maitland et al., 2015).

Fish biodiversity and genetic variability benefit society because fish tissues (i.e., skin) and other molecules have been processed and improved for *medical treatment provision*. Researchers in Brazil are experimenting with an innovative treatment using tilapia skin (e.g., glycerol-preserved skin, dermal matrix) in the treatment of burn wounds (Lima Junior et al., 2019) to accelerate tissue recovery after hand surgery (Monte et al., 2022), to repair and protect the palate after the removal of grafts (in dentistry) (Manfredi et al., 2021), and to apply collagen in the cosmetology and nutrition fields (Alves et al., 2018). Many tilapia species (e.g., *Oreochromis niloticus* (Linnaeus, 1758), *Sarotherodon melanotheron* Rüppel, 1852 and *Tilapia guineensis* (Günther, 1862)) already inhabit or shall be introduced in coastal lagoons for aquaculture (Achoh et al., 2018), with potential for this medical provision. Interestingly, the pufferfish (Tetraodontidae) endosymbiotic bacteria produce a potent neurotoxin (tetrodotoxin; Lago et al., 2015), with a potential disservice to humans since it can provoke intoxication (Hagen et al., 2017). However, due to medical research and development, it can now be used in the medical field as a powerful analgesic to treat cancer pain (Hagen et al., 2008, 2017).

All the ecosystem services mentioned above stimulate human development around coastal lagoons and subsidize traditional populations with economic, physical and experimental interactions with the natural environment. The population that directly depends on fish from coastal lagoons and those attracted as consumers and users enhance *cultural diversity* within these systems. Fish supply *Cultural Services* via *recreational activities* such as sport fishing of wild and stocked fishes (Alberini et al., 2007) and snorkelling (e.g., Yal Ku Lagoon, in Mexico and Tambaquis' Lagoon in Brazil). *Sacred and religious rituals* are also important for fishers, that ask for safety high catches during fishing trips. In Irakkam island, fishers participate in religious rituals to ask for supernatural powers, good catch, security and prosperity, which include using new fishing boats and worshipping clan deities (Reddy, 2020). In Brazil, records show fishers using sun-dry sea-horse *Hippocampus reidi*

Ginsburg, 1933 as a pendant for good luck and good fishing (Pinto et al., 2015).

Fish biodiversity (i.e., genetic, biomass and abundance) of coastal lagoons promotes *socialization areas* and provide *territorial identity and belonging* because fishers and local population use coastal lagoon since childhood, and the attraction to coastal lagoons is often connected to fish. Some of the most harvested species in coastal lagoons in terms of biomass (provisioning services) are also used in local culinary specialty with a rich history of use that is appropriated as *cultural heritage* (Almeida et al., 2021). For example, during mullet (*Mugil liza* Valenciennes, 1836) migration in southern Brazil (Lemos et al., 2014), some beaches are closed for other use (i.e., navigation or surfing) to prevent shoals from driving away from the coast, and to facilitate fish access to coastal lagoons. Fishers mobilize, prepare spotting huts and induce the opening of coastal lagoon sand bars to drive mullets inside the lagoons for further fishing. Spotting fish knowledge are passed along to young generations. Fishers commercialize fishes directly on the beach and nearby coastal lagoons, attracting tourists and residents. They also commercialize in fish markets and provide fish for local *cultural festivities*. Other traditional festivals take place in Europe. In Portugal, species such as the eel (*Anguilla anguilla* Linnaeus, 1758) and European flounder (*Platichthys flesus* (Linnaeus, 1758)) are considered “a pride of the local gastronomy” and are the main attraction of the Festival da Enguia da Lagoa de Santo André and Festa das Solhas de Lanhelas, respectively (Caminha, 2022; Santiago do Cacém, 2022). In the Iberian Peninsula, Sea lamprey (*Petromyzon marinus* Linnaeus, 1758) has been harvested for centuries. Dozens of gastronomic festivals take place every year in Portugal, during which hundreds of thousands of lampreys are consumed and belong to Portuguese and Galician *cultural heritage* (for further details, see Almeida et al., 2021). These festivals strengthen ties between the community and coastal lagoons, strengthening the *symbolic meaning* of fishing and increasing the *sense of belonging* of fishers and local populations.

Another important cultural service is the scientific one (Lillebø et al., 2015). Fish from coastal lagoons are subject of interest for research (Brehmer et al., 2013; Azevedo et al., 2017; Andrade-Tubino et al., 2020). Several scientific topics addressing fish in

coastal lagoons are investigated, such as community structure (García-Seoane et al., 2016; Manzo et al., 2016; Petry et al., 2016; Azevedo et al., 2017), fisheries (Pauly & Yáñez-Arancibia 1994, Pérez-Ruzafa & Marcos, 2012, FAO 2015, Haimovici & Cardoso 2017), functional diversity (Mouillot et al., 2007; Franco et al., 2021) and population aspects (Franco et al., 2014), significantly increasing *scientific knowledge* and attracting researchers for different studies. Although scientific and technical knowledge have been done with fishes from coastal lagoons, their ecology and ecosystem services provisioning still lack recognition among citizens and educators. This situation represents an important gap to be filled by the scientific and educational sectors to introduce relevant concepts in *formal education* and through Ocean Literacy resources, such as the Environmental Education Network for Ecosystem Services in Portugal (Barracosa et al., 2019). Finally, fishes are already used as *bioindicators* to assess aquatic habitat degradation in different ecological levels (Santhanam et al., 2010; Verdiell-Cubedo et al., 2012), and this knowledge could be easily translated to formal education activities. Physiological alteration can aid the comprehension of potential risks to wildlife and humans, while population and community alterations can be an early-warning signals of anthropogenic stress that need to be managed by decision-makers (Reis-Filho & Giarrizzo, 2016).

## Birds

Birds comprise a diverse group with a broad range of diets and foraging behaviour, from nectar-eating birds (Trochilidae) to piscivorous species consuming almost every type of fish prey (Gheler-Costa et al., 2018; Dalsgaard et al., 2021). In coastal lagoons, the bird assemblages may be organized in foraging habits guilds, such as dabbling birds (ducks), diving birds (cormorants), waders (Ciconiiformes and some Charadriiformes), fishing birds (Kingfishers, gulls and Sterns), filter feeders (Flamingos and some ducks) and insectivorous birds (Flycatchers and some passerines), evidencing the broad range of resources used by birds on coastal landscapes (Tavares et al., 2015). Coastal lagoons support a high diversity of residents and migrating birds due to their high biological productivity and habitat heterogeneity (Kennish

& Paerl, 2010), which provides nests, roosting and foraging sites (Sánchez & Rodríguez, 2000; Kularatne et al., 2021). The diversity of birds on coastal lagoons is affected by seasonality, waterbody ecological features and anthropogenic activities, such as habitat degradation, unsustainable hunting and the presence of exotic species (O'Connell, 2000; Dias et al., 2019). Still, stochastic events, such as storms, winds and floods, potentially generate perturbations that may affect birds or the resources they depend upon (Kennish & Paerl, 2010).

Birds feeding over aquatic organisms create a direct link between terrestrial and aquatic systems, assisting with *nutrient exchange between habitats* through birds' excretion. Feeding activities of seabird and waterbird guano influence *nutrients cycling* and enhance *primary production* (i.e., supporting services) from benthic component in favour of the planktonic pathway in inland coastal aquatic ecosystems (Gagnon et al., 2013; Vizzini et al., 2016). The bird droppings in nesting and roosting sites adjacent to coastal lagoons generate guano deposits, changing soil composition, vegetation, and microbial communities (Kolb et al., 2015), which comprises a supporting service by *soil formation* and *nutrient cycling* (Costanza et al., 2017). Seabird and waterbird guano are known as seabird white gold because it has high contents of nitrogen and phosphorus and has been used as a natural fertilizer for over 2000 years (Schnug et al., 2018; de la Peña-Lastra, 2021), providing an important *biochemical* product to society. The guano production in coastal lagoons is associated mainly with colonial birds, such as cormorants, terns and gulls (Palomo et al., 1999; Gagnon et al., 2013), which is a valuable raw material to agricultural activities (i.e., provisioning service), generating *income* to local communities.

Bird predation also provides *biological control* of pests or dominant species in the aquatic ecosystems, especially on closed coastal lagoons (Esteves et al., 2008; Green & Elmer, 2014). For instance, *Nannopterum brasiliense* (Gmelin, 1899) (neotropical cormorant) have broad plasticity on feeding habits, and its predation controls the invasive exotic salmonids in Patagonian freshwater ecosystems (Alarcón et al., 2012). Likewise, diving ducks have the potential to control the exotic zebra mussels, reducing the invasive species biomass drastically (Hamilton et al., 1994). Because neotropical cormorants and diving

ducks have a wide distribution on Neotropical ecosystems, encompassing coastal lagoons, these species undoubtedly play a role in controlling the abundance of invasive species.

Bird predation generates top-down effects on the food chain that shape fish and invertebrates' communities in coastal ecosystems (Rodríguez-Pérez & Green, 2012; Gheler-Costa et al., 2018), promoting the coexistence of species from different taxa, like fish, shrimp, and crabs (Rodríguez-Pérez & Green, 2012; Östman et al., 2013). Considering that predation can remove top-predator aquatic animals, secondary consumers abundance and biomass enhances.

Coastal lagoons avifauna can enhance biodiversity-based *cultural activities* (Sánchez & Rodríguez, 2000; Graves et al., 2019). *Birdwatching* is an activity that results in high economic benefits, potential conservation management, and collaborative science (Greenwood, 2007; Santos et al., 2019). A very illustrative case is the Celestum Lagoon (Mexico), where Flamingo watching tourism was evaluated in US\$16 million/year (Galicia et al., 2018). Birdwatching can be associated with several cultural services, such as *knowledge systems*, *education*, *aesthetics*, *social relations*, and *recreation/tourism*. Due to their conspicuousness, beauty, and vocalizations, birds are appreciated and fed in recreational activities, generating benefits to human welfare (Whelan et al., 2008), which might be associated with *spiritual and religious*, educational, inspiration, aesthetic and recreation/tourism services.

Public interest in some waterbirds such as ducks, swans and geese has opened the door to protection and conservation of many water bodies, including coastal lagoons, as well as the creation of conventions and non-governmental organizations, such as the Ramsar Convention in 1971 and Wildfowl & Wetlands Trust (UK) (Green & Elmberg, 2014). Such initiatives promote *education* (educational values, social relations) and environmental awareness (*sense of place*) activities for the protection of wetlands areas, as the Detwah coastal lagoon (Yemen), an important island to biodiversity in the Arabian Sea (Veettil et al., 2020).

Birds on coastal lagoons also have *religious* importance for ancient and contemporaneous society. Two illustrative examples are the greater flamingos, *Phoenicopterus roseus* Pallas, 1811, illustrated

in Palaeolithic caves in Spain (Lazarich et al., 2019) and the sacre-ibis, *Threskiornis aethiopicus* (Latham, J 1790), a waterbird species revered that was found mummified and illustrated on Egyptian walls (Wasef et al., 2015). In both cases, it is assumed that these bird species provided *inspiration*, *knowledge systems* and *spiritual and religious values* to ancient civilizations, while currently, besides spiritual values, these illustrations are an important cultural and *educational heritage* for humanity.

### Aquatic mammals

Aquatic and semi-aquatic mammals comprise a diverse group of species that share anatomical (e.g., integument and body shape) and physiological (e.g., thermoregulation, musculoskeletal systems) specializations according to their level of dependence on water (Reidenberg, 2007). Coastal lagoons contain a mosaic of wetlands, mangroves, saltmarshes and seagrass meadows (Basset et al., 2013), which provides vital habitats for a rich diversity of lower trophic level species (i.e., invertebrate and fish) and, consequently, favourable foraging environments for some species of aquatic and semi-aquatic mammals. Interestingly, aquatic and semi-aquatic mammals are not a common component in coastal lagoons. For example, a search in the EcoBase platform (Colléter et al., 2015)—a repository for data from ecosystem models based on the Ecopath framework (Polovina, 1984)—shows that only one from the eighteen models built for coastal lagoons has mammals in its trophic network; see Milessi et al., 2010).

Although the occurrence of aquatic and semi-aquatic mammals in coastal lagoons is occasional, when it happens, they can modulate the structure and stability of these habitats, in particular by their feeding activity. Their high trophic levels and prey consumption rate regulate the abundance of prey populations (Heithaus et al., 2008) in which their depletion can trigger a series of cascading events through lower trophic levels (Terborgh & Estes, 2013). In addition, aquatic mammals can also forage on a variety of food resources, from different trophic levels, which turn it into a challenge to predict their ecological role and consequences for an ecosystem. For instance, the semi-aquatic *Lontra longicaudis* (Olfers, 1818) is a top predator in the Laguna de Rocha ecosystem that

feeds on crabs and freshwater (e.g., *Hoplias malabaricus* (Bloch, 1794)) and marine (e.g., Flatfishes) fish species (Milessi et al., 2010). The bottlenose dolphin (*Tursiops truncatus* Montagu, 1821) is a generalist predator (Rossman et al., 2015), that feeds on fish species (e.g., Mugilidae) and molluscs (e.g., *Sepia officinalis* Linnaeus, 1758) in coastal lagoons and estuarine ecosystems (dos Santos et al., 2007).

Due to their relatively high metabolic rates (Bowen, 1997; Estes, 2009), aquatic and semi-aquatic mammals consume a significant amount of biomass and release a high amount of nitrogen in their faecal plumes (Roman & McCarthy, 2010; Roman et al., 2016), enhancing *primary production* (supporting ecosystem service) on their foraging grounds. They can also provide *supporting services* in coastal lagoons by increasing the *cycling of nutrients* through horizontal movements carried out between seascape's ecosystems and their microhabitats (Katona & Whitehead, 1988; Roman et al., 2014; Kiszka et al., 2022). These large-sized animals also provide *regulating services* by accumulating tons of carbon during their long lives that will not only generate food and habitat for communities of micro and macro-organisms (Pershing, 2010) but also release all the stored carbon to the atmospheric cycle (Quaggiotto et al., 2022) when their carcasses eventually sink to the bottom habitats.

The biomass of aquatic mammals' populations is also associated with *provision services* to several indigenous coastal communities (Reeves & Smith, 2006) where hunting is supported and managed by the International Whaling Commission. The beluga whale *Delphinapterus leucas* (Pallas, 1776) and harbour seal *Phoca vitulina* Linnaeus, 1758, for example, are some of the Arctic marine mammal species harvested by Chukchi communities in coastal Arctic lagoons (Neakok, 1985; Wolfe et al., 1999) to be primarily used as food resource, while skin and other raw materials are used for clothing, equipment and ornamental on a local and small scale.

Non-consumptive interactions with aquatic mammals, such as cooperative fishing between fishers and delphinids in coastal lagoons also represent significant *cultural services* in some regions of Australia, Mauritania, Myanmar and Brazil (Fairholme, 1856; Pryor et al., 1990, Machado et al., 2019; Smith et al., 2009, Kumar et al., 2012). For example, the threatened Irrawaddy dolphin *Orcaella brevirostris*

(Owen in Gray, 1866) population from Ayeyarwady river, in Myanmar, herd fish schools (mainly mullet) from murky or deeper waters towards cast-net fishers standing in small canoes awaiting specific behaviours by the dolphins perceived as cues or 'signal' to where and when casting their nets, increasing catching rate (Smith et al., 2009). A subset of small and highly resident Lahille's Bottlenose dolphin *Tursiops truncatus gephyreus* Lahille, 1908 populations from Laguna and Barra de Imbé/Tramandaí, southern Brazil, also engage in such cooperative behaviour with local artisanal fishers (Simões-Lopes et al., 1998). Similarly, these dolphins detect, aggregate and drive fish schools (mainly mullet) towards shallow waters where fishers stand in line or on moored canoe. Then, dolphins also display behavioural cues that fishers understand as a signal to cast their nets. For both cases, although the benefits to dolphins remain inconclusive, it is hypothesised that dolphins are more easily able to access fish schools disrupted by barriers or fishing gear (Simões-Lopes et al., 1998). Interestingly, the artisanal fishers from Laguna perceive and recognize that this human-dolphin cooperation provides not only food but also *recreation leisure to tourists*, as well as a *sense of place, social relations, aesthetics, cultural heritage values, knowledge system, and cultural diversity* to their community (Machado et al., 2019).

### Impacts on coastal lagoon biodiversity and consequences in ecosystem services provision

Coastal lagoons provide a wide spectrum of ecosystem services (Newton et al., 2018). In a recent effort, Pérez-Rufafa et al., (2019) highlighted 58 ecosystem services related with processes and attributes from coastal lagoons. Also, the authors highlighted the importance of geomorphological features and ecological processes to coastal lagoons functioning. In our review, we aimed to complement this knowledge, through a more specific understanding of how species functions generate ecosystem processes and services in coastal lagoons. By specific examples, we highlighted how the fauna that inhabits coastal lagoons perform a broad range of ecological functions and may have broad-scale implication for a variety of services. However, both species and ecosystems have been subject to a continuous intensification of human pressures worldwide (Tundisi et al.,



2015; He & Silliman, 2019). Coastal areas are the most populated regions of the world (Harley et al., 2006), and are subjected to multiple human-driven impacts associated with regional and local land-use changes (i.e., industrialization, urbanization, agriculture and aquaculture). In addition, the potential future effects of global climate changes and ocean acidification will extensively impact the functioning, survival and spatial distribution of the aquatic (and aquatic-dependent) fauna in coastal lagoons accelerating species loss—a primary and readily worrying threat to ecosystem services provision (Díaz et al., 2006; Cardinale et al., 2012; Loreau & de Mazancourt, 2013).

The stability and resilience of coastal lagoon ecosystems are affected by biodiversity loss (Bec et al., 2011; Loreau & de Mazancourt, 2013; Thibaut & Connolly, 2013), because biodiversity components and ES have an intricate co-dependent complex relationship (Loreau et al., 2001; Hooper et al., 2005; Balvanera et al., 2006; Gamfeldt et al., 2008; Cardinale et al., 2012). Hence, linking socio-economic systems with the uses of ecosystem services necessarily encompasses the historical transformations of human occupations, land use reclamation, and the related impacts—direct or indirect—on biodiversity (He & Silliman, 2019; Pérez-Ruzafa et al., 2019; Thanh et al., 2020).

Direct causes of biodiversity loss in coastal lagoons include nutrient enrichment, pollution with pesticides and heavy metals, alteration of morphology and hydraulics (with consequent physical and chemical water changes), overfishing and the invasion of exotic species (Newton et al., 2014; Vasconcelos et al., 2017; Teichert et al., 2018; Elliott et al., 2019). All of these threats occur simultaneously, with distinct frequency and magnitude depending on the coastal lagoon. So, in this section we intend to highlight general patterns and specific examples, that are not meant to cover all possible impacts to these ecosystems and their related services.

Nutrient enrichment can derive from different human activities and sources (e.g., input of sewage, fertilizer leaching and runoff from agricultural fields, and mariculture). Increases in nutrient concentrations are more intense in shallow lagoons, and in those with intermittent or no connection with the sea, due to little water renewal (Glibert et al., 2007; Wazniak et al., 2007; Fertig et al., 2013). Increased nutrient concentration boost primary production (i.e.,

a process known as eutrophication) and the consequent outcome are context-dependent (i.e., landscape, proximity to river inputs), because the composition of primary producers may differ following nutrients enrichment and change the energetic base of the food web (Nixon, 2009; Glibert et al., 2010). For example, studies conducted in Florida Bay and the Chincoteague Bay, in the United States, showed that lagoons in which food webs are based on diatoms presented more zooplankton grazers, ultimately supporting a large biomass of secondary producers. In contrast, in lagoons where phytoplankton biomass is dominated by flagellates or cyanobacteria (i.e., *Prorocentrum cordatum* (Ostenfeld) Dodge, 1976, *Microcystis* sp.), the system sustains a proportionately greater flow through the microbial loop (Legendre & Rassoulzadegan, 1995; Glibert et al., 2010). Eutrophic conditions may lead to a decrease in fish richness while enhancing fishery yield in coastal lagoons (Pérez-Ruzafa et al., 2007). The higher fishing resource availability may foster food, income, and cultural provision values in coastal lagoons. However, in chronic eutrophication cases, the effects are deleterious, including hypoxia or anaerobiosis, harmful algal blooms, massive animal mortalities and changes in species patterns (Pérez-Rufaza et al., 2012), which may impact longstanding and negatively the provision of ecosystem services.

In some coastal lagoons, rooted macrophytes may be replaced by macroalgae or phytoplankton after nutrient enrichment (Wazniak et al., 2007), and because the structural complexity provided by macrophytes are vital for the recruitment of many coastal fish species, such as *Rutilus rutilus* (Linnaeus, 1758) and *Perca fluviatilis* Linnaeus, 1758 (Snickars et al., 2009), their abundance and biomass might be severely reduced, preventing coastal communities of maintaining fisheries, tourism and cultural heritage activities. Eutrophication in coastal lagoons also drives hypoxia because algal blooms form mats in the water surface and reduce light availability underwater, and prevents submerged primary producers to carry out photosynthesis, driving both submerge fauna and flora death (D'Avanzo & Kremer, 1994). In Negombo lagoon, in Sri Lanka, hypoxic events have been frequently registered in both wet and dry seasons, and were related to high seawater temperature, poor water circulation and high nutrient loadings (Hsieh et al., 2021). Raw faces and uncollected solid waste have been dumped

into the lagoon's water, reducing water quality and fishing stocks due to unfavorable ecosystem conditions, imposing real threats to tourism and fisheries in the lagoon (Hsieh et al., 2021). Additionally, cyanobacterial blooms have the potential to release toxins (i.e., microcystin) that are incorporated into the coastal lagoon's food web (Bukaveckas et al., 2017). Elevated microcystin levels have persisted 7–8 years after cyanobacterial bloom in Curonian lagoon, and extended to several consumers including benthivorous, planktivorous and piscivorous fishes (Bukaveckas et al., 2017), imposing potential risk to human health and economic activities of coastal communities (Ferrão-Filho & Kozłowsky-Suzuki, 2011; El Mahrad et al., 2020).

Contamination of coastal water with pesticides and heavy metals are also a prominent threat because toxic and persistent substances have the potential to bioaccumulate along the food web and be retained in the sediment (Odjer-Bio et al., 2015), posing direct and chronic threats to human health. Amphipod species (i.e., *Orchestia montagui* Audouin, 1826 and *Porcellio scaber* Latreille, 1804), for example, grow less in heavy metal-contaminated lagoons in Tunisia because they invest more energy to avoid contamination and are less able to survive due to biochemical alterations and cellular mutations from the intoxication (Jelassi et al., 2020). And while feeding in the sediment, amphipods can make toxic compounds previously retained in the sediment available in the food web. Fish and crustacea are also vulnerable to intoxication in contaminated lagoons, and poses additional risk to coastal communities that relies mostly on the food and income provisioning of fisheries and mariculture within the lagoons (Márquez et al., 2008; Ramírez-Ayala et al., 2021).

Fish and crustaceans, are the two most important resource for the livelihoods of local communities and to regional economies, harvested through fishing and mariculture. Nevertheless, overfishing is a major threat to coastal lagoons due to the removal of biomass of specific taxa (i.e., with commercial values) to attend economic needs, but prevents the ecosystem to maintain the natural balance through species interactions (especially trophic ones). The commercially exploited wild population of the manila clams, *Venerupis (Ruditapes) philippinarum* (A. Adams & Reeve, 1850) have been declining in the Pialassa Baiona lagoon due to low recruitment and

low population recovery due to overfishing (Ponti et al., 2017), reducing water purification service (i.e., through filtering) and food and income provisioning to coastal communities. In Langebaan lagoon, during stock assessment of the southern mullet *Chelon richardsonii* (Smith, 1846), the authors found that overfishing reduced current spawner-biomass-per-recruit to only 24% of the pristine (unfished) levels, indicating a stock at risk of recruitment failure (Horton et al., 2019).

Alteration of morphology and hydraulics can occur due to embankments for construction purposes and artificial sand bar opening. In Mar Menor lagoon, in Spain, dredging and enlarging of its inlets led to the colonization of the algae *Caulerpa prolifera* (Forsskal) J.V.Lamouroux, 1809, changing the lagoon's bottom sediment, that was previously dominated by the phanerogam *Cymodocea nodosa* (Ucria) Asch. And benthic microalgae. The progressive increase in the organic matter content of the sediments lead to changes in the faunal assemblages and strong decrease in fishing yields, especially of mugilids and sparids (Pérez-Ruzafa et al., 2020). Recreational boating and the support infrastructure (i.e., marinas) can also degrade coastal lagoons habitat through aquatic vegetation removal (Hansen et al., 2019), which in turn reduce sediment stabilization, nutrient uptake and storage (Moksnes et al., 2018), and ultimately reduce densities of fish (i.e., pike [*Esox lucius* Linnaeus, 1758] and juvenile perch [*Perca fluviatilis*] (Diehl & Eklöv, 1995; Craig, 2008). Interestingly, Hansen et al., (2019) compared the effects of boating-macrophyte removal to that of eutrophication.

Artificial sand bar opening justification are many-fold, such as to improve fisheries, to reduce water level to avoid inundation of residences nearby, to improve water quality by exporting nutrients to the sea and to reduce hypoxia risks (Esteves et al., 2008). However, negative consequences include osmo-regulatory stress of species adapted to low salinity gradients (Esteves et al., 2008 and reference therein), reduction of photosynthesis of phytoplankton due to increased UV radiation (Conde et al., 2000), and inefficient effect on eutrophication control, because internal loads of sediment phosphorus regeneration quickly enhance phosphorus concentrations in the water column and maintain eutrophic conditions in some lagoons (Esteves et al., 2008). For example, in Iquipari lagoon, sand bar opening undergone

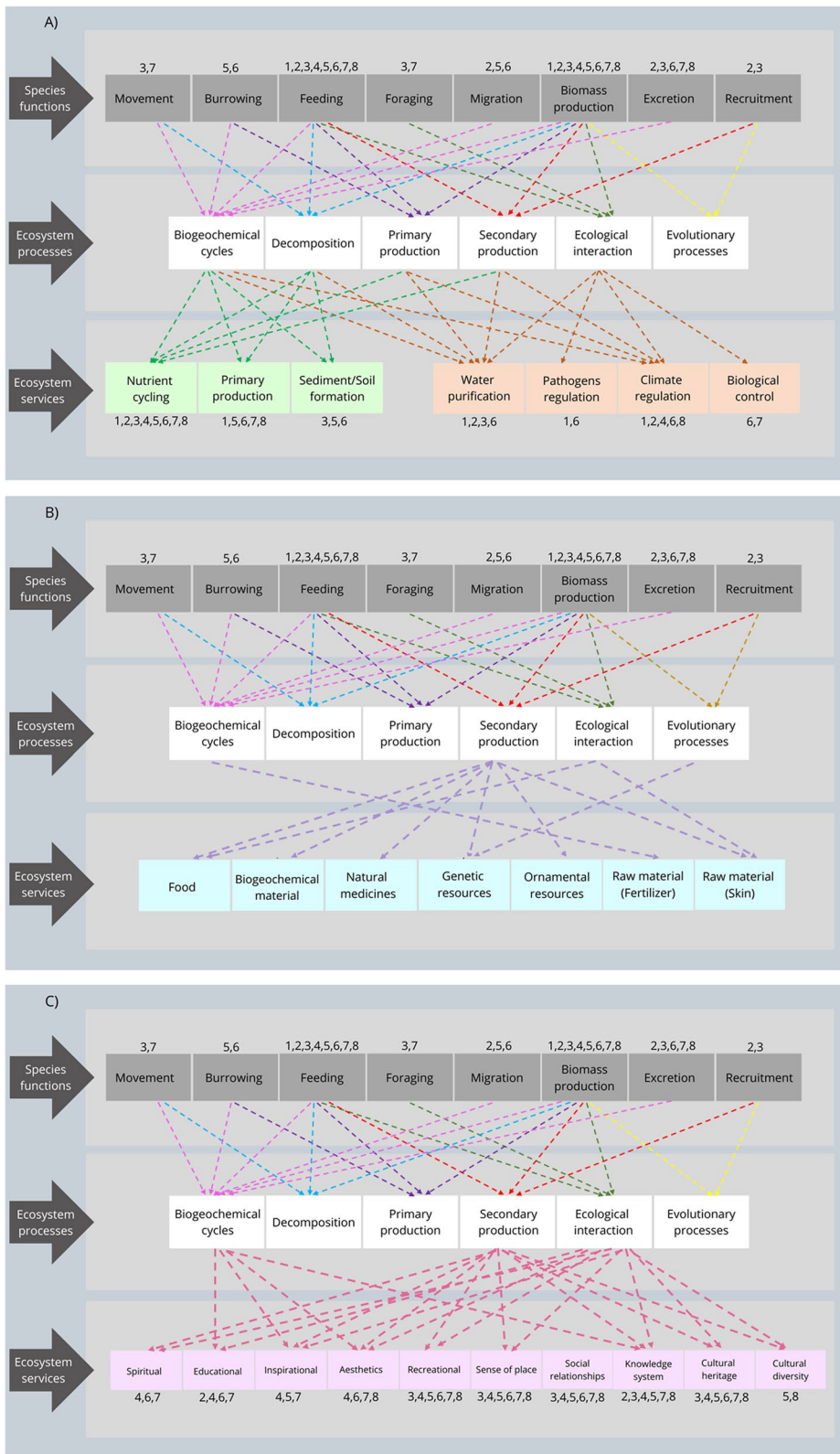
a regime shift from a macrophyte-dominated system to an opportunistic phytoplankton dominated system (Suzuki et al., 2002), altering the entire ecosystem metabolism, changing species biodiversity and composition and ultimately affecting nutrient cycling (i.e., support service), and food and tourism provision.

In addition to the physical habitat and water quality alterations, coastal lagoons can be more susceptible to species invasion because of its connectivity with terrestrial, freshwater and marine ecosystems. Negative effects from invasions on coastal shallow lagoons are expected to rise, because brackish invasive species are stress-tolerant to a broader range of stressors (e.g., *Cercopagis pengoi* (Ostroumov, 1891); *Mnemiopsis leidyi* A. Agassiz, 1865; *Tilapia* sp.; *Moina macrocopa* (Straus, 1820)) (Katsanevakis et al., 2014; Franco et al., 2021; Macêdo et al., 2022). The introduction of fishes in coastal lagoons, such as *Tilapia*, can cause both services and disservices to society (Deines et al., 2016). *Tilapias* can enter the coastal lagoons due to evasion from aquaculture in the vicinity or be introduced for mariculture (Watanabe et al., 2010). These species are of high commercial value to artisanal and sports fisheries, generating income to local communities (Agbekpornu et al., 2016). The “grain-to-feed conversion rates” for fish are equivalent to those of chicken, and far more economical than pork or beef (Canonico et al., 2005). It can cause disservices because it can promote decline in many native fishes, through predation, parasitism or competition (Canonico et al., 2005). It can also cause reduction of aquatic plants and the habitat they provide to native species (Canonico et al., 2005).

In Vistula lagoon, in Poland, the introduction of the alien gammarid species (*Gammarus tigrinus* Sexton, 1939, *Dikerogammarus haemobaphes* (Eichwald, 1841), *Pontogammarus robustoides* (Sars, 1894) and *Obesogammarus crassus* (G.O. Sars, 1894)) induced nearly total decline of native populations of the marine crayfishes *Gammarus zaddachi* Sexton, 1912 and *Gammarus duebeni* Lilljeborg, 1852. The authors attributed it to competitive exclusion, but also to a lowered biotic resistance of the recipient community, mostly associated with increasing pollution and eutrophication of the lagoon (Grabowski et al., 2006). In contrast, in preserved coastal lagoons, such as the Taman Bay, the native macrozoobenthos community was resilient to the alien *Anadara kagoshimensis* (Tokunaga, 1906). The alien arrived in 2003,

and a decade later macrozoobenthos abundance did not depend on whether the alien or indigenous species were dominant, and the authors attributed this outcome to the absence of persistence disturbances in the lagoon (Kolyuchkina et al., 2019). Intermediate outcomes have also been reported. For example, the introduction of the dark false mussel *Mytilopsis leucophaeata* (Conrad, 1831) into an urban coastal lagoon in Brazil improved lagoon water quality, and this was perceived as a good outcome. However, it could also increase phosphorus availability through excretion because the species forms dense clusters in newly invaded areas, and might induce additional prejudices to native species in the long term (Neves et al., 2020). The consequences of species invasion in coastal lagoons are context-dependent and data-poor, which limits our ability to draw conclusive inferences about ecosystem services loss due to invasion. However, as an overall pattern, in the long term, alien species are most likely to change ecosystem metabolism and food web structure with direct changes in the supporting capacity of coastal lagoons.

If not enough, beyond local and regional changes to coastal lagoons, we are facing a global changing climate, in which coastal lagoons may experience significant variation in rainfall, temperature, and fluctuations in sea level that could also change the salinity and thermal regime of the habitat (Hawkins, 2012, 2016)—key drivers of biodiversity in coastal lagoons. Nevertheless, if climate change predictions become true (IPCC, 2021), floristic and faunistic composition and ecosystem structure are likely to collapse since future conditions could be unable to accomplish the main processes needed to mitigate impacts or provide ecosystem services. For example, global warming is predicted to indirectly affect coastal lagoons from nutrient uptake and resistance to eutrophication (Lloret et al., 2008) to the timing and route of migrating birds (Gatter, 1992). The combined effects of increased temperature, ocean acidification and sea-level rise (Range et al., 2012; Roberts et al., 2017), combined with local stressors (Mahapatro et al., 2013), will likely stress human communities that value the presence of particular lagoons. Predicted abrupt climatic variability through higher water evaporation leading to extreme shallowness will increase salinity resulting in the loss of nursery and mating habitats, affecting commercially important taxa (e.g., shrimps, crabs, and many fish). These conditions can



◀**Fig. 2** Diagram of the pathways from species functions to ecosystem processes and services in coastal lagoons. The most relevant functions assumed for the biological groups described in this study are responsible for a number of processes which in turn are crucial for the provisioning and regulating (A), supporting (B) and cultural (C) services. The numbers from 1 to 8 represent each of the biological groups (1: microbes; 2: zooplankton; 3: polychaetas; 4: mollusks; 5: macro-crustaceans; 6: fishes; 7: birds; 8: aquatic mammals). Dashed arrows represent the proposed links connecting the pathways

influence the bioavailability and toxicity of contaminants as metals (Vazquez et al., 1999) and the hydrocarbons derived from petroleum (Ramachandran et al., 2006). Impacts have led to increasing specialization and adaptation to a narrower range of abiotic conditions, such as those that can be experienced within lagoonal habitats (Telesh et al., 2011), there is nevertheless an increasing risk of population declines and local extinctions, considering unknown effects of multiple stressors acting together (Martínez-Megías and Rico, 2021).

## Final remarks

Coastal lagoons connect freshwater-brackish-marine and terrestrial habitats and support a high diversity of animal assemblages that ranges from microbes to aquatic mammals. From the review of these assemblages (we did not exhaust all of biodiversity components), we could clarify through a cause-effect perspective how species trophic interactions and habitat use (i.e., species functions) are intrinsically linked with ecosystem processes and services provided by coastal lagoons (Fig. 2). We identified 26 ecosystem services categorized as supporting (5), regulating (4), provisioning (7) and cultural (10) services that are associated with functions performed by several animal groups, highlighting a high functional redundancy between them. Besides, it was notorious that species functions from distinct groups might be complementary to compose ecosystem processes and services, evidencing that the species loss might affect both (i.e., processes and services).

Owing to animal assemblages having temporal and spatial asynchrony to use coastal lagoons habitats and that these ecosystems suffer from

deleterious impacts from point and nonpoint sources, the conservation and management of coastal lagoons should be carried out through broad lens, to ensure species diversity, habitat heterogeneity and ecosystem functioning. The use of the ecosystem services' approaches on the watershed scale with multi-actors' collaboration should be adopted in management plans, to maximize the ecosystem services provision by lagoons and, consequently, the well-being of human societies, especially in coastal zones and densely populated areas worldwide.

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**Declarations**

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