Current knowledge of New Caledonian marine and freshwater ichthyofauna, SW Pacific Ocean: diversity, exploitation, threats and management actions

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Regular paper

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by

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Abstract. – Located in the Southwest Pacific Ocean, the New Caledonian archipelago hosts a diversified and original ichthyofauna. Marine ecosystems host 2,339 species of fish, including ~1,450 for coral reefs alone and a total of 94 endemics, especially in deep environments. The proximity of the centre of biodiversity (the "coral triangle"), as well as a great variety of coastal habitats and their relatively good "state of health" are probably major reasons for this high species richness. Freshwaters (excluding estuaries and brackish water) have 94 species, including 12 introduced and 8 endemics. Most of these species are diadromous, essentially amphidromous, and illustrate biological traits adapted to local rivers. New Caledonian ichthyofauna is subject to various disturbances of varying intensity and/or frequency. Some disturbances are natural and affect habitats rather than the fish species, such as cyclones, which can affect both coastal ecosystems (coral reefs, seagrass beds, mangroves) and freshwater ecosystems. Anthropogenic pressures on ichthyofauna are of several natures. Fishing is widely practiced, both in rivers and in coastal environments and in the EEZ, but does not currently seem to pose a serious threat to targeted populations. New Caledonian aquaculture is largely focused on shrimp farming, but fish farming (currently marginal) could develop in the near future. Mining activities related to the extraction of nickel ore (and cobalt to a lesser extent) are however a much more serious problem. The potential impacts of these mining activities differ from those of cyclones, in particular by their regular (if not permanent) and non-punctual nature on the one hand, and by the fact that they considerably increase the risk of contamination of freshwater and coastal environments by metallic trace elements on the other hand. These metallic elements as well as various organic contaminants (pesticides and PCBs) are indeed found in coral reef fish. Other more specific threats concern freshwater fish, such as hydraulic developments or the proliferation of certain introduced and invasive species. For all New Caledonian aquatic ecosystems, the major issue of climate change cannot be ignored, but its impacts still remain poorly documented. About 15,000 km² of coral reef and lagoon areas have been listed as UNESCO World Heritage since 2008 and are therefore protected and regulated, with regard to the activities authorized within these areas. In addition, there are more informal protections in other coastal areas where the Melanesian tribes have a customary management. Finally, various regulations exist at local authority level (environmental codes) to protect certain sensitive species.

Résumé. – État actuel des connaissances sur l'ichtyofaune marine et dulçaquicole de la Nouvelle-Calédonie, SO océan Pacifique : diversité, exploitation, menaces et mesures de gestion.

Situé dans le sud-ouest de l'océan Pacifique, l'archipel néo-calédonien héberge une ichtyofaune diversifiée et originale. Les milieux marins rassemblent 2339 espèces de poissons, dont ~1450 pour les seuls récifs coralliens et un total de 94 endémiques, surtout en milieux profonds. La proximité du centre de biodiversité (le "triangle de corail"), ainsi que la très grande variété des habitats côtiers et leur relatif bon "état de santé" sont probablement des raisons majeures pour expliquer cette richesse spécifique élevée. Les eaux douces (hors estuaires et eaux saumâtres) comptent 94 espèces, dont 12 introduites et 8 endémiques. La plupart de ces espèces sont diadromes et surtout amphidromes et illustrent un mode de vie adapté aux rivières locales. L'ichtyofaune néo-calédonienne est soumise à différentes perturbations d'intensité et/ou de fréquence variables. Certaines perturbations sont naturelles et vont affecter les habitats plus que les espèces de poissons elles-mêmes, comme par exemple les cyclones qui peuvent affecter à la fois les écosystèmes côtiers (récifs coralliens, herbiers de phanérogames, mangroves) et d'eaux douces. Les pressions anthropiques sur l'ichtyofaune sont de plusieurs natures. La pêche est largement pratiquée, tant en rivière qu'en milieux côtiers et dans la ZEE, mais ne semble pas actuellement constituer une grave menace pour les populations ciblées. L'aquaculture néo-calédonienne est très largement focalisée sur la crevetticulture, mais la pisciculture (actuellement marginale) pourrait se développer dans les années à venir. Les activités minières en lien avec l'extraction du nickel (et accessoirement du cobalt) sont une problématique nettement plus sérieuse. Les impacts potentiels de ces activités minières diffèrent de ceux des cyclones notamment par leur côté régulier (sinon permanent) et non ponctuel d'une part, et par le fait qu'ils accroissent considérablement le risque de contamination des milieux dulçaquicoles et côtiers par des éléments traces métalliques d'autre part.

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Ces éléments métalliques ainsi que divers contaminants organiques (pesticides et PCBs) sont en effet retrouvés dans les poissons coralliens. D'autres menaces plus spécifiques concernent les poissons d'eau douce, comme les aménagements hydrauliques ou encore la prolifération de certaines espèces introduites et invasives. Pour tous les écosystèmes aquatiques néo-calédoniens, l'enjeu majeur du changement climatique ne peut être ignoré, mais ses impacts restent encore peu documentés. Environ 15 000 km^2 de zones récifo-lagonaires sont inscrites au Patrimoine Mondial de l'UNESCO depuis 2008 et sont, de ce fait, protégées et règlementées. À ceci s'ajoute des protections plus informelles dans d'autres secteurs côtiers où les tribus mélanésiennes assurent une gestion coutumière. Enfin, diverses règlementations existent au niveau des collectivités locales (codes de l'environnement) pour protéger certaines espèces sensibles.

INTRODUCTION

Knowledge of biodiversity is one of the major challenges of our time, both for scientists who describe species and seek to better understand their roles in the functioning of ecosystems, and for managers in charge of the environment who need updated data to make the best possible decisions. Tropical island environments, such as New Caledonia, are largely concerned by such issues. This article focuses on aquatic environments, and its objectives are i) to present current knowledge on the diversity of marine and freshwater fish, ii) to make an inventory of fishing and aquaculture activities, iii) to assess the main threats to fish as well as present the current protection measures and iv) discuss the main research perspectives.

GEOGRAPHICAL SETTING

New Caledonia includes a set of islands in the Southwest Pacific Ocean (21°30'S, 165°30'E). Located in the Coral Sea, approximately 1,400 km east of Australia and 1,800 km northeast of New Zealand, the territory is bordered by the Solomon Islands to the north, Vanuatu to the northeast and the Fiji Islands to the east (Fig. 1). Covering an area of 18,575 km^2 (Bonvallot *et al*., 2012) and bordered by approximately 3,400 km of coastline, New Caledonia is the third largest island in the South Pacific after Papua New Guinea and New Zealand. Three large groups compose the archipelago: the mainland (named "Grande Terre") and its coral reef-lagoon complex, the Loyalty Islands (Ouvéa, Lifou, Tiga and Maré), small islands/islets in the far south EEZ (Walpole, Mathew and Hunter), plus the coral reef-lagoon complex of Chesterfield-Bellona and Lansdowne-Fairway (Fig. 1). Grande Terre stretches over 400 km long along a south-east / north-west axis (between 20° and 22°30'S), on around 50 to 70 km wide and has a lagoon area that extends over nearly 800 km from north to south. It is crossed by a mountain range, peaking at more than 1,600 m (ISEE, 2012). This asymmetrical massif separates Grande Terre into two regions with different characteristics: wide plains characterize the western coast, while the eastern coast is steep and interspersed with deep valleys. At the ends of Grande Terre are the Isle of Pines to the south and the Huon and Surprise atolls (forming the Entrecasteaux reefs) to the north.

Positioned about 100 km to the east, the Loyalty Islands line up on an axis parallel to that of Grande Terre. Lifou is the largest of the islands (1,196 km^2), followed by Maré (642 km^2), Ouvéa (132 km^2) and Tiga (11 km^2). The Loyalty Islands are divided into two groups: the raised islands (Lifou, Maré and Tiga) and the atolls or pseudo-atolls (Ouvéa, Beautemps-Beaupré, Petrie and Astrolabe reefs; Fig. 1). The elevated islands form large limestone plateaus of coral origin, surrounded by a generally narrow fringing reef. There are no barrier reefs around these islands, nor any river, which reduces terrigenous inputs. The atolls are of various sizes and types: Ouvéa is a relatively large tilted atoll surrounded by a barrier reef and a belt of islets on two thirds of its perimeter, the last third being constituted by the main island of coral limestone. The other atolls are much smaller, only Beautemps-Beaupré is well closed and has an islet. Finally, the Chesterfield archipelago is located 550 km northwest of Grande Terre. This wide plateau of coral origin, surrounded by its string of islets, is divided into two large areas: Chesterfield and Bellona. Its western facade is largely bordered by a barrier reef, while in the east the barrier reef is continuous only south of Bellona. The Chesterfields and Bellona plateaus are dotted with sometimes very large coral pinnacles. All of these reefs are halfway between Grande Terre and Australia and little frequented by boats and fishermen. Several seamounts are located within the EEZ, mainly in its southern part (Fig. 1).

New Caledonia crosses the Tropic of Capricorn, and therefore undergoes both tropical and temperate seasonal influences. The island is subject to the prevailing south-eastern trade winds (60 to 70% of the winds), which moderate its climate described as tropical oceanic. The annual variations determine two main seasons, (i) the hot and humid austral summer (mid-November to mid-April) characterized by prevailing south-eastern winds and periods of tropical depressions or cyclones and (ii) the cooler and drier austral winter (mid-May to mid-September) with western winds generated by subtropical to polar air masses. These two main seasons are interspersed with two inter-seasons; a transition period from mid-April to mid-May and a dry season from mid-September to mid-November. The main rainy season occurs in summer from January to March (rainfall 140-218 mm) and

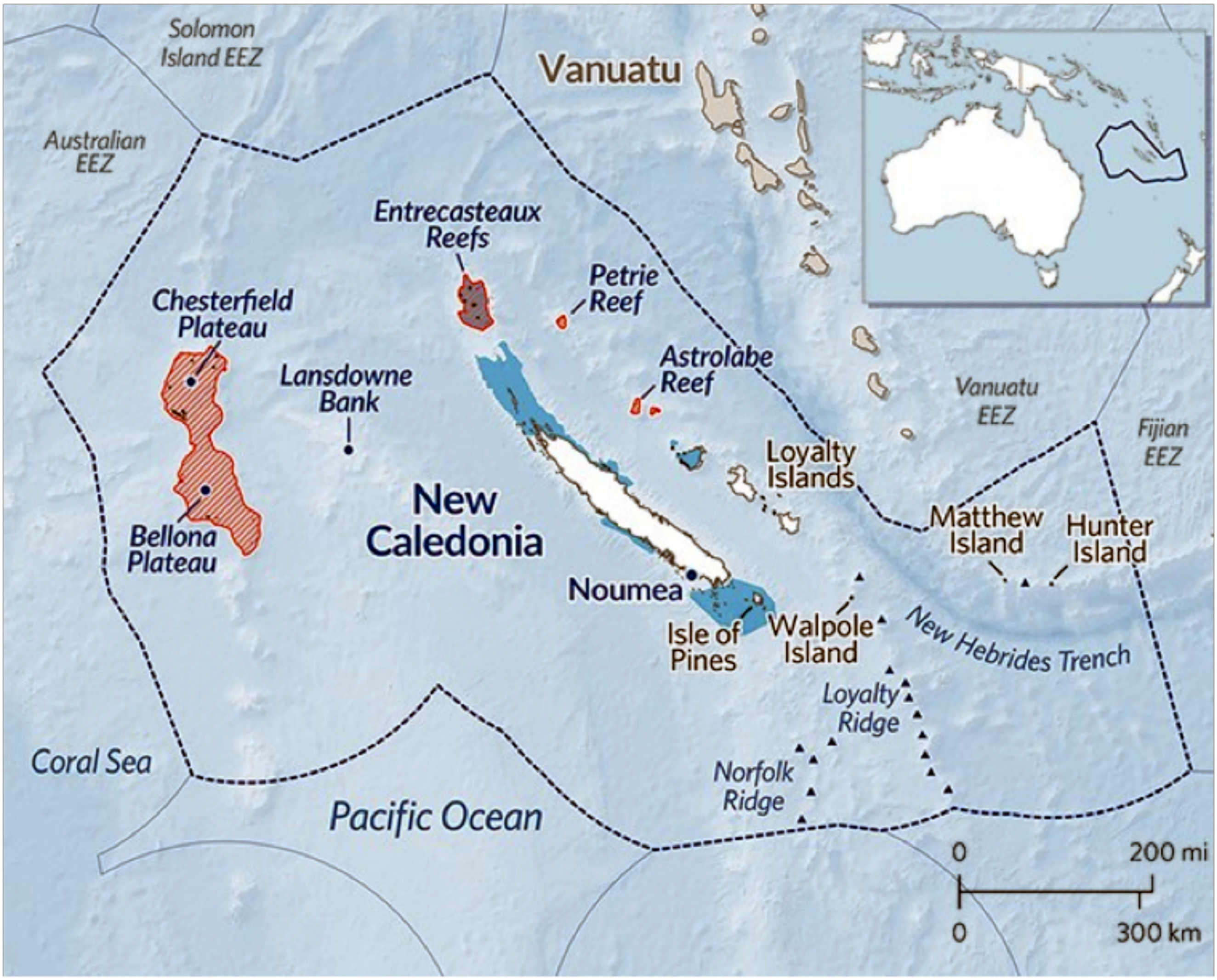

Figure 1. – Location of New Caledonia in the southwest Pacific. Dotted lines: limits of the New Caledonian EEZ, triangles: main seamounts, blue zones: UNESCO world heritage areas, and red hatched zones: fully protected marine areas. Modified from New Caledonian Government, Global seamounts database, The Pew charitable trust.

a second, more modest, occurs in the cool season around July (rainfall 120 mm). The rains are unevenly distributed on Grande Terre, because its asymmetry generates more rainfall on the east coast than on the west coast. The season alternation, as well as the extension in latitude of the island, has as a direct consequence a spatio-temporal variability of surface water temperature. It usually ranges between 26 and 28°C in the hot season (sometimes > 29°C in the north and ~25°C in the south), against 22 to 24°C in the cool season (sometimes > 25°C in the north and ~20°C in the south) (Rougerie, 1986). This general pattern can be, however, distorted by the La Niña and/or El Niño phenomenon.

New Caledonia is an Oceanian territory attached to France. Its current institutional organization benefits from a particular status of broad *sui generis* autonomy (*i.e.* "of its own kind"), established by the Nouméa agreement on May 20, 1998. The organic law resulting from this agreement provides in particular a gradual transfer of powers from mainland France to the local New Caledonian government. The institutional organization of the territory is composed of the Congress and a Government, as well as three Provinces: the Loyalty Islands Province, the North Province and the South Province.

Since the 1970s, New Caledonia has experienced a significant demographic growth, resulting in 85% of the natural balance and 15% of the migratory balance mainly linked to the exploitation of the nickel ore, the main resource of New Caledonia. This growth mainly concerns the South Province, moderately the North Province, while the Loyalty Islands tend to present a population decrease. New Caledonia currently has ~270,000 inhabitants, 75% of whom live in the South Province, 18% in the North Province and 7% in the

Loyalty Islands (ISEE, 2020). This concentration in the South Province is mainly explained by the growing attractiveness of the population for the city of Nouméa, the only large city on the island with ~95,000 inhabitants in 2019. This polarization of the population is increasing by the urbanization of the neighbouring municipalities, forming the "Grand Nouméa" and encompassing two thirds of the people inhabiting the archipelago.

MARINE FISH DIVERSITY

Fricke *et al.* (2011) recorded 2,320 native marine species belonging to 241 families, in New Caledonia. Since this study, 19 new marine species were recorded (Fricke *et al.,* 2015; Moléana *et al.*, 2016), resulting in 2,339 species now known from New Caledonian marine waters. The ten most diversified families are Gobiidae (161 species, excluding diadromous species), Labridae (128), Pomacentridae (112), Serranidae (100), Apogonidae (80), Blenniidae (64), Scorpaenidae (54), Myctophidae (53), Macrouridae (52) and Muraenidae (49) (Fricke *et al.*, 2011, 2015). Among these marine species, Kulbicki (2007) estimated that ~1,450 are coral reef associated (possibly up to ~2,000; Kulbicki *et al.*, 2018); the other marine species being mostly pelagic or deep-water fish and, in a relatively smaller number of cases, mangroves, soft-bottom or seagrass associated species.

This high fish diversity is driven by several factors of both regional and local importance. The proximity of the "coral triangle", *i.e.* the area around Indonesia-Philippines-Salomon Islands, known as the most diversified area from the marine realm, is obviously a key-factor (Harmelin-Vivien, 1989). New Caledonia is also characterized by a wide number of types of coral reefs (fringing reefs, reefs around isolated islets in the lagoon, barrier reefs, atolls, scattered pinnacles, etc.) and reef-associated habitats (seagrass and algal beds, mangroves, lagoonal soft-bottoms), all present in a wide area (~23,000 km^2) that represents the second widest coral reef complex ecosystem of the world. Thus, such a situation offers numerous habitats and microhabitats for fish allowing a high diversity of available ecological niches (Letourneur *et al.*, 1997). In addition and despite episodic natural and anthropogenic pressures, New Caledonian coral reefs globally present a good "state of health" with median to high coral cover and generally a high coral diversity (Wantiez, 2008; Job, 2018). These healthy conditions offer diverse habitats and wide capacities of resource use for fish species (Bell and Galzin, 1984; Chabanet *et al.*, 1997).

Fricke *et al.* (2011) mentioned 94 marine endemic species in New Caledonia, equivalent to ~4.0% of its marine ichthyofauna, but the authors recognized this value could be likely overestimated due to low sampling efforts in neighbouring islands thus preventing a real assessment of endemism. These endemic species are mostly deep-species (*sensu* deeper than 200 m) with 55 species (~58.5% of marine endemics). In terms of biogeographical affinities and considering only species found between the 0-80 m depth-range, the ranking of the most speciose families in New Caledonia is unsurprisingly very similar to those found in other sites from the region, such as Vanuatu, Fiji, Tonga, Papua New Guinea and the Great Barrier Reef of Australia (Fricke *et al.*, 2011).

FRESHWATER FISH DIVERSITY

Fricke *et al.* (2011) recorded 125 native freshwater species in New Caledonia, a value that included fish species using what the authors called "transitional waters", *i.e.* brackish waters. In fact, most of these species are marine species using occasionally estuaries or mangroves, most often at their juvenile stages or for episodic entrances in rivers in search of food. An on-going work taking into account uncertainties regarding the determination and misidentifications of freshwater fish species and the detection of cryptic species indicates that there are 82 native freshwater (*sensu stricto*) species including 8 endemics, plus 12 introduced species (Keith *et al.*, in prep.). Based on the latter values, the endemism of New Caledonian freshwater fish is ~10%. The most diversified families are Gobiidae (30 species, including Gobionellinae, Gobiinae and Sicydiinae), Eleotridae (9) and Syngnathidae (7) (Keith *et al.*, in prep.). Rivers are mainly colonised by diadromous fish, *e.g.* migrant amphihaline species performing a part of their biological cycle in freshwaters. These are represented by catadromous (Anguillidae and Kuhliidae) and amphidromous fish (Gobiidae, Eleotridae and Rhyacichthyidae); the latter category being dominant in New Caledonian freshwaters (Keith, 2003). Indeed, river systems are mainly colonised by fish with a life cycle typically adapted to the conditions that prevail in New Caledonian habitats, *i.e.* young oligotrophic rivers, subject to extreme climatic and hydrological seasonal variations. These species spawn in freshwater, the free embryos drift downstream to the sea where they undergo a planktonic phase during 2-3 months, before returning to the rivers to grow and reproduce (Keith, 2003). These species contribute most to the diversity of fish communities and have the highest levels of endemism. Amphidromy is considered as a major adaptation to insular, young environments (Keith *et al.*, 2015; Mennesson *et al.*, 2018).

In addition, there are two main ecoregions in New Caledonia that structure the freshwater fish species richness, *i.e.* metamorphic units in the north-eastern part of the island and peridotite nappes, in the southern part of the island, from which nickel ore is extracted (Maurizot *et al.*, 2020). The rivers on the north-east coast have numerous steeply sloping sectors which bring a wide range of rheophile species, preferring fast, well-oxygenated sectors under forest cover. In this area, there is a relationship between the stream flow and the species found within each zone. The majority of species occupy moderate flow habitat. On the contrary, populations found in facies where the current is very strong (rapids or waterfalls) are characterised by the presence of species having specific adaptations. For instance, this is the case for gobies of the Gobiidae-Sicydiinae group that are capable of resisting very strong currents by sticking to the substrate with their ventral suction cup (Keith *et al*., 2015). The majority of the species live exclusively in the lower and medium courses, whereas others are found only in the higher course. The rivers in the south have the highest rates of endemic species, which are adapted to live in poor and oligotrophic rivers with a high level of metallic trace elements such as nickel. Here the majority of species occupy moderate flow habitat and live mainly in the lower and middle courses. Unlike New Caledonia, all the neighbouring archipelagos (Vanuatu, Fiji, etc.) are of volcanic origin and therefore have only basaltic or raised coral reef watersheds. Their freshwater fish fauna is rather similar to those of the New Caledonian north-east coast with which they share several species.

FISHERIES

Fishery activities in New Caledonia currently concern ~690 fishermen, for ~520 boats (GVT-NC, 2019, 2021). These activities are dominated by artisanal fisheries (~550 fishermen, ~500 boats and ~85% of the whole fishing effort in New Caledonia) operating mostly within lagoonal waters and on coral reef outer slopes. Total catches did not vary much over years, fluctuating between ~840 and ~990 tonnes within the five last years (GVT-NC, 2019). The catches represented ~940 tonnes in 2019, including ~270 tonnes of holothurians (mostly *Holothuria scabra* Jaeger, 1833), ~90 tonnes of crustaceans (mostly the mud crab *Scylla serrata* (Forsskål, 1775)) and ~15 tonnes of shells (mostly the troca *Tectus niloticus* (Linnaeus, 1767)). Apart from holothurians that are exported towards the Asian markets, the catches are fully intended to the local market (GVT-NC, 2019). The most targeted fish were mullets (family Mugilidae; ~150 tonnes), snappers (Lutjanidae; ~65 tonnes), spangled-emperor (*Lethrinus nebulosus* (Forsskål, 1775), considered separately from the other emperors ~57 tonnes), other emperors (Lethrinidae, except *L. nebulosus*; ~43 tonnes), groupers (Serranidae; ~50 tonnes), the unicornfish (*Naso unicornis* (Forsskål, 1775)), small mackerels (mostly *Selar* spp.) and parrotfish (Scarinae) with ~35 tonnes each, followed by "picots", a local name often associating surgeonfish and rabbitfish (Acanthuridae and Siganidae, respectively) with ~33 tonnes. Deep fish caught on the outer slope reached ~28 tonnes, mostly deep snappers (*Etelis* spp., *Pristipomoides* spp.). In total, fish captures (all categories pooled) represented a commercial value of ~520 million of Pacific francs in 2019, *i.e.* ~4.3 million € (GVT-NC, 2019). Deep *Beryx* spp. populations were targeted during the 90s but this fishery does not exist anymore due to a drastic and rapid decrease in that resource (Payri *et al*., 2019).

The offshore fishing fleet operates with longlines mostly in the western part of the New Caledonian EEZ, and to a lower extent near the Loyalty Islands (Fig. 2). This fishing fleet comprised 3-5 boats (operating ~0.6 million hooks/year) until the mid-90s, whereas it currently reached 18-20 boats (operating ~5 million hooks/year) in the last years (GVT-NC, 2019). Overall in 2019, their catches represented ~2,530 tonnes, for a commercial value of ~1,080 million of Pacific francs (*i.e.* ~9 million €). The main targeted fish species are tunas, mostly *Thunnus alalunga* (Bonnaterre, 1788) (~1,680 tonnes) and *T. albacares* (Bonnaterre, 1788) (~555 tonnes) (GVT-NC, 2019). Other important species are *T. obesus* (Lowe, 1839) and marlins; dolphinfish, swordfish and few other species constituted a small fraction of catches. Overall, 80% of these catches are intended to the local market, 11% are exported to Japan, 7% to the US (including American Samoa for a local cannery) and the remaining 2% to Europe (GVT-NC, 2021).

Subsistence fishing, for both auto-consumption and customary gifts, remains difficult to assess. A first attempt was done to quantify this phenomenon in the Northern Province at the end of the 90s (Letourneur *et al*., 2000; Labrosse *et al*., 2006). These authors estimated that catches for auto-consumption in that Province ranged from ~1,050 to ~1,200 tonnes/year in that period. More recently, another work estimated the subsistence catches by Melanesian tribes at ~3,700 tonnes for the three Provinces pooled (Sourisseau *et al*., 2020). Approximately 55% of theses catches came from the Northern Province, *i.e.* 2,035 tonnes, and ~65% of this latter value (*i.e.* ~1,320 tonnes) are marine fish, thus indicating a trend to an increase in fishing pressure on coral reef fish during the last decades. In the same study in the Northern Province, freshwater catches were estimated at ~480 tonnes, mainly eels (*Anguilla* spp.), the introduced invasive tilapia (*Oreochromis mossambicus* Peters, 1852), and freshwater shrimps (*Macrobrachium* spp.) (Sourisseau *et al*., 2020).

AQUACULTURE

Aquaculture in New Caledonia is mainly dedicated to the non-native blue shrimp, *Litopenaeus stylirostris* (Stimpson, 1871). This activity picked in 2005 with a production of ~2,300 tonnes, but progressively decreased afterwards to ~1,300-1,500 tonnes/year, mainly due to *Vibrio* spp. induced mortalities (Lemonnier *et al*., 2006). Currently, shrimp

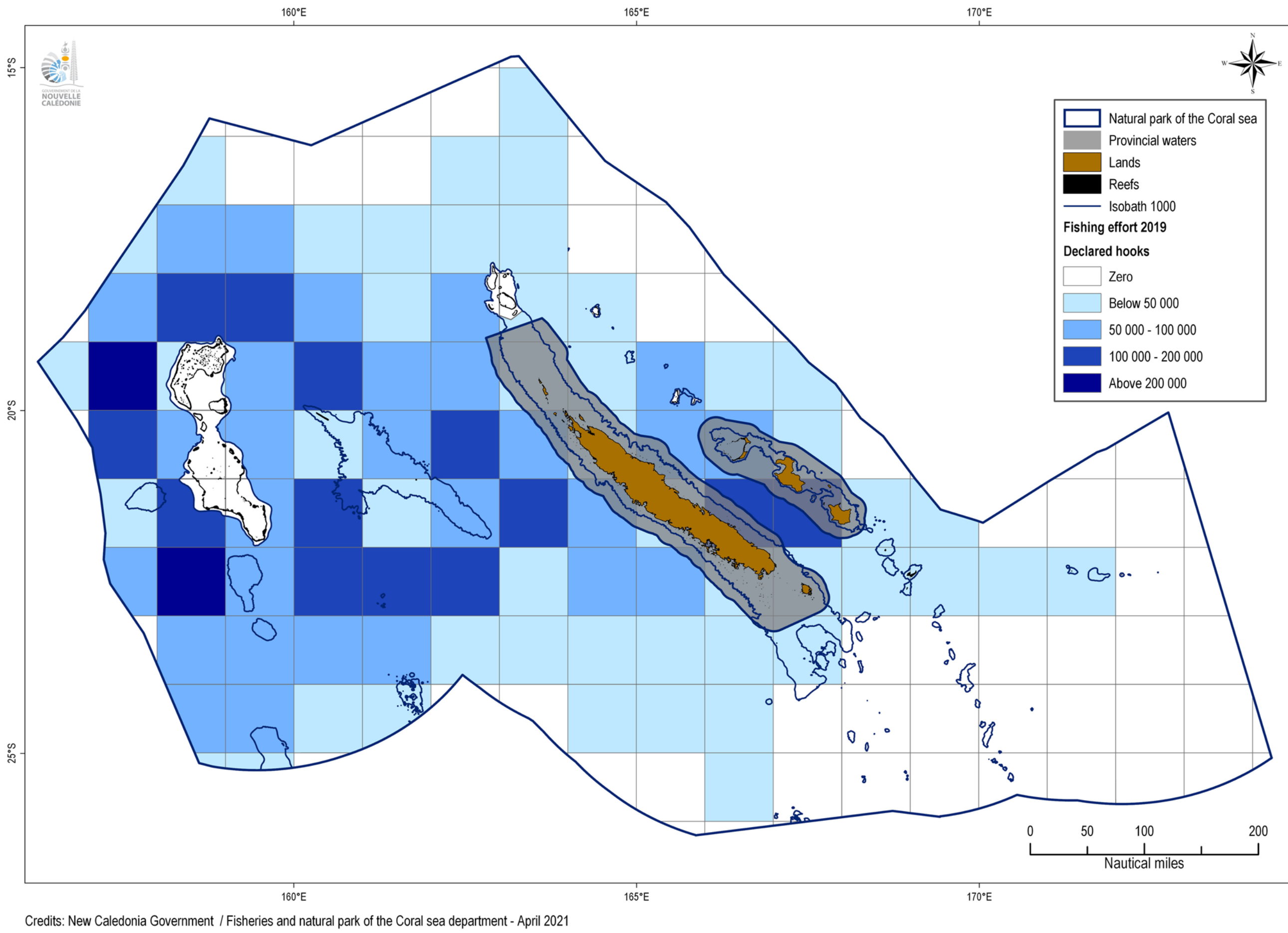

Figure 2. – Location of fishing effort of the offshore fishing fleet in the New Caledonian EEZ in 2019 (Source: GVT-NC, 2021; modified by Léa Carron).

aquaculture takes place in 19 farms totalling ~585 hectares (GVT-NC, 2019). Approximately 55-60% of the production is intended to the local market; the other part is exported (Japan, Europe and US). Fish farming is by far less developed mainly due to the diversity and abundance of lagoonal and offshore fish provided by local fisheries. However, for the last 7-8 years, attempts were made to develop fish farming dedicated to relatively high priced species (from local standards, *i.e.* ~10 €/kg) and/or highly demanded fish, such as *Siganus canaliculatus* (Park, 1797), *S. lineatus* (Valenciennes, 1835) (Siganidae) and *Lutjanus sebae* (Cuvier, 1816) (Lutjanidae). These activities are still at an experimental stage but offer interesting production development prospects. Currently, the production of these species remains marginal with, respectively, ~0.5, ~1 and ~7 tonnes in 2019 (GVT-NC, 2019). A previous attempt to develop fish farming of *Cromileptis altivelis* (Valenciennes, 1828) (Serranidae) was recently abandoned.

Freshwater fish farming does not exist anymore, but several attempts were made in the 50s-60s. The main attempt concerned the tilapia, *O. mossambicus*, that escaped from its ponds and now colonizes numerous rivers and ponds all over New Caledonia, and even some coastal brackish waters (Keith, 2005; Lefeuvre *et al.*, 2007). Others attempts concerned the carp *Cyprinus carpio* Linnaeus, 1758 (that also escaped from their ponds and then colonized some rivers), and the trout *Oncorhynchus mykiss* (Walbaum, 1792), a species for which the cultivation attempt was unsuccessful.

THREATS AND PROTECTION MEASURES

Major threats on marine ichthyofauna

Marine fish are subject to recurrent natural disturbances such as hurricanes, or outbreaks of the coral-eating sea star *Acanthaster solaris* (Schreber, 1793) on coral reefs. Hurricanes remain an usual disturbance in tropical regions, and their frequency and intensity may significantly shape coral reef habitats, by reducing live coral cover, generating high number of dead coral fragments, increasing hyper-sedimen-

Table I. – Major threats to marine fish.

Threats	Contributing processes
Bleaching events due to high sea surface temperature	Alteration can mostly be indirect (through habitat changes): – decrease of live coral cover (alteration or rupture of the dinoflagellate-coral symbiosis); – increase of internal and external bioerosion on dead corals, reducing the structural complexity of coral reefs, thus reducing habitat use and food resources for fish; – increase of algal populations that compete with corals for space, potentially implying a shift from coral reef towards algal reef.
Temperature increase, ocean acidification and/or deoxygenation	Alteration can be direct or indirect: – alteration of key-biological processes such as reproduction or food behaviour; – alteration of key-physiological processes such as digestive processes and maintenance of homeostasis; – alteration of calcification processes (skeleton, otoliths).
Fish habitat degradation	Alteration can mostly be indirect: – alteration of habitats from dredging, sand / debris extraction, or constructions / extensions of ports, marinas etc.; – removal of/damage to watershed (riparian, forests) or coastal (mangroves) vegetation increasing terrigenous runoffs, and decreasing surface filtration processes and trapping of pollutants; – sedimentation resulting from the above activities, mining activities, deforestation and/or watershed development, smothering habitats and spawning sites.
Pollutions altering water quality	Alteration can be direct or indirect: – chemical contaminants in mangroves, seagrass beds and/or coral reef fish issued from agricultural runoffs (nutrients and pesticides), metallurgic factories and mines (metals), and/or industry/urban discharges (metals, organic compounds, endocrinian disruptors); – increased sedimentation that affect fish habitats, fish physiology, food resources, reproduction and larval recruitment / settlement.

tation possibly burying coral reefs close to river mouths and/or enhancing algal growth through nutrient inputs (river runoffs, "internal resuspension") (Letourneur *et al*., 1993; Harmelin-Vivien, 1994). New Caledonia regularly faces such type of disturbances, but hurricanes having highly significant impacts on a large spatial scale remained scarce until now; the last really severe hurricane was Erica in 2003 (Wantiez *et al*., 2006; Guillemot *et al*., 2010).

By strongly reducing live coral cover, *Acanthaster solaris* outbreaks significantly impact benthic habitat characteristics and their three-dimensional structure (Adjeroud *et al*., 2018), thus having potentially drastic consequences on fish populations, especially those having a clear benthic-related behaviour. Although impacts of such outbreaks on corals were documented in New Caledonia (Adjeroud *et al*., 2018), their consequences on coral reef fish populations remain unstudied in that territory to our knowledge. A current debate, also shared for hurricanes, is to know if such events will become more frequent in the coming decades in relation to global changes.

Fishing activities remain currently identified as not of strong concern in most lagoonal sectors for most species, and checks are carried out to verify compliance with regulations, including for recreational fishing (see below). The pelagic fish stocks from EEZ waters are currently also not in danger (despite an increase in efforts and catches over the last decades), but special attention will have to be maintained, if not reinforced, in order to manage sustainable captures, particularly on the most commercially profitable species (*T. obesus*) and to prevent illegal catches within EEZ by fishing fleets from some Asian countries.

However, marine fish are facing several major threats, such as the consequences of bleaching events, temperature increase, various pollutions and habitat degradations (Tab. I). Bleaching events may have consequences similar to those mentioned above for *A. solaris* outbreaks. However, they act at much wider surface areas than *A. solaris* outbreaks and their expected increase in frequency / amplitude in the coming decades due to climate change, notably the increase of sea surface temperatures, might significantly alter the resilience of coral reefs (Hugues *et al*., 2018, 2019) and thus raise questions about the persistence of all coral reef communities including fish (Souter *et al*., 2021). Other "complementary" threats could be associated to the on-going temperature increase, such as ocean acidification and deoxygenation. The potential consequences of both phenomena on tropical fish remain poorly known. Wilson *et al*. (2010) pointed out 17 questions of interest linked to these topics that could enhance our understanding of the effects of ocean acidification and deoxygenation on fish biology / physiology as well as on population dynamics. To our knowledge, these questions however remain subjects of research.

Table II. – Major threats to native freshwater fish (adapted from Keith *et al*., 2013).

Threats	Contributing processes
Altered flow regimes and loss of longitudinal and lateral connectivity	– Water pumping for domestic or agricultural use; often related to the installation of structures such as dams and weirs; – Land use change such as forest and native vegetation clearance in the catchment altering water balance (through increased evaporation and decreased water retention).
Physical barriers	Direct alteration through: – the construction of dams, weir; – the often poor design of culverts, fords and urban structures such as channels creating high velocities and/or enhanced erosion and reduced wet margins.
Fish habitat degradation	Alteration can be direct or indirect: – alteration of in-stream habitats from mining, gravel extraction or constructions of dams and roads; – removal of/damage to riparian vegetation altering surface filtration processes and reducing shade, cooling and oxygenation of water; – sedimentation resulting from above activities and from adjacent land and/or catchment development, smothering stream bed substrate and spawning sites.
Lowered water quality	– chemical contaminants in streams and estuaries/river mouths from agricultural run-off (nutrients and pesticides) and/or industry/urban discharges (metals, organic compounds, endocrinian disruptors); – increased suspended sediments that affect fish physiology, reproduction and migrations – especially at larval and post larval phases.

Various contaminants, metallic trace elements as well as PCBs and pesticides, are found in almost all coral reef fish (Bonnet *et al*., 2014; Briand *et al*., 2014, 2018; Fey *et al*., 2019). These authors showed that the origin of those compounds is unsurprisingly linked to several human activities, such as either insufficiently controlled wastewaters or river runoffs that thus transport contaminants from urbanization and agricultural practices into the lagoon. Another serious risk is related to mining activities to extract nickel ore (open sky mines), but also bush fires and deforestation (Richmond, 1993; Letourneur *et al*., 1998; Burke *et al*., 2011; Briand *et al*., 2018). In addition to potential transport of pollutants into the lagoon, such disturbances most often generate a high level of soil erosion during rainfalls, and a drastic sedimentation on coasts that, in turn, may strongly affect fish habitats (Letourneur *et al*., 1993, 1998, 1999). The presence of such contaminants in fish from the remote Entrecasteaux atolls (Letourneur, unpubl. data), ~300 km north of New Caledonia and far from any known potential source of pollution, suggests that compounds might be transported over long distances through marine currents and/or atmospheric deposit at a regional scale rather than only local scale. The situation might be different for pelagic fish (mainly tunas), notably for contamination by mercury (Hg). Indeed and even if the hypotheses evoked above can partly explain Hg concentration in tunas, the role of complex biochemical processes in the mercury cycle is better and better understood. In particular, the preferential formation of methyl-mercury (MeHg) in the 400-600 m deep layer can explain why tunas' preys living in those depths are more concentrated in Hg than sub-surface preys (Houssard *et al*., 2019). Thus, species feeding preferentially on deep preys, such as *Thunnus obesus*, are more contaminated by Hg than other species feeding on preys in shallower layers, such as *T. alalunga* and *T. albacares*.

Major threats on freshwater ichthyofauna

Freshwater native communities exhibit behaviours that are fostered by environmental factors such as free passage (along the river), natural vegetation cover, unmodified flows, quality of estuaries, and/or the absence of introduced species. Most freshwater fish in New Caledonia are amphidromous, having a larval migrant stage and use different parts of streams and rivers at different phases in their life cycle. The larvae need to move freely downstream. When they return to freshwater as post-larvae after weeks at sea, those that live in upper reaches of the catchments must have free passage to ensure the success of their adult populations (Keith *et al.,* 2013, 2015). Physical structures, altered flow regimes, degraded habitats (in-stream and riparian) and lowered water quality can all play a role in affecting behaviour and enabling or not fish passage (Tab. II). It is thus critical to consider major threats that potentially affect habitat characteristics and/or fish movements, in order to protect the freshwater biodiversity of insular streams (Keith *et al.,* 2013, 2021). For the species living specifically in rivers with a peridotite watershed, the physical deterioration and water pollution from nickel mining and deforestation are blamed. A recent study showed that the marble eels (*Anguilla marmorata*) are impacted *in situ* by metals issued from mining activity (Germande *et al*., 2022). Among organs, the liver was found to be the most affected with average nickel concentrations of 5.14 mg/kg *versus* 1.63 mg/kg for eels away from mines leading to dysregulation of numerous genes involved in oxidative stress, DNA repair, apoptosis, reproduction and both lipid and mitochondrial metabolisms (Germande *et al.*, 2022). Silt deposits on rocks prevent algal growth, eliminating predominant food source; for Sicydiine gobies for example it also prevents fish adhesion to rocks, thus a decreasing access to headwater habitats and spawning grounds availability (Lord and Keith, 2006, 2008).

The impacts of freshwater introduced species on native fauna remain poorly known in New Caledonia. However, it should be hypothesised that the most widespread introduced species, *Oreochromis mossambicus*, and the most aggressive one (as generalist predator), *Micropterus salmoides* (Lacepède, 1802), likely represent the most serious potential threats for native freshwater fish. Overall, introduced species mainly colonised the lower reaches of rivers, lakes and brackish ponds. Thus, rheophile species in New Caledonia, which are often endemic and mainly colonise upstream areas (for instance, the Sicydiinae genera *Lentipes, Sicyopus, Sicyopterus, Stiphodon, Smilosicyopus*), might therefore be less affected by introduced species in their upstream adult habitats. However, the indigenous species all have a planktonic marine larval phase followed by colonisation of the river from the estuary and predation by exogenous species, as well as the occupation of niches by introduced taxa, could have an unfavourable impact on the recruitment of these species and therefore on stocks (Keith *et al.,* 2013).

The potential impacts of climate change on freshwater species were discussed in tropical islands (Gehrke *et al.*, 2011; Keith *et al.*, 2013, 2015). Increased temperatures, decreased dissolved oxygen levels, increased toxicity of pollutants along with altered hydrologic regimes (in lotic systems) or more pronounced stratification and eutrophication (in lentic systems) are likely to occur. This would affect food webs and change habitat availability and quality as well as the physiology and life histories of fish. In addition, endemic species in fragmented habitats will be less able to cope. All freshwater habitats in New Caledonia could become affected by changes in the timing, intensity and frequency of rainfall and resulting changes in flow variability characteristics (Gehrke *et al.*, 2011). Several climate change scenarios could be considered (Bell *et al.*, 2011; Gehrke *et al.*, 2011). These authors concluded that most rivers in the Pacific islands will likely receive more run-off as a result of the expected increases in rainfall of 5-20% by 2035 and 10-20% by 2100. New Caledonia will likely be an exception with an expected decline of up to 20% during winter by 2100, increasing the variability of seasonal flow in the rivers there. Flow being a major driver of New Caledonian stream ecosystems, such rainfall variations need to be carefully monitored in the coming decades, especially in middle and upper reaches of catchments where increased flows and flow variability will create greatest exposure. Surface water temperatures are expected to increase (up to 3°C by 2100) and the maintenance of shade provided by the riparian vegetation will become even more crucial. Increased temperatures and the impacts of modifications in ocean currents might also affect freshwater diadromous fish: currents in the western Pacific might vary over seasons in both intensity and direction (Ganachaud *et al.*, 2011), possibly influencing the larval dispersal and the recruitment of a number of diadromous species.

Protection measures

Since the creation of the first marine protected area (MPA) in 1970, New Caledonia encompassed 23 implemented MPAs in the mid-2000s (ranging from 13 to 17,150 ha), totalling ~42,000 ha within lagoonal waters (Wantiez, 2008). Several Melanesian tribes also protect their coastal waters through a customary management that most often significantly reduce and/or control fishery activities in those areas. A key-step in protection measures occurred in 2008: the good “state of health” of New Caledonian coral reefs is at the origin of the inscription of six parts of the coral reef complex, totalling ~15,000 km², in the UNESCO world heritage. Finally and after a strong local and national support, the “Parc Marin de la Mer de Corail” was created in 2014. With the whole New Caledonian EEZ (except lagoonal waters), it constitutes one of the widest marine protected area of the world, with ~1.25 million km².

In order to avoid excessive recreational fishing pressure in the most populated part of New Caledonia (*i.e.* the South Province), a maximum of 40 kg of catches (pooling fish, shells and crustaceans) per day and per boat is authorized in the lagoon, or a maximum of 15 individuals of pelagic fish, if fishermen operate outside the lagoon (Province Sud, 2019). In addition, some species are protected all year round (for instance the Napoleon wrasse *Cheilinus undulatus* Rüppell, 1835, Serranidae over 1 m long or > 15 kg, and all shark species) or during the reproduction period such as *Siganus* spp. from September to the end of January. Serranidae cannot be fished during reproductive aggregations, usually in passes also from September to end of January (Province Sud, 2019). Regarding sharks, recent fatal attacks, most likely due to *Carcharinus leucas* (Müller & Henle, 1839) and/or *Galeocerdo cuvieri* (Péron & Lesueur, 1822), led local authorities in 2019-2020 to allow spatially and numerically limited animal catches in order to reduce the risks for stakeholders. Finally, in October 2021, these two shark species have been removed from the list of protected species from the “Code de l’Environnement” of the South Province (Province Sud, 2021).

Several species of freshwater fish, including the endemic and the most endangered species, are protected in New Caledonia in the North Province (22 species) (Code de l’Environnement, Titre V, Chap 1, article 251-1) and in the South Province (17 species) (Code de l’Environnement, Titre IV, article 240-1). But no area was specifically protected for the conservation of freshwater fish, and only a few studies were done on endangered species (for example see Mennesson *et al.*, 2017 for *Protogobius attiti* Watson & Pöllabauer, 1998 and *Schismatogobius fuligimentus* Chen, Séret, Pöllabauer & Shao, 2001).

RESEARCH PERSPECTIVES

The on-going integrative taxonomic studies will continue to resolve the uncertainties regarding the determination of both marine and freshwater fish species (Fricke *et al.*, 2015), and possibly allow to detect cryptic species. It was indeed necessary to adapt the fish taxonomic reference system and to update the knowledge and tools used by the environmental agents and the various water stakeholders. The change in the number of species or their validity may have direct consequences on the legal regulation (protected species, fishing, management and conservation), on the IUCN red lists, but also on the species management plans. The use of complete or partial mitogenomes in the study of the cryptic biodiversity of freshwater fishes has considerably increased the number of species known from New Caledonia, including new species (+15%) (Keith *et al.*, in prep.). The use of eDNA in such a context could also be very useful. For instance, some shark species are usually not seen in visual censuses, baited cameras or not caught through experimental fishing, and the use of eDNA in New Caledonian coral reefs gave new insight on shark diversity (Bakker *et al.*, 2017; Boussarié *et al.*, 2018).

Due to high fish diversity on New Caledonian coral reefs, it could be really challenging to detect the true diversity and abundance values during visual surveys, for example during a program to monitor the effectiveness of an MPA. This is a reason why several efforts were implemented by local researchers the last decade towards automatic video systems, which then allow a more precise analysis of richness, densities or biomasses (Mallet *et al.*, 2014). An improvement in these biodiversity assessment techniques involving artificial intelligence for an automatic recognition of species and individual fish size is currently under development (Villon *et al.*, 2021). Recent work and others still in progress also concern research on emblematic species such as sharks (Boussarié *et al.*, 2018; Juhel *et al.*, 2021) and manta rays (Lassauce *et al.*, 2022), both for conservation issues and for understanding the role of these species in the functioning of marine ecosystems.

New Caledonian authorities seek to tend more and more towards food self-sufficiency, and fisheries are one of the potential levers to achieve this objective. In most Pacific Island Nations, fish intake is two to four times the worldwide average, contributing up to 90% of animal protein intake (Charlton *et al.*, 2016). Coastal reef fish make approximately 70% of species consumed, with the remainder consisting of primarily tuna (Bell *et al.*, 2013). The recent COVID-19 pandemic has brought this dependence and connection into sharp focus as many community members (re)turn to subsistence fishing as a source of livelihood and/or food. This is in large part due to severe disruptions to import supply chains, associated hikes in food prices, and catastrophic declines in key economic sectors such as tourism and remittances. Not all fish are equal. Indeed, the nutritional composition (*i.e.* macro-, micro-nutrients and fatty acids) of fish varies considerably among species (Hicks *et al.*, 2019; Robinson *et al.*, 2022). Thus, the nutritional benefits derived from fish consumption depend on both the quantities and diversity of fish consumed. However, metallic trace elements and organic pollutants (pesticides and PCBs) are widely distributed in Pacific coral reef species (Fey *et al.*, 2019), potentially having direct and/or indirect impact on human nutrition and well-being. Climate change stands to exacerbate these risks, impairing both food and nutrition security. Among others, climate change may lead to changes in the nutritional content and contaminant level of consumed marine resources due to changes in fish species composition, biological processes (*e.g.* growth, fecundity) (Hugues *et al.*, 2018), access to commonly harvested species and ocean productivity. Of particular concern for contaminant loading is increased runoff because of increased rain rates and associated total local rainfall (Kossin, 2018). Given this context, a research project has been recently built to assess the often cited but rarely deeply investigated trade-off in risks *versus* benefits in consuming fish (Letourneur *et al.*, unpubl. report) and research actions just began.

For the species found only in ultramafic rivers in New Caledonia, their environmental requirements restrict their natural distribution to this type of rivers, which are particularly limited in the area. A large amount of basic biological and ecological information still needs to be collected, including reproduction, development, larval life, etc. Habitat requirements and distribution patterns in the ocean or coastal waters would be key steps for a better understanding of the pelagic larval phase, the dispersal abilities of endemic and widespread species and the evolution of the amphidromous life cycle. This is of a particular interest to understand the species resilience and propose reliable tools for the management and conservation of patrimonial species. This may support the restoration and conservation of ecological corridors. A key-issue is to implement conservation measures required to protect the remaining populations of the most endangered species and to rehabilitate lakes and rivers that could house these species (protection of the last remaining habitats, control of the nickel mining and of the deforestation in surrounding habitats).

CONCLUSIONS

Although our knowledge of New Caledonian marine fish has significantly improved in the past decades, the "state of the art" remains contrasted when considering different marine ecosystems. For instance, deep fish are globally poorly studied due to logistic and economic constraints, while it is suspected that a large part of deep fish biodiversity (including trophic and functional interactions) remains to be discovered. In the EEZ, *i.e.* pelagic ecosystem, most research concerned assessment and monitoring of *Tuna* spp. stocks as well as their contamination by mercury (Houssard *et al*., 2019; Moore *et al*., 2020), but other components of the system remains largely unstudied although efforts recently began to focus on micronekton (Receveur *et al*., 2020). On coastal zones, fish communities within some habitats are relatively scarcely investigated until now such as soft-bottoms (Wantiez *et al*., 1996; Kulbicki *et al*., 2000) or mangroves (Thollot 1992; Letourneur *et al*., 2017). Despite coral reefs attracted by far most of the ichthyological research during the past decades, it should be recognized that functional interactions between coral reefs and adjacent ecosystems, such as seagrass beds, soft-bottoms and mangroves did not generate significant investigations, except for a few specific cases (Paillon *et al*., 2014; Briand *et al*., 2015; Letourneur *et al*., 2017). These various observations simply underline that, despite the research efforts on the New Caledonian marine ichthyofauna, vast fields of studies still constitute a stimulating challenge to improve our knowledge and our understanding of the functioning of these very speciose ecosystems.

Amphidromous species colonising the rivers are a major component of New Caledonian streams. They are distributed along the river from the estuary to the higher reaches according to their ecology. Some are therefore only found at a certain altitude according to the water temperature, its physical and chemical parameters and its hydrological properties. The majority of the species encountered are rheophile; in order to maintain a high level of biodiversity, it is therefore necessary to maintain high flow rates (Keith *et al*., 2015). The seasonal variability favours massive freshwater flow in estuaries, thus allowing post-larvae from the sea to colonise the rivers. Moreover, the shorter the river and the steeper its slope, the higher the success of the downstream migration of larvae to the sea as, according to several authors, larvae have less than three days after hatching to reach the estuary (Ellien *et al*., 2016). In these kinds of rivers, the colonisation of the rivers by post-larvae will also be more successful: as they return, they must climb upstream as fast as possible in order, on the one hand, to flee predators that are in greater number in the lower course, and, on the other hand, to find a suitable territory (Keith *et al*., 2021). In our current state of knowledge on the life cycle of the amphidromous species (biology, ecology) the impact of humans on freshwater species is highly significant, from estuaries to lower or elevated reaches; all habitats are crucial to many amphidromous species. As these have to undertake two migrations between freshwaters and the sea. The success of such a life cycle, is contingent on maintaining the mountain/forest-river-ocean corridor and maintaining an open channel to allow free movement between both habitats. Estuaries must be preserved as they represent areas where certain species transit, where larvae of amphidromous species exit to sea, and where post-larvae and juveniles enter to colonise the rivers (Keith *et al*., 2021).

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