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1 **Harbours as unique environmental sites of multiple anthropogenic stressors**
2 **on fish hormonal systems**

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5 Emma Gairin^{a,#,*}, Mélanie Dussenne^{b,#}, Manon Mercader^{a,#}, Cécile Berthe^{c,d}, Mathieu Reynaud^{a,d}, Marc
6 Metian^e, Suzanne C. Mills^{c,d}, Philippe Lenfant^f, Laurence Besseau^b, Frédéric Bertucci^g, David
7 Lecchini^{c,d,□}

8
9 ^aMarine Eco-Evo-Devo Unit, Okinawa Institute of Science and Technology, 1919-1 Tancha, Onna-Son,
10 Kunigami District 904-0495, Okinawa, Japan

11 ^b Sorbonne Université, CNRS UMR Biologie Intégrative des Organismes Marins (BIOM), F-66650
12 Banyuls-sur-Mer, France.

13 ^c Laboratoire d'Excellence "CORAIL", France

14 ^d PSL Université Paris, EPHE-UPVD-CNRS, UAR3278 CRIOBE, 98729 Moorea, French Polynesia

15 ^e International Atomic Energy Agency - Environment Laboratories, 4a Quai Antoine 1er, MC-98000,
16 Principality of Monaco, Monaco

17 ^f Université de Perpignan Via Domitia, Centre de Formation et de Recherche sur les Environnements
18 Méditerranéens, UMR 5110, 58 Avenue Paul Alduy, F-66860 Perpignan, France

19 ^g Functional and Evolutionary Morphology Lab, University of Liège, 4000 Liege, Belgium
20

21
22 * Corresponding author: emma.gairin@hotmail.fr

23 # Equal first authors

24 □ Equal last authors

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27 **ABSTRACT**

28 Fish development and acclimation to environmental conditions are strongly mediated by the
29 hormonal endocrine system. In environments contaminated by anthropogenic stressors, hormonal
30 pathway alterations can be detrimental for growth, survival, fitness, and at a larger scale for population
31 maintenance. In the context of increasingly contaminated marine environments worldwide, numerous
32 laboratory studies have confirmed the effect of one or a combination of pollutants on fish hormonal
33 systems. However, this has not been confirmed *in situ*. In this review, we explore the body of knowledge
34 related to the influence of anthropogenic stressors disrupting fish endocrine systems, recent advances
35 (focusing on thyroid hormones and stress hormones such as cortisol), and potential research perspectives.
36 Through this review, we highlight how harbours can be used as “*in situ* laboratories” given the variety
37 of anthropogenic stressors (such as plastic, chemical, sound, light pollution, and invasive species) that
38 can be simultaneously investigated in harbours over long periods of time.

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40 ***Keywords: fish, harbours, hormones, anthropogenic stressors, pollution, plastics, ALAN***

41

42 **Introduction**

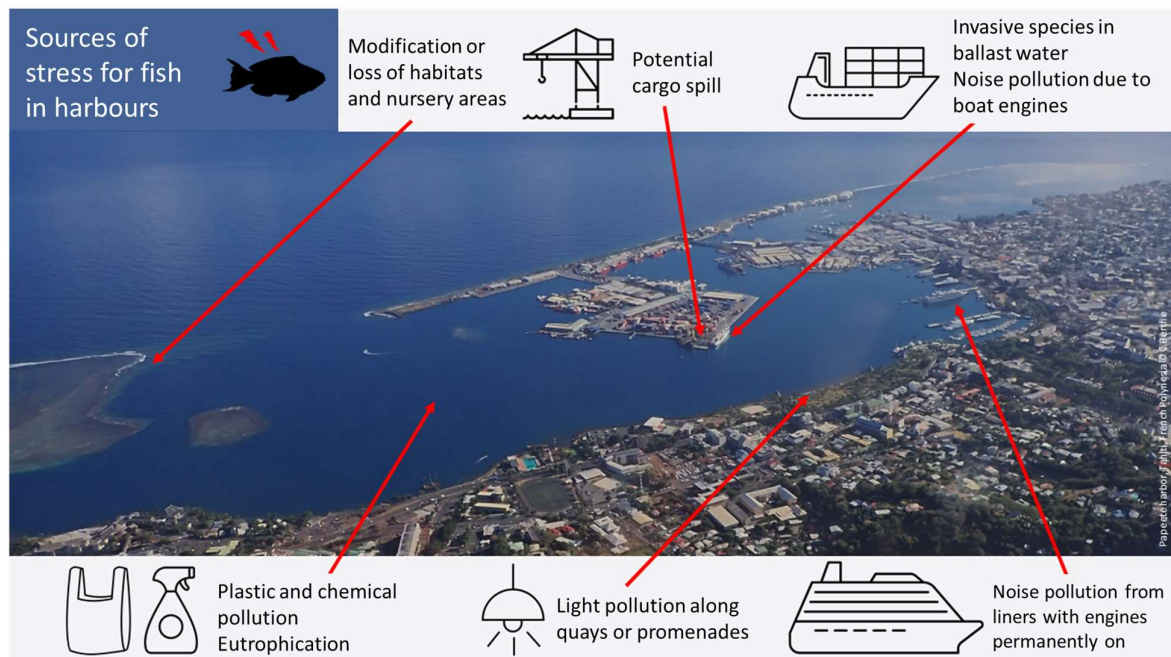
43 Coastlines – the interface between the land and the sea – have been increasingly subjected to
44 anthropogenic pressures such as fishing, boating, pollution, coastal construction, and tourism since the
45 end of the 19th century (*e.g.*, Crain et al., 2009; Dugan et al., 2011). Marinas, harbours, and ports are
46 among the most common man-made structures along coastlines worldwide (*e.g.*, Hardaway and
47 Duhring, 2010; Dafforn et al., 2015). Harbours are often hotspots of human-mediated environmental
48 pressures which significantly affect the quality of surrounding coastal and marine waters, as well as the
49 native *vs.* non-native species assemblages (Mayer-Pinto et al., 2015). For example, Harik et al. (2017)
50 assessed anthropogenic stressors along the Mediterranean coastline using a multi-criteria index . The
51 study showed that harbours along the Mediterranean coastline are the third largest cause of stress to
52 marine ecosystems, behind landfills and industrial sites (Harik et al., 2017). The construction and
53 presence of harbours not only directly destroy natural coastal habitats, but also indirectly damage
54 neighbouring ecosystems through changes in currents and sediment loads which dramatically impact
55 the composition of benthic communities (Meinesz et al., 1991; Martin et al., 2005; Li et al., 2010), as
56 well as fish larval dispersal and recruitment (Roberts, 1997). Within harbours, direct stressors include
57 pollutants from maritime activities (*e.g.*, diesel spills during vessel refuelling, hydrocarbon pollution
58 from boat traffic - Steen et al., 2004 in Danish harbours; Bergen et al., 2005 in the USA; Ingole et al.,
59 2009 in India; Li et al., 2010 in China; Mayer-Pinto et al., 2015 in Australia; Harik et al., 2017 in
60 Mediterranean harbours), and pollution generated by neighbouring cities and agricultural activities.
61 These can lead to high levels of heavy metals and organic pollutants (*e.g.*, high polychlorinated biphenyl
62 levels such as in New Bedford Harbour - Bergen et al., 2005; Nogales et al., 2011; Mali et al., 2017),
63 affecting the composition and function of microbial (Nogales et al., 2011) and macro-faunal
64 communities (Martínez-Lladó et al., 2007) in the water and sediments in harbours and marinas. Overall,
65 although the legislative framework concerning marine pollution control and prevention has been increasingly
66 enforced in harbours since the early 2000s (AAPA, 2003; ESPO/EcoPorts, 2009; US-EPA, 2009),
67 harbours remain man-made structures in which intense human usage impacts coastline environments.
68 Nonetheless, harbours and marinas contain marine communities and therefore constitute sites of interest
69 for ecologists and endocrinologists working on fish populations.

70 In their review of 200 environmental studies on Sydney harbour, Mayer-Pinto et al. (2015)
71 found that 109 focused on contamination, 58 on habitat modification, 11 on invasions by non-indigenous
72 species, and only 8 on fish and fisheries. This relative gap in studies on fisheries from Sydney harbour
73 mirrors the lack in knowledge of the impact of harbours on fish worldwide. Elsewhere, although many
74 studies have been conducted on intertidal sessile organisms living in harbours (*e.g.*, Yung et al., 1999;
75 MacFarlane and Burchett 2003), only a few have monitored mobile species such as fish (*e.g.*,
76 Wooldridge et al., 1999; Mercader et al., 2017a; Mercader, 2018). The low number of studies looking
77 at fish species may be due to practical aspects such as the danger of boat traffic when swimming, as well
78 as fishing restrictions in harbours (Ferreira et al., 2020). In addition, harbours are seldom considered of

79 interest for fish studies as they are rarely viewed as key habitats in terms of ecological function along
80 coastlines and islands and are often only referred to as polluted and artificial habitats (Mayer-Pinto et
81 al., 2015). These multiple reasons may explain the paucity of scientific papers focusing on the ecology
82 and physiology of fish living in harbours. However, harbours could be considered as unique habitats of
83 key scientific interest. Indeed, they concentrate uncommonly high and varied levels of pollutants. These
84 urbanised centres, previously absent from coastlines, completely differ from the ecosystems they
85 replaced as well as from the surrounding natural areas in terms of abiotic composition (*e.g.*, substrate
86 type, water quality, hydrodynamics). They represent a novel ecosystem (Hobbs et al., 2013) with their
87 own functional groups of living organisms. These make them unique areas in which to study the
88 synergistic effects of multiple anthropogenic stressors on the ecology, biology, and physiology of fish.
89 In addition, from an adaptive and evolutionary point of view, they provide a setting for long-term field
90 experiments impossible in mesocosm conditions (*e.g.*, Viard et al., 2020; Le Moan et al., 2021). The
91 aim of our review is to encourage future research on the biology (with a focus on endocrinology) and
92 ecology of fish affected by multiple stressors encountered in harbours. To do so, we (i) identify the
93 different stressors present in harbours and their potential impacts on marine fauna, (ii) present baseline
94 knowledge on the effect of multiple anthropogenic stressors on two endocrine pathways in marine fish
95 (stress and thyroid hormones), and (iii) propose a framework to conduct integrated research that could
96 provide crucial insights for ecosystem management, as well as a better understanding of hormonal
97 responses in fish under stressful conditions.

98 99 ***1. Harbours as fish habitats and potential nurseries***

100 Harbours are semi-closed coastal marine areas with limited water mixing with the open sea, in
101 which marine organisms are exposed to multiple stressors (*e.g.*, chemical contamination, elevated
102 nutrients, turbidity, marine debris, microplastics, invasive species, habitat modification, boat traffic and
103 noise and artificial light at night – Li et al., 2010; Mayer-Pinto et al., 2015; Fig. 1). In this review, we
104 focus on six major anthropogenic stressors that can affect the hormonal system of fish: plastic pollution,
105 chemical contamination, invasive species, boat noise, artificial light at night, temperature variation, as
106 well as their combined effects.



109

110 Fig. 1: Illustration of the different anthropogenic stressors present in the port of Papeete, Tahiti, French
 111 Polynesia (illustration by C. Berthe).

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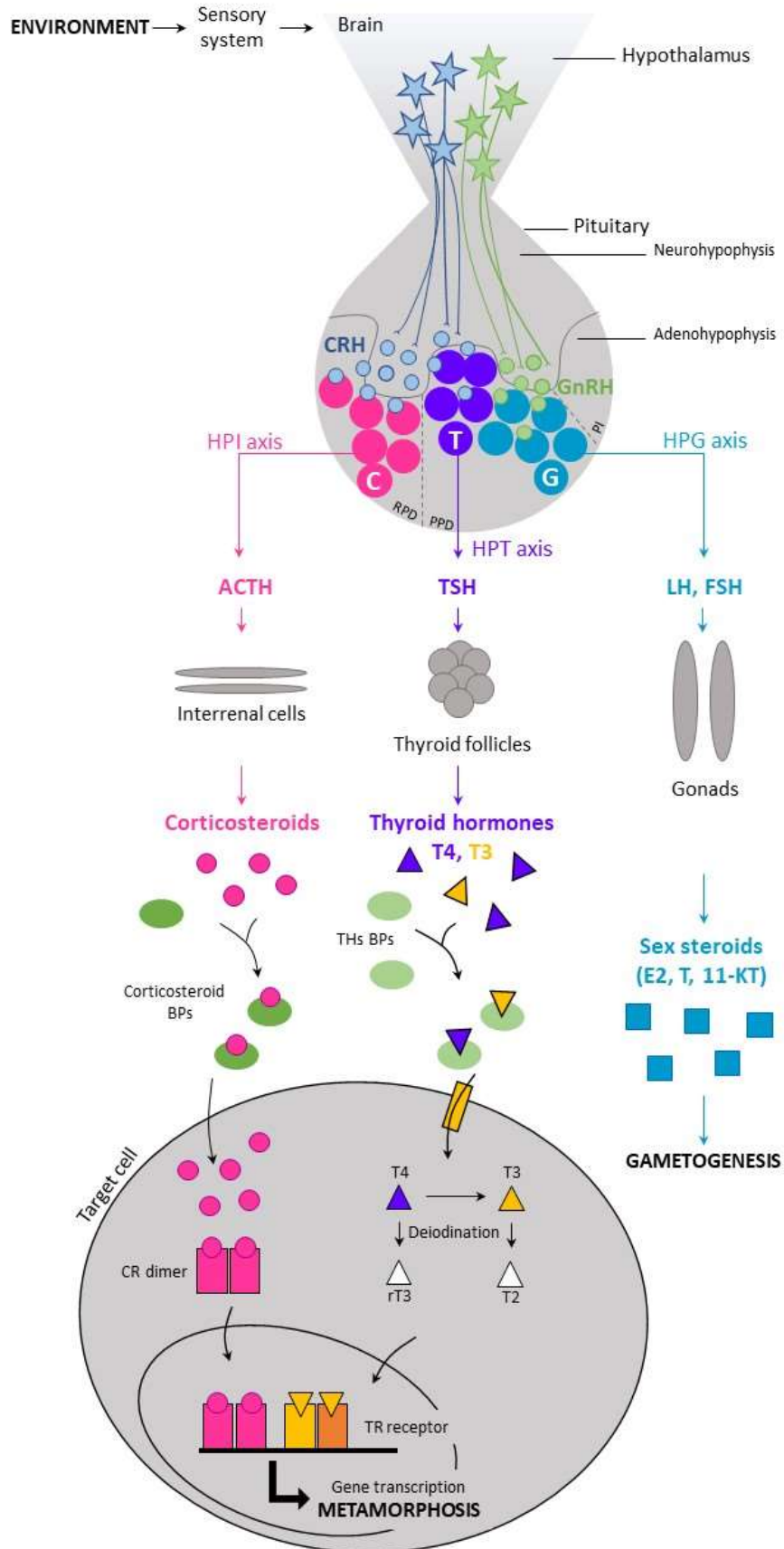
Despite the numerous anthropogenic stressors present in harbours, studies have found that harbours can be marine biodiversity hotspots, but these have mostly focused on macro-invertebrates (Johnston et al., 2015; Mayer-Pinto et al., 2015). The existing quantitative data on fish populations does not paint a similar picture for fish biodiversity (Edgar and Shaw, 1995; Clynick, 2006; Hutchings et al., 2013). However, recent studies have highlighted that some harbours with artificial habitats (mainly in temperate regions) could be nursery areas for fish (Bouchoucha et al., 2016; Dufour et al., 2009; Mercader et al., 2017b; Patranella et al., 2017; Mercader, 2018). Breakwaters host high densities of juvenile fish (Ruitton et al., 2000; Pizzolon et al., 2008; Dufour et al., 2009) and in some areas (e.g., in Sydney harbour; Clynick 2008) adult fish species richness and abundance inside marinas are close to those found on natural rocky habitats. Mercader (2018) surveyed juvenile fish populations on various artificial infrastructures and natural sites along a 100-km section of the French Mediterranean shoreline. Juvenile fish densities were highly variable between harbours depending on the type of small-scale habitats, with juvenile densities on ripraps or jetties higher or equivalent to those on natural sites. Port and marina jetties might in some cases provide suitable nursery grounds for juvenile fish, at least by comparison with highly urbanized neighbouring sections of the coastline (Dufour et al., 2009; Bouchoucha et al., 2016; Mercader et al., 2017b; Patranella et al., 2017; Mercader, 2018). Therefore, marinas, harbours, and ports may play a surprisingly vital role in the life cycle of some fish species. This is important when it comes to emblematic protected species, for instance the dusky grouper along the

131 French Mediterranean coastline. This species, which almost disappeared from the French coasts, is
132 almost exclusively found in marine protected areas, and there are very few juveniles. Projects to restore
133 the nursery function in several French and Moroccan Mediterranean ports have led to an increase in
134 observed juveniles (Mercader et al., 2017a; Selfati et al., 2018).

135 Many marine fish species have structured life histories with two distinct stages: first, a pelagic larval
136 stage capable of long-distance dispersal, followed by a relatively sedentary benthic stage (usually
137 juveniles and adults in reefs or along coastlines; Leis and McCormick, 2002). After the oceanic dispersal
138 phase, larvae settle in a suitable recruitment site. Recruitment is a critical phase in the life cycle of fish
139 as its success is decisive for population maintenance. Fish must undergo an abrupt transformation from
140 larvae to juvenile during this transition phase (Laudet, 2011). This transformation, called
141 metamorphosis, is usually quite spectacular and includes changes in behaviour, morphology, and
142 physiology, including biochemical and histological remodelling that affect several tissues at different
143 levels (McCormick et al., 2002; Parmentier et al., 2004; Frédérick et al., 2012; Holzer and Laudet, 2015;
144 Besson et al., 2020). Metamorphosis is usually triggered by physiological and environmental cues
145 (Holzer et al., 2017). Indeed, thyroid hormones (TH, notably thyroxine (T4) and triiodothyronine (T3));
146 Holzer et al., 2017) and cortisol (Jesus et al., 1991) act in concert to control and modulate
147 metamorphosis. TH levels increase during post-embryonic development to reach a peak which induces
148 metamorphosis; TH then coordinate ontogenetic transformations from the larval to the juvenile stages
149 (Gilbert et al., 1996; Wada, 2008; Isorna et al., 2009; McMenamin and Parichy, 2013; Campinho, 2019;
150 Klann et al., 2021). As TH signalling is critical for neurogenesis and the development of sensory organs,
151 it may play a role in determining the "quality" of future juveniles, *i.e.*, their capacity to select suitable
152 habitats, feed efficiently, as well as detect predators and escape from them, which are all crucial for fish
153 to successfully recruit into adult populations (Besson et al., 2020).

154 **2. Effects of multiple anthropogenic stressors on the hormonal system of fish living in** 155 **harbours**

156 In this review, we discuss on the effect of pollutants and stressors on fish endocrinology, with a
157 focus on three major hormonal axes: the hypothalamo-pituitary-interrenal (HPI), hypothalamo-pituitary-
158 thyroid (HPT), and hypothalamo-pituitary-gonadal (HPG) axes, as described by Fig. 2.



160 Fig. 2 Modified from Dusseigne et al., d2022. Illustration representing the hypothalamo-pituitary-
161 interrenal (HPI), hypothalamo-pituitary-thyroid (HPT), and hypothalamo-pituitary-gonadal (HPG) axes
162 in non-mammalian species (pink, purple and blue, respectively). Environmental cues are perceived by
163 sensory organs and processed in the brain, where corticotropin-releasing hormone (CRH) and
164 gonadotropin-releasing hormone (GnRH) are secreted. In non-mammalian species, CRH is thought to
165 control both the HPI and HPT axes. CRH acts on the pituitary cells to stimulate the synthesis and release
166 of i) adrenocorticotrophic hormone (ACTH) from corticotrophic cells (C, pink circles) and ii) thyroid-
167 stimulating hormone (TSH) from thyrotrophic cells (T, purple circles). HPI axis: ACTH stimulates the
168 secretion of glucocorticoids (GCs) by the interrenal cells. Once secreted, GCs are transported in the
169 blood by corticosteroid binding proteins (BPs). GCs enter target cells where they bind to corticosteroid
170 receptor dimers which then translocate into the nucleus where they bind to specific DNA regions to
171 induce gene expression. HPT axis: TSH stimulates the production of thyroid hormones (THs, T4 and
172 T3) by thyroid follicles. THs are transported to target cells via their specific BPs. Inside target cells,
173 THs are substrates of deiodinase enzymes which can both activate (i.e., forming T3) or inactivate (i.e.,
174 rT3 and T2) THs. THs are transported to the cell nucleus where they bind to TR receptors, which activate
175 gene transcription, in fine resulting in metamorphosis. HPG axis: GnRH reaches gonadotropic cells to
176 induce synthesis and release of gonadotropins (LH and FSH). LH and FSH both reach the gonads where
177 they stimulate gonadal maturation and function (i.e., synthesis of sex steroids: E2, T and 11-KT). The
178 balance between these sex steroids, in turn, regulates gametogenesis. RPD: rostral pars distalis, PPD:
179 proximal pars distalis, PI: pars intermedia of the adenohypophysis.

180 **2.1 Plastic pollution**

181 Plastic pollution in the marine environment has become a global environmental concern (Coyle
182 et al., 2020). Plastics are derived from raw natural substances such as petroleum, coal, and gas (Gabbott
183 et al., 2020) and can absorb multiple pollutants from the aquatic environment. The mechanical or
184 chemical impacts of plastics on marine organisms are well documented (Jacob et al., 2020; Welden,
185 2020). Multiple mechanical impacts have been directly or indirectly linked to plastics including
186 entanglement in macro-plastics (impeding mobility, leading to starvation or drowning), and the
187 ingestion or inhalation of smaller plastic debris, such as micro-plastics (MPs) and nano-plastics (NPs;
188 Welden, 2020). In fish, most ingested MPs and NPs are eventually excreted, but a small fraction can
189 accumulate in organs and tissues (mainly in the intestine and liver) causing severe tissue damage and
190 inflammation (e.g., Jovanović 2017; Wang et al., 2019; Araújo et al., 2019; Jacob et al., 2021; Marana
191 et al., 2022).

192 Beyond mechanical risks, marine plastic debris can also act as a reservoir of chemicals that pose
193 potential threats to wildlife. A wide array of contaminants may be contained in plastics: additives such
194 as flame retardants and plasticisers that can leach out from the plastic, or contaminants that get absorbed
195 into plastics from seawater. More than 250 organic compounds have been identified on plastic debris
196 (Campanale et al., 2020). Bisphenol A (BPA), used in the manufacturing of plastics, is found in aquatic

197 environments worldwide, notably harbours, and its concentration is positively correlated with the
198 amount of plastic waste generated in the region (Wu and Seebacher, 2020). BPA is a xenoestrogen, *i.e.*,
199 an endocrine disruptor capable of mimicking natural estrogens (Matozzo et al., 2008; Rubin, 2011).
200 BPA and its congeners can alter testis maturation and decreased sperm quality in fish (Chen et al., 2017;
201 Yang et al., 2017) and can induce gonad feminisation (Drastichová et al., 2005; Gonzalez et al., 2021).
202 Males exposed to BPA show increased plasma vitellogenin (VTG) levels or increased *vgt* gene
203 expression in the liver (Sohoni et al., 2001; Van den Belt et al., 2003; Yang et al., 2017; Frenzilli et al.,
204 2021; Gonzalez et al., 2021). VTG is a precursor of the egg-yolk protein; in females, VTG is synthesised
205 in response to estrogens and stored in oocytes. In males, the gene coding for VTG is normally not
206 expressed; its induction is thus used as a marker of estrogen exposure (Matozzo et al., 2008). Together
207 with increased estrogen levels, exposure to BPA is also associated with decreased androgen levels (T
208 and / or 11-KT; Yang et al., 2017; Gonzalez et al., 2021). Bisphenol also acts on the HPG axis, a
209 hormonal cascade starting with the release of gonadotropin-releasing-hormone (GnRH) from GnRH
210 neurons in the pituitary, stimulating the synthesis of gonadotropins, namely luteinising hormones (LH)
211 and follicle-stimulating hormone (FSH). Both hormones together stimulate gonad maturation and the
212 production of sex steroid hormones (in fish, mainly estradiol (E2), testosterone (T) and 11-
213 ketotestosterone (11-KT); Mills et al., 2010, 2018; Zohar et al., 2010). Moreover, in fish, kisspeptin
214 (Kiss) neurons are thought to control the synthesis of gonadotropins, acting either directly on the
215 pituitary cells or indirectly on GnRH neurons (Somoza et al., 2020). Following bisphenol exposure
216 (BPA, bisphenol S, bisphenol F), the expression of *Kiss1*, *Kiss receptor*, *GnRH2*, *GnRH3*, *GnRH*
217 *receptors*, *fsh β* , *lh β* , and *aromatase* genes increases, whereas the expression of genes involved in
218 steroidogenesis decreases (Ji et al., 2013; Qiu et al., 2016; Yang et al., 2017; Gonzalez et al., 2021).
219 BPA and their congeners can have profound effects on fish reproductive systems, raising questions about
220 population persistence in the future.

221 Other studies have evaluated the effects of BPA on the thyroid system and found disruption of
222 the HPT axis (Zhang et al., 2017; Wei et al., 2018; Lee et al., 2019) initiated by thyrotropin-releasing
223 hormone (TRH) in mammals and corticotropin-releasing hormone (CRH) in non-mammalian species
224 (see Laudet, 2011; Denver, 2017). In fish, when the HPT axis is stimulated, hypothalamic CRH neurons
225 release CRH in the anterior pituitary, which synthesises and releases thyroid-stimulating hormone (TSH)
226 into the global circulation. In turn, TSH reaches thyroid follicles and stimulates the synthesis of
227 thyroxine (T4), which can be converted into its active form triiodothyronine (T3) in peripheral tissues
228 under the action of deiodinase enzymes (Laudet, 2011; Denver, 2017). Several studies have found
229 altered circulating levels of T4 and T3 in individuals exposed to bisphenols compared to control
230 individuals, suggesting a disruption to the HPT axis (Zhang et al., 2017; Wei et al., 2018; Lee et al.,
231 2019). In addition, BPA causes regulatory changes in genes involved in all steps of the HPT axis, for
232 which gene transcription occurs mainly in the brain, pituitary, thyroid, peripheral tissues, and liver (Lee
233 et al., 2019). Interestingly, BPA on one hand and BPS – BPZ on the other hand may have different

234 modes of action on the HPT axis. For example, *in vivo* (zebrafish embryos) and *in vitro* experiments
235 have shown that exposure to BPA upregulated the expression of several genes involved in TH synthesis
236 as well as genes involved in thyroid development (Gentilcore et al., 2013). These results were further
237 confirmed in zebrafish embryos exposed to BPA (*i.e.*, upregulation of genes directly implicated in
238 thyroid development and function; Lee et al., 2019). On the contrary, BPS and BPZ may deregulate
239 gene expression in the brain and pituitary, notably causing the upregulation of *crh* and *tsh β* gene
240 transcription (at levels above 0.68 mg/L; Lee et al., 2019, higher than those observed in harbours, which
241 are in the few ng/L range; Robinson et al., 2009; Emnet et al., 2020).

242 A transgenerational experiment showed that the thyroid hormone disruption – lower T4 and
243 higher T3 circulating levels– seen in F0 zebrafish females exposed to BPS from 2 hours to 120 days
244 post-fertilisation was transferred to eggs, leading to higher T3 circulating levels in F1 embryos, causing
245 adverse effects (delayed hatching, decreased swimming speed and escape behaviour, and reduced
246 pigmentation; Wei et al., 2018).

247 Overall, studies have highlighted numerous significant negative consequences of plastics on
248 fish, either mechanically or through chemical impacts on several hormones. BPA is one of many plastic
249 components that cause endocrine disruptions in marine organisms. However, there has been no study
250 on fish living in harbours, although these zones are often exposed to high concentrations of plastics and
251 associated chemicals (Claessens et al., 2011; Naidoo et al., 2015; Romeo et al., 2015; Chen et al., 2021);
252 characterising the effects of plastics on fish in harbours would be an informative research avenue.

253

254 **2.2 Chemical contamination**

255 In many coastal areas, including marinas, harbours, and ports, the legacy of past industrialisation
256 and the past absence of regulations on emissions is still present. Coastal regions are part of the
257 catchment-coast continuum, where catchment areas are often dominated by intense agriculture, may
258 contain dump sites or landfills, and wastewater discharge is carried across drainage basins into the
259 marine environment. It is therefore unsurprising that chemical contamination is increasing in many
260 harbours and ports across the world (*e.g.*, USA: Dauer et al., 2000; Hong Kong: Nicholson et al., 2011;
261 Brazil: Hatje and Barros 2012; Australia: Mayer-Pinto et al., 2015). Chemical contamination is one of
262 the greatest threats to marine species, leading to impairments in development and reproduction
263 (Rochman et al., 2014), the emergence of diseases (Kiesecker, 2002), declines in biodiversity and
264 ecosystem function (Johnston and Roberts, 2009; Johnston et al., 2015), and numerous chemical
265 pollutants are thyroid hormone disruptors (Jarque and Piña, 2014).

266

267 **2.2.4 Persistent organic pollutants**

268 Among the multiple pollutants recorded in harbours, persistent organic pollutants, such as
269 polychlorinated biphenyls (PCBs) and polycyclic aromatic hydrocarbons (PAHs), are the most
270 commonly detected (Casado-Martínez et al., 2009; Ghosh et al., 2003; Mali et al., 2016). Persistent

271 organic pollutants are organic compounds that are resistant to environmental degradation through
272 chemical, biological, or photolytic processes (Jones and De Voogt 1999). These persistent contaminants
273 are usually found only in trace amounts in water but tend to adsorb onto inorganic and organic material
274 settled in sediments (Jones and De Voogt 1999). Persistent organic pollutants are remobilised by human
275 activities such as dredging, rendering them bioavailable (Martins et al., 2012). Consequences on aquatic
276 organisms are numerous: they are immunotoxic, genotoxic, mutagenic, and carcinogenic, and have the
277 potential to disrupt hormonal systems (Tanabe, 2002; Vega-López et al., 2007; Luch and Baird, 2010)

278 Polychlorinated biphenyls (PCBs), along with other organic pollutants (dioxins, and polycyclic
279 aromatic hydrocarbons PAHs, a diverse group of organic molecules produced through the incomplete
280 combustion of fossil fuels, petroleum, or petrochemical materials), have been strictly regulated since
281 2001, yet remain present in harbour sediments worldwide (Connell et al., 1998; Adami et al., 2000;
282 Barakat et al., 2002; Ghosh et al., 2003). In Sydney Harbour, 13 of 19 seafood species studied presented
283 tissue concentrations of organic pollutants above standard thresholds for human consumption (Manning
284 et al., 2017).

285 Leatherland and Sonstegard (1978) reported changes in thyroid histological appearance and
286 decreased plasma TH levels in coho salmon (*Oncorhynchus kisutch*) and chinook salmon
287 (*Oncorhynchus tshawytscha*) after PCB exposure. Since then, the thyroidal responses of fish to PCBs
288 have shown variable results in different studies, depending on the species and the type of PCB congeners
289 (Brown et al., 2004). A 30-day laboratory exposure to PCB in the diet of juvenile rainbow trout *O.*
290 *mykiss* reported several detrimental effects, such as oxidative stress, thyroid system dysfunction – higher
291 T4 levels and more active deiodination (Buckman et al., 2007). A similar exposure in young-of-the-year
292 Atlantic croaker *Micropogonias undulatus* decreased both T4 and T3 levels (LeRoy et al., 2006). Altered
293 reproductive physiology has been documented in numerous species (review by Henry, 2015): for
294 instance, female fish fed with PCB mixtures at environmentally realistic concentrations showed
295 impaired ovarian maturation, delayed reproduction, and produced fewer viable eggs (Daouk et al., 2011;
296 Horri et al., 2018).

297 Life history transitions, such as metamorphosis, are hugely sensitive to endocrine disruption.
298 Larval and juvenile Japanese flounder (*Paralichthys olivaceus*) exposed to PCBs show declines in T3
299 and T4 levels as well as changes in deiodinase gene expression levels, which were associated with
300 slower growth and delay metamorphosis (Dong et al., 2014, 2017). The effects of PAHs on the thyroid
301 function in fish remain poorly studied (Brown et al., 2004; Kim et al., 2016; Price and Mager, 2020).
302 Nevertheless, a few studies have reported adverse effects on TH. For example, in juvenile common carp
303 (*Cyprinus carpio*), levels of plasma T3 and T4 were reduced in response to PAHs exposure (Shirdel et
304 al., 2016), and similar results were found in zebrafish larvae (Kim et al., 2016). In addition, short-term
305 exposures of water-soluble fractions from oil (PAH compounds) to larval and juvenile turbot
306 (*Scophthalmus maximus*) increased whole-body concentrations of T4, but not T3 (Stephens et al., 1997).
307 Overall, the effects of persistent organic pollutants on the thyroid system are varied and depend on the

308 compound and species. Changes in TH levels in both larvae and juveniles may reflect a complex
309 disruption of biological processes, both in terms of TH synthesis and of their biotransformation in
310 peripheral tissues, which may result in developmental deformities of adults.

311

312 **2.2.2 Metals**

313 Developing fish (embryos, larvae, and juveniles) are particularly sensitive to heavy metal
314 exposure (Sfakianakis et al., 2015), and certain metals such as Cadmium (Cd) or Copper (Cu) are often
315 present in harbours and ports (Broman et al., 1994; Jupp et al., 2017). Fish embryos exposed to Cd or
316 Cu have lower hatching rates and survival, while young individuals (larvae and juveniles) notably suffer
317 from severe skeletal deformities, impairments of the lateral line, and cardiac oedema (Sfakianakis et al.,
318 2015). Moreover, Cd exposure negatively impacts the function of both the HPT and the HPI axes (HPI
319 ends with the synthesis and release of corticosteroids, mainly cortisol). Indeed, fish larvae exposed to
320 Cd show complete disturbance of gene expression in the HPT axis and reduced circulating plasma levels
321 of T4 (Jancic and Stosic, 2014; Li et al., 2014). Cd can also disturb cortisol synthesis by suppressing the
322 expression of genes coding for proteins which are essential for corticosteroid production (i.e. StAR
323 (steroidogenic acute regulatory protein) and MC2R (Melanocortin 2 receptor, which triggers steroid
324 biosynthesis following activation by ACTH); Sandhu and Vijayan, 2011). Cadmium could potentially
325 have detrimental effects on the metamorphosis and development of young fish and alter the reproductive
326 system of adults. Persistent organic pollutants, such as PCBs, and metals, such as Cd, are examples of a
327 large number of contaminants with varied and potentially cumulative effects.

328

329 **2.2.3 Pesticides**

330 A commonly used insecticide, chlorpyrifos (CPF), significantly decreases thyroid hormone
331 levels of exposed fish juveniles, thus altering their metamorphosis, leading to decreased intestine
332 lengthening and impaired grazing behaviour (Holzer et al., 2017). Besson et al. (2020) also showed that
333 CPF and increased temperature, independently as well as synergistically, affect sensory development
334 and predator avoidance behaviour in a coral reef fish (Besson et al 2020). Their results suggest that TH
335 signalling might be the underlying physiological process impacted by these different stressors, however,
336 each stressor might affect physiological process in unique ways. Increased temperature impacts T4
337 levels, suggesting an alteration at the neuroendocrine level – before T4 is converted to other compounds
338 such as T3. In contrast, CPF is thought to have a more downstream effect, possibly by acting on T3
339 metabolism (Besson et al., 2020; Holzer et al., 2017). Fish exposed to these stressors had impaired anti-
340 predator behaviour, similar to that of pre-metamorphosed larvae, and experienced higher mortality from
341 predation. The disruption of TH signalling during fish metamorphosis can cause neurological defects,
342 with possible community-level consequences that may even threaten the maintenance of a species
343 (Crane et al., 2006; Noyes et al., 2009; Laudet, 2011; Holzer et al., 2017; Pinsky et al., 2019). Indeed,
344 changes in survival rates during this transition and post-settlement can have drastic effects on population

345 replenishment. This is of particular concern as nurseries are mainly located in shallow coastal waters
346 and some harbours are even qualified as nurseries (Bouchoucha et al., 2016; Mercader et al., 2017b;
347 Patranella et al., 2017; Mercader, 2018) despite containing multiple stressors that can affect fish
348 metamorphosis and subsequent juvenile quality. As such, harbours are ideal sites to study the impact of
349 multiple stressors on fish endocrine pathways “*in situ*”, in an ecologically relevant context.
350 Understanding how harbours effect fish hormonal systems during metamorphosis is of great importance
351 from a conservation perspective.

352

353 **2.2.4 Wastewater discharge**

354 In addition to pesticides, many other contaminants can reach the coast and harbours (endocrine
355 disruptors, pharmaceuticals, etc.) through wastewater discharge (Mossa, 2006; Hamdhani et al., 2020).
356 Among these, triclosan (TCS) is a synthetic chlorinated bactericide used in a vast number of personal
357 care (soaps, toothpastes, deodorants, etc.) and textile products (Adolfsson-Erici et al., 2002). TCS has
358 been monitored in US streams (Kolpin et al., 2002) and coastal waters (*i.e.*, in the Narragansett Bay:
359 Katz et al., 2013; the San Francisco Bay: Jackson and Sutton, 2008; Kerrigan et al., 2015). TCS has
360 structural similarities with THs, suggesting it could disturb thyroid function (Adolfsson-Erici et al.,
361 2002). Studies have investigated the toxicity of TCS on various organisms and reported high mortality
362 rates, deformities, perturbations of behaviour, and reproductive failure (Orvos et al., 2002; Oliveira et
363 al., 2009; Nassef et al., 2010; review by Dann and Hontela 2011). However, few studies have
364 investigated the effects of TCS on fish metamorphosis. In the sheepshead minnow *Cyprinodon*
365 *variegatus*, the T3 peak observed in control fish (indicative of metamorphosis climax) is absent in fish
366 exposed to TCS, resulting in delayed metamorphosis (Schnitzler et al., 2016). Zebrafish larvae exposed
367 to TCS also displayed delayed metamorphosis (Stenzel et al., 2019). In the sole *Solea senegalensis*, TCS
368 had the opposite effect and accelerated metamorphosis (Araújo et al., 2019). The mechanisms of action
369 of TCS remain unclear but are thought to modulate the expression of several genes involved in the HPT
370 axis, notably affecting the expression of TH receptors α and β in the North American bullfrog *Rana*
371 *catesbeiana* (Veldhoen et al., 2006), and upregulating of the expression of the *tsh* gene in adult zebrafish
372 (Pinto et al., 2013). TCS is detected in the environment worldwide, and has been recorded in various
373 organisms, including humans (Dann and Hontela, 2011). A better understanding of the risks associated
374 with its use is urgent.

375

376 **2.2.5. Antifouling compounds**

377 Antifouling compounds are used on many submerged structures (*e.g.*, ship hulls, buoys) to
378 prevent the recruitment of marine organisms, but have many unintended impacts. Tributyltin (TBT)
379 used to be a widespread antifouling agent. Its use became regulated in the 1980s and was banned in
380 2008 (IMO, 2005) after it was linked to a global decline in marine molluscs, likely causing reproductive
381 failure (Gibbs and Bryan, 1996; Antizar-Ladislao, 2008). TBT has been shown to delay tadpole

382 metamorphosis and growth in amphibians (Shi et al., 2014) and studies reported altered T4 and T3 levels
383 and HPT gene expression in the zebrafish *Danio rerio*, goldfish *Carassius auratus* as well as in marine
384 rockfish *Sebastes marmoratus* (Zhang et al., 2013, 2016; Li and Li 2021). Recently, medetomidine,
385 a veterinary anaesthetic, has emerged as a new antifouling agent (Dahlström et al., 2000). It is widely
386 used (Wendt et al., 2016) even though its ecotoxicological effects are poorly understood. Recent studies
387 on amphibians showed that tadpoles exposed to medetomidine experienced delayed metamorphosis
388 (Barr et al., 2018; Fong et al., 2018). Medetomidine induces paleness in fish (Bellas et al., 2005;
389 Hilvarsson et al., 2007; Lennquist et al., 2010), which may be due to altered thyroid function, as TH
390 regulates fish pigmentation (McMenamin et al., 2014; Saunders et al., 2019; Salis et al., 2021).

391

392 **2.2.6 Case study of chemical contaminants: the San Francisco Bay**

393 The San Francisco Bay features on the “303(d)” list of impaired water bodies in the US from
394 the federal Clean Water Act. Chemical contaminants found in the San Francisco Bay include pesticides
395 (diazinon, chlordane, dieldrin, dichlorodiphenyltrichloroethane), polyaromatic hydrocarbons, and
396 chlorinated compounds. Several of the compounds monitored in the bay as well as in marine organisms
397 are sometimes found in concentrations higher than the screening values established by the US EPA
398 (Fairey et al., 1997; Davis et al., 2007; Greenfield and Allen, 2013). To our knowledge, only one study
399 investigated fish TH levels in the vicinity of a harbour in the area (Brar et al., 2010). In this work, young
400 individuals of two fish species, the shiner surfperch (*Cymatogaster aggregate*) and the Pacific staghorn
401 sculpin (*Leptocottus armatus*), were sampled in several locations across the San Francisco Bay and over
402 two consecutive years. Over the 2-year sampling period, both species had reduced T4 concentrations in
403 locations with concentrated human activities (among which the Oakland inner harbour and the San
404 Leandro Bay) compared to other locations (Brar et al., 2010). Fish liver analyses revealed the presence
405 of over 85% of existing PCB congeners, with concentrations inversely correlated to T4 levels. Fishes
406 also had significant differences in T3 concentrations and T3/T4 ratios across the study locations, which
407 might reveal an alteration of deiodinase activity in peripheral tissues. The sampled sculpins may have
408 been undergoing metamorphosis at the time of sampling (as indicated by their body size; Goto 1990).
409 The altered TH levels due to contaminant exposure in the long term and notably during metamorphosis
410 may lead to thyroid dysfunction, alter metamorphosis, and threaten population persistence.

411

412 **2.3. Invasive species**

413 Harbours, in addition to being subjected to anthropogenic stressors, are very susceptible to
414 invasions of aquatic species. Boets et al. (2012) showed that one fourth of all crustacean species across
415 four Belgian harbours were non-native. Invasive species in harbours mainly arrive in ballast water or
416 from hull fouling (Carlton, 1985; Ruiz et al., 2000; Boets et al., 2012). They can also originate from
417 aquaculture or the aquarium trade (Naylor et al., 2001). The arrival of new species in a harbour can
418 cause interspecific competition with native species, leading to increased predation and stress. In fish,

419 stress is mediated by glucocorticoids, among which cortisol is often measured as an indicator of stress
420 (e.g., Beldade et al., 2017). During a stressful situation, the HPI axis is stimulated, leading to the release
421 of cortisol into the organism (Wendelaar Bonga, 1997). During acute stress, cortisol release is
422 considered adaptive because it stimulates the catabolism of lipids, mobilising energy to cope with the
423 stressful event (Van Weerd and Komen, 1998). However, prolonged stress can have detrimental effects
424 on organisms, including impaired disease resistance, loss of appetite, reduced growth, and altered
425 reproduction (Wendelaar Bonga, 1997; Van Weerd and Komen, 1998). The presence of invasive species
426 which could induce stress in native species has never been explored in fish living in harbours or
427 elsewhere. The only insight available is from a mammal, the Eurasian red squirrel (*Sciurus vulgaris*),
428 faced with the invasion of grey squirrels (*S. carolinensis*; Santicchia et al., 2018). The presence of the
429 invader induced high physiological stress in the native species: faecal glucocorticoid levels of native
430 individuals were related to the abundance of invasive individuals. Whether alien species can induce
431 physiological stress in fish has not yet been studied. Given the highly mobile nature of fish, and because
432 cortisol levels fluctuate extremely rapidly (within a few minutes; Pankhurst 2011), it will be particularly
433 challenging to assess stress levels in response to invasive species from blood samples in harbours.

434

435 **2.4. Boat noise**

436 Sound travels faster and further underwater compared with in air, and the frequency and
437 intensity of anthropogenic underwater sounds overlap with the ranges of natural biological sounds
438 (Hastings and Popper, 2005; Slabbekoorn et al., 2010). Anthropogenic underwater sounds have
439 therefore been defined as pollutants. Within the EU Marine Strategy Framework Directive (MSFD)
440 (2010/477/EU European Commission Decision), two indicators have been proposed to monitor this
441 pollution: impulsive noise and continuous noise. The anthropogenic contribution to the soundscapes of
442 many harbours worldwide, notably in the northern hemisphere, is dominated by continuous noise caused
443 by commercial shipping (Hildebrand, 2009; McKenna et al., 2013). In the northeast Pacific, noise from
444 commercial shipping in inshore waters is also the most persistent type of anthropogenic noise, notably
445 in large ports such as Vancouver and Seattle (Erbe et al., 2014). In addition, tourism and recreational
446 boating also add a substantial amount of noise to coastal underwater soundscapes (e.g., McDonald et
447 al., 2006; Hermanssen et al., 2019; McCormick et al., 2019). During a lockdown put in place by
448 governments worldwide to slow the spread of COVID-19 (April-May 2020), the vocal activity of a
449 range of coral reef fish living in the marina of Pointe-à-Pitre (Guadeloupe, French West Indies), located
450 next to a major maritime harbour, was reduced as a response to the lower levels of anthropogenic noise
451 they experienced (Bertucci et al., 2021).

452 Several studies have highlighted the effect of noise on fish physiology, although none have
453 directly tested this on fish living in harbours. The potential stressors caused by anthropogenic
454 underwater noise include behavioural responses, which are mediated through androgen and
455 glucocorticoid pathways (Mills et al., 2020) and may ultimately lead to hearing impairment or habitat

456 abandonment. Noise can affect physiology as early as the embryonic stage in fish, with heart rates shown
457 to increase in staghorn damselfish embryos (*Amblyglyphidodon curacao*) exposed to noise from boats
458 with 2- and 4-stroke engines (Jain-Schlaepfer et al., 2018). This study also demonstrated that heart rate
459 doubled with playbacks of 2-stroke engines compared to 4-stroke engine playbacks. Similarly, heart rate
460 increased by approximately 10% when sounds of small boats powered by 2-stroke engines were played
461 back to embryos of damselfishes *Amphiprion melanopus* and *Acanthochromis polyacanthus* (Fakan and
462 McCormick, 2019). Similar exposures to anthropogenic noise in starved green Chromis (*Chromis*
463 *viridis*) and spiny damselfish (*A. polyacanthus*) caused a heightened corticosteroid stress response
464 (Armstrong-Smith, 2016). Besides the Pomacentridae family, which has received most attention, boat
465 noise playbacks also increased whole body cortisol levels of a Labridae species, the slippery dick
466 (*Halichoeres bivittatus*; Staaterman et al., 2020). Should this exposure be prolonged, elevated cortisol
467 levels might ultimately impact immune responses and weaken responses to diseases and parasites (Fast
468 et al., 2008). While elevated cortisol levels drove fish to hide in their shelter during anthropogenic noise,
469 circulating androgens such as testosterone, correlated with aggression in orange-fin anemonefish
470 (*Amphiprion chrysopterus*) when exposed to both 30 min and 48 hours of boat noise (Mills et al., 2020).
471 In freshwater environments, playbacks of underwater boat noise recorded from the Danube River and
472 in two Austrian lakes led to increased cortisol secretion in the common carp (*Cyprinus carpio*), the
473 gudgeon (*Gobio gobio*), and the European perch (*Perca fluviatilis*; Wysocki et al., 2006). However, no
474 increase was observed when fish were exposed to continuous random noise. This indicated that irregular
475 noises such as those caused by ship engines, with fluctuations in amplitude and frequency, constitute
476 important stressors. This study also did not find differences in response between species possessing
477 excellent (common carp and gudgeon) or poor (perch) hearing abilities. Nevertheless, species-specific
478 sensitivities and ranges of hearing capacities may alter the extent to which anthropogenic noise impacts
479 them. Motorboat noise also affects interspecies interactions. Bluestreak cleaner wrasses (*Labroides*
480 *dimidiatus*) inspected their fish clients for longer and were significantly less cooperative during exposure
481 to boat noise (Nedelec et al., 2017). Furthermore, clients did not retaliate as expected (*i.e.*, by chasing)
482 in response to increased cheating by cleaners, suggestive of cognitive impairments due to distraction by
483 both parties. The effects of noise may also depend on multiple acoustic factors, such as sound frequency,
484 intensity, and duration (Slabbekoorn et al., 2010; Hawkins and Popper, 2016).

485 While some fish species appear to somewhat acclimate to noise in terms of behaviour – with
486 behaviours returning to control levels after continuous noise exposure (Nedelec et al., 2016; Holmes et
487 al., 2017; Staaterman et al., 2020) –, hormonal effects could be long-lived. This has been documented
488 through the increase in aggressiveness and hiding behaviour of *A. chrysopterus*, linked to heightened
489 levels of testosterone and cortisol respectively, after short thirty-minute boat noise playbacks, but also
490 over longer two-day playbacks, throughout which *A. chrysopterus* did not show any habituation or
491 reduction in response (Mills et al., 2020). It illustrates that changes in the physiological state in response
492 to noise could result in prolonged behavioural effects in reef fish species, which might ultimately lead

493 to alterations in individual fitness and behavioural changes at the population level (Radford et al., 2016;
494 Popper and Hawkins, 2019).

495

496 **2.5. Artificial light pollution at night**

497 Harbours are one of the largest sources of permanent light on coastlines with light emitted from
498 homes, resorts, and streetlights (Davies et al., 2014). Shallow waters in harbours experience light
499 intensities up to 150–200 lux (Bolton et al., 2017), compared to intensities of 0.03 to 2.5 lux due to
500 skyglow in other zones (when scattered light from streetlights is reflected by clouds; Perkin et al., 2014),
501 0.1–0.3 lux during full moonlight on a clear night, and only 0.00003–0.0001 lux on a cloudy night (Rich
502 and Longcore, 2013). The consequences on living organisms are multiple as artificial-light-at-night
503 (ALAN) could affect functions related to orientation in space (phototropism, phototaxis) and in time
504 (circadian rhythms; Falcón et al., 2020).

505 Circadian clocks are systems that translate environmental information, mainly the alternation of
506 light and darkness (or photoperiod), into the hormonal signal melatonin to orchestrate a myriad of
507 downstream biochemical, physiological, and behavioural events so that the right process occurs at the
508 right time (Falcón et al., 2009; Falcón et al 2020). In fish, the main source of information on photoperiod
509 and light is from the photosensitive pineal organ, situated at the surface of the brain underneath a
510 translucent window in the skull. The pineal photoreceptors are responsible for the nocturnal production
511 of the time-keeping hormone melatonin, the duration of this nocturnal signal reflecting the duration of
512 the night, while the amplitude varies with temperature in a species-specific manner. Consequently, daily
513 and annual variations in melatonin production provide internal information of daily and annual time, for
514 the orchestration and synchronization of numerous physiological and behavioural processes (Falcón and
515 Meissl, 1981; Underwood, 1989; Falcón et al., 1992, 2009; Grubisic et al., 2019). Other tissues that
516 produce hormonal signals include deep brain photoreceptors, the saccus vasculosus, or photoreceptors
517 in the retina (Kojima et al., 2000; Philp et al., 2000; Peirson et al., 2009; Falcón et al., 2010; Nakane et
518 al., 2013). The main hormone controlling circadian activities, pineal melatonin, is produced during the
519 night and released in the cerebrospinal fluid and blood to control locomotor activity, food intake,
520 shoaling, and diel vertical migration (Ekstrzm and Meissl, 1997, 2004; Ryer and Olla, 1998; Mehner,
521 2012; Vowles et al., 2014). Pineal melatonin also regulates seasonal rhythms including reproduction,
522 growth and development, sleep rhythms, rhythmicity of locomotor activity, and immune responsiveness
523 (Duston and Bromage, 1986; Fairey et al., 1997; Boeuf and Le Bail, 1999; Downing and Litvak, 2002;
524 Wiechmann and Sherry, 2013). However, more and more studies warn about the potentially disruptive
525 effects of ALAN on the synchronization of biological functions and life cycle of species, questioning
526 their sustainability on impacted areas, such as harbours.

527 Almost all studies in fish have shown that broad-spectrum white light, even as little as 1, 0.1
528 and 0.01 lux, reduces the nocturnal production of plasma melatonin across fish species. ALAN reduced
529 melatonin in temperate freshwater fish such as goldfish (*C. auratus*; Kezuka et al., 1988; Iigo et al.,

530 1997), pike (*Esox lucius*; Falcón et al., 1987, 1989), zebrafish (Khan et al., 2018) and other freshwater
531 species (Porter et al., 2001; Vera et al., 2005; Brüning et al., 2015, 2018b), as well as in marine species
532 such as the Atlantic salmon (*Salmo salar*), European sea bass (*Dicentrarchus labrax*) and Arctic charr
533 (*Salvelinus alpinus*; Porter et al., 2001; Bayarri et al., 2002; Rahman et al., 2004; Vera et al., 2005;
534 Nikaido et al., 2009; Park et al., 2014; Choi et al., 2017; Liu et al., 2019). Tropical marine species have
535 shown some of the strongest responses to light at night of 1 lux (e.g., Rahman et al., 2004; Nikaido et
536 al., 2009; Carazo et al., 2013; Park et al., 2014). Increasing light intensity had little to no effect
537 suggesting that there is likely a threshold level of ALAN near 1 lux that alters the circadian rhythm in
538 fish (Brüning et al., 2015, 2016, 2018a). Even lower light levels, such as skyglow (0.01–0.1 lux),
539 suppress nocturnal melatonin levels (Kupprat et al., 2020): the strong light pollution observed in
540 harbours can be expected to suppress melatonin secretion at night in fish.

541 The pineal gland develops early and detects light even during early embryonic stages (Ekström
542 et al., 1983; Östholm et al., 1987; Ekström and Meissl, 1997). Egg hatching, which normally takes place
543 under the cover of darkness, is impacted by the disturbance of the circadian rhythm by ALAN. Egg
544 hatching was delayed in the European perch *Perca fluviatilis*, roach *Rutilus rutilus*, and bleak *Alburnus*
545 *alburnus* (Brüning et al., 2011) and completely prevented in laboratory studies of tropical fish species
546 (Fobert et al., 2019). One explanation may be that the modified ratio of prolactin (a pituitary hormone)
547 and melatonin resulted in a change in the egg hatching enzyme (Brüning et al., 2011).

548 Melatonin also regulates the secretion of several components of the HPG axis, such as
549 gonadotropins, sex steroids or gonadal maturation (Khan and Thomas, 1996; Amano et al., 2000;
550 Chatteraj et al., 2005; Bhattacharya et al., 2007; Sébert et al., 2008; Carnevali et al., 2011). Experimental
551 white light levels as low as 1 lux (but not other wavelengths of light such as blue, green, red) as well as
552 street-lighting in a natural setting (13.3–16.5 lux) suppress mRNA expression of LH and FSH in male
553 and female European perch and roach (Brüning et al., 2016, 2018b). ALAN also reduces circulating sex
554 hormones, 17 β -estradiol in female European perch and roach (Brüning et al., 2018b), Senegalese sole
555 (*Solea senegalensis*, García-López et al., 2006), and in male and female perch (Migaud et al., 2004), as
556 well as 11-ketotestosterone in male European perch and roach (Brüning et al., 2018b), sea bass
557 (Rodríguez et al., 2005; Felip et al., 2008) and Senegalese sole (García-López et al., 2006). The
558 cascading impacts of ALAN on sex hormones cause a subsequent failure in gonad maturation for several
559 fish species, including sea bass (Rodríguez et al., 2005), Atlantic cod (*Gadus morhua*, L.; Taranger et
560 al., 2006), turbot (*Scophthalmus maximus*; Imsland et al., 2003) and Nile tilapia (*Oreochromis niloticus*;
561 Rad et al., 2006).

562 The impact of ALAN on fish cortisol levels, a commonly measured indicator of stress
563 (Mommensen et al., 1999), has been mixed. ALAN increased plasma cortisol and glucose in farmed
564 Atlantic salmon (Migaud et al., 2007) but did not affect cortisol levels in dispersing Atlantic salmon fry
565 (Newman et al., 2015). There was also no effect of ALAN on the cortisol response of European perch
566 (Brüning et al., 2015), red sea bream (*Pagrus major*) and striped knifejaw (*Oplegnathus fasciatus*;

567 Biswas et al., 2006, 2008), Bluefin tuna (*Thunnus orientalis*; Honryo et al., 2013) or juvenile bonefish
568 (*Albula vulpes*, Szekeres et al., 2017). To date, the evidence shows that the hormonal impacts of ALAN
569 in fish are driven by the changes of melatonin levels rather than cortisol levels.

570 In most cases, all the above experiments on ALAN were completed in laboratory settings
571 lacking many environmental and ecological factors, such as species interactions between predators and
572 prey, as well as refuges linked to habitat complexity (Brüning et al., 2015; Schligler et al., 2021). It is
573 therefore unclear whether ALAN in more natural settings, and over longer periods of time, will lead to
574 similar alterations to hormone levels. However, one recent study in a natural setting showed that long-
575 term exposure to light pollution over 18–23 months negatively impacts the survival and growth of a
576 wild coral reef fish (Schligler et al., 2021). The higher mortality of orange-fin anemonefish, *A.*
577 *chrysopterus*, in the wild (Schligler et al., 2021) agrees with a laboratory study showing increased
578 predation under ALAN of coral reef fish larvae, the convict tang, *Acanthurus riostegus* (O'Connor et
579 al., 2019). Despite no studies to date on the impact of ALAN specifically in harbours, the disruption to
580 hormonal rhythms, including those associated with gonadogenesis, as well as the impacts of growth and
581 survival, strongly suggests that the high levels of light pollution in harbours will have downstream
582 consequences for fitness and population dynamics (Brüning et al., 2018b).

583

584 **2.6. Temperature variations in water exchange-limited harbours**

585 The often-enclosed topography of harbours can prevent efficient water cycling with the open
586 ocean. This can cause higher variation in temperature than in “open” coastal areas (*i.e.*, the water tends
587 to be colder in the winter and warmer in the summer). Harbours can hence potentially provide a natural
588 setting in which to study of the effects of temperature variation on hormones and hormone-dependent
589 physiological processes. Multiple studies have highlighted the effect of temperature on a range of
590 processes – *e.g.*, metabolic rates in zebrafish, ATP production in mosquitofish *Gambusia affinis* –
591 controlled by thyroid hormone action in organisms (cf. review by Little 2021). In addition, temperature
592 variation in harbours will only be heightened by climate change. Fish are most commonly ectotherms
593 (Little, 2021), and thus do not regulate their internal temperatures, but rather adapt their metabolic
594 processes to environmental conditions. This fine-tuning is strongly reliant upon the thyroid axis for
595 numerous taxa: it can be based on the regulation of T3 and T2 levels (in zebrafish; Little et al., 2013)
596 but it also depends on other parts of the signalling cascade, such as the temperature-sensitive differential
597 expression of nuclear thyroid receptors (in tadpoles; Nakajima et al., 2020). Variations in temperature
598 thus have direct effects on the thyroid hormone signalling cascade and can be expected to modify the
599 physiological responses controlled by thyroid hormones (higher T2 and T3 levels in warm conditions,
600 higher metabolic rate, and transcription of ATPase in cold conditions; Little et al., 2013). Furthermore,
601 the combination of other stressors impairing thyroid hormone pathways and heightened temperature
602 variability can have negative impacts on fish. For instance, hypothyroid zebrafish have been found to
603 have impaired swimming performances under cold conditions (Little et al., 2013). Harbours can thus be

604 key sites to study the cumulative consequences of numerous stressors and stronger temperature
605 variability than in natural coastlines with more efficient water renewal.

606

607 **2.7. Combined effects of anthropogenic stressors**

608 Anthropogenic stressors (*e.g.*, chemicals, plastics, boat noise, ALAN, and invasive species) thus
609 occur in harbours and some of their effects on fish endocrine systems are already documented, mostly
610 based on laboratory studies (non-exhaustive list in Table 1). Laboratory studies are particularly suited
611 to isolate causal relationships between a type of contaminant and physiological issues (*e.g.*, Grinwis et
612 al., 2000), and these relationships are extrapolated to predict field conditions (Ankley and Villeneuve
613 2006). However, laboratory studies have numerous limitations when compared to field studies, which
614 is an issue raised by ecotoxicologists over the past decades (Kimball and Levin, 1985, Chapman 2002):
615 they consist of artificial set-ups, with exposure routes differing between the laboratory and field-exposed
616 fish, chemical contaminants often at higher concentrations than those found in harbours, restrained times
617 of exposure to one or multiple contaminants, low number of successive generations, and limited
618 experimental set-up and space. Crucially, they do not replicate all conditions experienced by wild
619 organisms, in particular combinations of numerous stressors (Crain et al., 2008) at various levels of
620 acuteness through time (*e.g.*, varying bioavailability of chemical pollutants depending on water
621 parameters (Ankley and Villeneuve 2006). Wider-scale laboratory studies with microcosms or
622 mesocosms have been suggested (Kimball and Levin, 1985) but involve complex protocols and are
623 again limited in scope. Experimental manipulations of whole ecosystems require numerous impact
624 assessments (*e.g.*, recent experiment with wastewater release into a confined stream, with before-
625 after/control-impact; Pereda et al., 2020) and would be difficult to put in place in open water or coastal
626 settings where target fish species grow. However, harbours can be considered as large-scale and long-
627 term ecosystem manipulations and thus provide an ideal study ground to assess the effects of combined
628 anthropogenic stressors on fish.

629 Indeed, combinations of stressors may have cumulative effects on resident organisms. In the
630 laboratory, synergistic effects of chemical pollutants on TH homeostasis have been identified in rats
631 exposed to a range of endocrine disruptors (dioxins, PCBs, polybrominated diphenyl ethers), with
632 combined impacts higher than in a simple dose additive manner (Crofton et al., 2005). The combination
633 of invasive species and heavy metal pollution in harbours has unexpected outcomes: copper and tin
634 contamination result in the recruitment and growth of various invasive species above ‘natural’ levels in
635 high traffic areas of Sydney harbour, while the recruitment of native species decreases (Piola and
636 Johnston, 2008; Dafforn et al., 2009). Increased larval recruitment of invasive species and increased
637 metal contamination may therefore act in combination to diminish the abundance of native species
638 (Dafforn et al., 2009). The additional impact of climate change and/or ocean acidification onto these
639 local anthropogenic stressors is also predicted to be largely additive. Increased temperature and
640 decreased pH may induce a higher toxicity of many common contaminants in harbours (Crain et al.,

641 2008). Due to the complexity and importance of understanding how global change and multiple local
642 anthropogenic stressors interact, determining the combined impacts of stressors on fish hormonal
643 systems should be a priority to inform managers and stakeholders and improve conservation practices
644 in harbours.

645

646 **Table 1: Examples of the impacts on endocrine systems of fish of different sources of stress that**
647 **can be found in harbours (non-exhaustive list).**

Category	Source of stress		Impact on endocrine systems	Consequences	Species	Developmental stage	Reference
Plastic pollution	Plastic chemical compounds	Bisphenol A and congeners	<i>HPT axis</i>	Altered circulating T4 and T3 levels, expression of HPT-related genes, hormonal disruption transferred to offspring	Zebrafish <i>Danio rerio</i>	Embryonic, larval, metamorphosis, adult	Gentilcore et al. (2012) Zhang et al. (2017) Wei et al. (2018) Lee et al. (2019)
Plastic pollution	Plastic-sorbed chemical compounds	Bisphenol A	<i>Reproductive system</i>	Altered testis maturation, gonad feminisation, decreased sperm quality, increased plasma vitellogenin levels, altered expression of genes related to the reproductive system	Fathead minnow <i>Pimephales promelas</i> Zebrafish <i>D. rerio</i> Rainbow trout <i>Oncorhynchus mykiss</i> Brown trout <i>Salmo trutta</i> Anemonefish <i>Amphiprion ocellaris</i>	Adult Adult Juvenile, adult Juvenile Adult	Sohoni et al. (2001) Van den Belt et al. (2003) Chen et al. (2017) Yang et al. (2017) Van den Belt et al. (2003) Frenzili et al. (2021) Gonzalez et al. (2021)
Chemical pollution	Persistent organic pollutants	Polychlorinated Biphenyl	<i>HPT axis</i>	Altered HPT function, decreased TH circulating levels, change in thyroid gland structure In young individuals: Decreased circulating TH levels, slower growth, and delayed metamorphosis	Coho salmon <i>O. kisutch</i> Flounder <i>Paralichthys olivaceus</i>	Juvenile Metamorphosis, juvenile	Leatherland et al. (1978) Dong et al. (2014) Dong et al. (2017)
Chemical pollution	Persistent organic pollutants	Polychlorinated Biphenyl	<i>Reproductive system</i>	Impaired ovarian maturation, delayed reproduction, fewer viable eggs	Zebrafish <i>D. rerio</i>	Embryonic, larval, metamorphosis, juvenile, adult	Daouk et al. (2011) Horri et al. (2018)
Chemical pollution	Persistent organic pollutants	Bactericide – Triclosan	<i>HPT axis</i>	Disruption of thyroid function, deformities, modified metamorphosis timing	Zebrafish <i>D. rerio</i> Medaka <i>Oryzias latipes</i> Sheepshead minnow <i>Cyprinodon variegatus</i> Sole <i>Solea senegalensis</i>	Embryonic, metamorphosis, adult Embryonic Metamorphosis Metamorphosis	Oliveira et al. (2009) Stenzel et al. (2019) Nassef et al. (2010) Schnitzler et al. (2016) Araújo et al. (2019)

Chemical pollution	Persistent organic pollutants	Polycyclic Aromatic Hydrocarbon	<i>HPT axis</i>	Altered T3, T4, and TSH levels	Turbot <i>Scophthalmus maximus</i>	Metamorphosis	Stephens et al. (1997)
					Caspian brown trout <i>Salmo trutta caspius</i>	Juvenile	Shirdel et al. (2016)
Chemical pollution	Heavy metals	Cadmium	<i>HPT axis</i>	Altered gene expression, reduced circulating T4 levels	Chinese rare minnow <i>Gobiocypris rarus</i>	Larval, adult	Li et al. (2014)
Chemical pollution	Heavy metals	Cadmium	<i>HPI axis</i>	Reduced expression of genes linked to corticosteroid production	Rainbow trout <i>O. mykiss</i>	Juvenile	Sandhu and Vijayan (2011)
Chemical pollution	Antifouling	Tributyltin	<i>HPT axis</i>	Altered T3 and T4 circulating levels and gene expression	Rockfish <i>Sebastes marmoratus</i>	Adult	Zhang et al. (2013)
					Goldfish <i>Carassius auratus</i>	Adult	Zhang et al. (2016)
					Zebrafish <i>D. rerio</i>	Adult	Li and Li (2021)
Chemical pollution	Antifouling	Medetomidine	<i>HPT axis</i>	Paleness in fish – pigmentation linked to TH (McMenamin et al., 2014; Saunders et al., 2019; Salis et al., 2021)	Lumpfish <i>Cyclopterus lumpus</i>	Larval	Bellas et al. (2005)
					Atlantic cod <i>Gadus morhua</i>	Larval	Bellas et al. (2005)
					Turbot <i>Psetta maxima</i> L.	Juvenile	Hilvarsson et al. (2007)
Chemical pollution	Pesticides	Chlorpyrifos	<i>HPT axis</i>	Decreased circulating TH levels, impact on T3 metabolism during metamorphosis. Impaired anti-predator behaviour post-metamorphosis.	Surgeonfish <i>Acanthurus triostegus</i>	Metamorphosis	Holzer et al. (2017) Besson et al. (2020)
Light pollution	Artificial light at night	Disruption of the circadian cycle	<i>Reproductive system</i>	Suppression of LH and FSH synthesis	European perch <i>Perca fluviatilis</i>	Juvenile	Brüning et al. (2016, 2018)
					Roach <i>Rutilus rutilus</i>	Juvenile	Brüning et al. (2016, 2018)
Light pollution	Artificial light at night	Disruption of the circadian cycle	<i>Reproductive system</i>	Reduction in circulating levels of male and female sex hormones (11-ketotestosterone for males, 17 β -estradiol for females)	European perch <i>P. fluviatilis</i>	Juvenile	Migaud et al. (2004)
					Seabass <i>Dicentrarchus labrax</i>	Juvenile	Rodriguez et al. (2005) Felip et al. (2008)

					Sole <i>S. senegalensis</i>	Juvenile	Garcia-Lopez et al. (2006)
					Roach <i>R. rutilus</i>	Juvenile	Brüning et al. (2018)
Light pollution	Artificial light at night	Disruption of the circadian cycle	<i>Reproductive system</i>	Altered gonad maturation	Seabass <i>D. labrax</i>	Juvenile	Begtashi et al. (2004)
					Atlantic cod <i>Gadus morhua</i>	Juvenile	Taranger et al. (2006)
					Turbot <i>Scophthalmus maximus</i>	Juvenile	Imsland et al. (2003)
					Nile tilapia <i>Oreochromis niloticus</i>	Juvenile	Rad et al. (2006)
Temperature	Uncommon temperature conditions	Temperature changes in semi-enclosed harbours	<i>All hormones</i>	Modification of hormone synthesis and tissue sensitivity, impact on numerous processes	Numerous fish species	Embryonic, larval, metamorphosis, juvenile, adult	Review by Little (2021)
Temperature	Uncommon temperature conditions	Increase in average temperature	<i>HPT axis</i>	Modified T4 levels. Impaired anti-predator behaviour post-metamorphosis)	<i>A. triostegus</i>	Juvenile	Besson et al. (2020)
Invasive species	Competitors with native species	Long term competition	<i>HPI axis</i>	Increased stress – release of cortisol, mobilisation of energy. In the long-term, impaired disease resistance, loss of appetite, reduced growth and reproduction, more hiding behaviour	No fish study yet. Squirrel <i>Sciurus vulgaris</i>	Adult	Santicchia et al. (2018)
Sound pollution	Boat noise	Long term engine noise exposure	<i>HPI axis</i>	Increased stress – release of cortisol, mobilisation of energy. In the long-term, impaired disease resistance, loss of appetite, reduced growth and reproduction, more hiding behaviour	Anemonefish <i>Amphiprion chrysopterus</i>	Adult	Mills et al. (2020)
					Wrasse <i>Halichoeres bivittatus</i>	Adult	Staaterman et al. (2020)
Sound pollution	Boat noise	Long term engine noise exposure	<i>Testosterone</i>	Higher aggressivity	Anemonefish <i>A. chrysopterus</i>	Adult	Mills et al. (2020)

649 **3. Recommendations for future studies**

650 Harbours are often considered as secondary sources of coastal pollution, notably when
651 compared with direct wastewater inputs. This review emphasises the lack of studies on the endocrine
652 systems of fish in harbours, despite harbours being potential *in situ* laboratories where multiple stressors
653 occur simultaneously. Characterising the interactions between the hormonal systems of fish and a wide
654 range of stressors in harbours can shed light on numerous issues: how are different endocrine pathways
655 affected by multiple stressors? What consequences do stressors have on the biology and fitness of fish
656 and on their distribution and abundance (*i.e.*, consequences from the molecular and organism level to
657 the population and ecosystem level)? Such integrative studies would provide insights for the
658 development of effective policies to manage and preserve marine biodiversity and would guide solutions
659 to enhance water quality in harbours. Recommendations for future studies are detailed below.

660

661 **3.1 Choice of target fish species**

662 To assess the need for harbour management plans, indicator species can be used. Ford et al.
663 (2005) focused on changes in the structure and function of the microbial community in New Bedford
664 Harbour (USA) in response to toxic contaminant exposure, with the goal of using microbes as
665 ecotoxicological tools. Sessile invertebrates are often used to monitor harbour environments as harbours
666 serve as sinks for pollutants that bind to sediments and contaminants, such as heavy metals and
667 hydrocarbons, accumulate in the tissues of benthic marine species (*e.g.*, marine mussels; Wade et al.,
668 1998; Corsi et al., 2005). Corals have also been identified as environmental indicators of heavy metal
669 contamination and have been used to identify pollution hotspots in Safaga harbour (Egypt; Shabib et al.,
670 2021). Mobile fish species can also be used as key species to reflect the water quality of harbours, as
671 organic contaminants and trace metals can also accumulate in fish tissue (Bolton et al., 2004). Studies
672 conducted in Vancouver Harbour and in the neighbouring Puget Sound estuary reported toxicopathic
673 liver lesions in the English sole *Pleuronectes vetulus*, a benthic species, which were associated with
674 sediment contaminant levels (Goyette, 1988; Myers et al., 1990, 1998). Velusamy et al. (2014)
675 confirmed that benthic species are well-suited to assess the impacts of sediment-associated pollution as
676 trace metals highly accumulated in demersal fishes, followed by neritic and pelagic fishes in Mumbai
677 harbour. Thus, benthic fish species (as opposed to pelagic and demersal fish species) could be used in
678 harbours not only as a bioindicator of marine ecosystem health, but also to study the relationship
679 between sediment contaminant concentrations and the prevalence of diseases. Benthic fish species, due
680 to their ecological niche, cannot avoid environmental stressors, and can be sensitive indicators of natural
681 and anthropogenic disturbances in harbours. Conversely, in the event of restoration action in ports, the
682 species to be favoured will be demersal species, which are independent of the substrate (*e.g.*, most
683 coastal fish typical of rocky substrate in the case of the Mediterranean Sea).

684

685 **3.2. Increasing larval recruitment in harbours**

686 Numerous management solutions for harbours have focused on promoting larval recruitment in
687 harbour areas. However, the relevance of such solutions can be questioned as harbours are generally
688 unfavourable habitats for fish growth and quality. Larval fish recruiting in harbours are exposed to
689 multiple stressors that may impact their ability to grow properly (deformity), to metamorphose, to
690 reproduce (sterility), or to protect themselves from predation. Why should fish recruitment be promoted
691 in harbours if fish survival and metamorphosis are uncertain, and hence if the renewal capacity of fish
692 stocks is not guaranteed? The first ecological restoration actions in ports to rehabilitate the nursery
693 function are encouraging as they show greater species diversity, greater abundance, and better survival
694 (Bouchoucha et al., 2016; Mercader et al., 2017). This is linked to the fact that the artificial habitats only
695 target demersal species which have food sources independent from polluted harbour substrates.
696 Bouchoucha et al. (2018) found little to no significant differences between the concentrations of some
697 heavy metals in the muscle tissues of seabream juveniles in a harbour and a natural area. Studies testing
698 the synergistic effects of the multiple stresses present in harbours on the hormonal systems of fish are
699 yet to be performed. Research must focus on these questions to clarify whether the restoration of juvenile
700 nursery areas in harbours is efficient in the long term to mitigate the impacts of coastal modifications.
701 Answering this question is crucial to implement relevant and efficient conservation actions. Indeed, even
702 if harbours attempt to limit their impacts, for instance by obtaining ecological labels (which should be
703 the direction to follow; Satir and Doğan-Sağlamtimur, 2018), the creation of a marine protected area in
704 their vicinity could be a better option. However, not all areas are suitable for the implementation of
705 protection measures and restoring degraded habitats in harbours should be considered as a
706 complementary step. Conservation and restoration actions must be adapted to local characteristics and
707 specificities. In any case, the priority remains preventing the degradation of ecosystems and associated
708 ecosystem services.

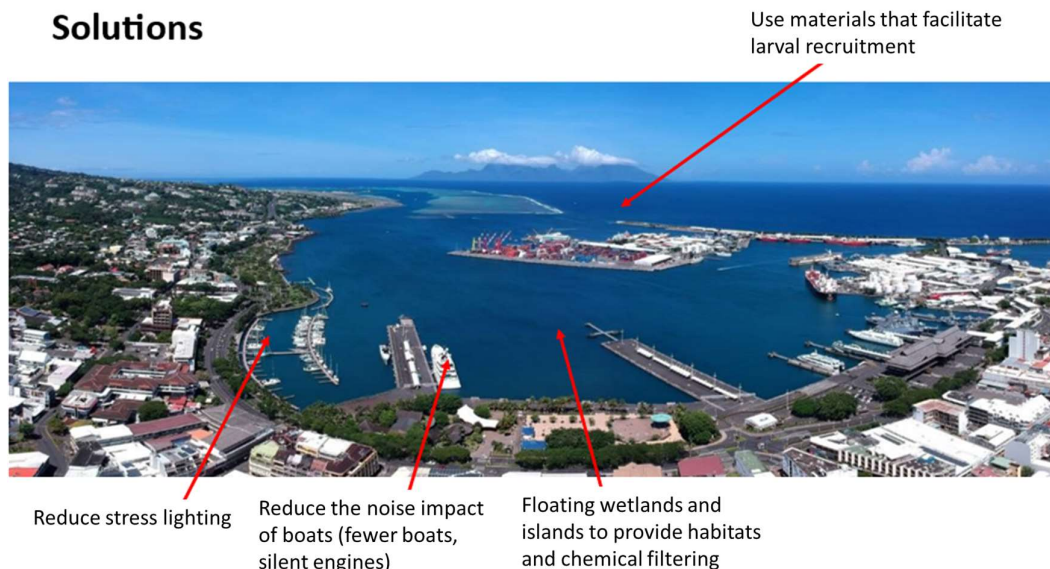
709

710 ***3.3. Recommendations to harbour authorities and researchers***

711 Environmental protection perspectives in harbours should focus around four themes: 1) an
712 analysis of the nursery function of the harbour, through a dynamic and quantitative description of the
713 recruitment of juvenile and of adult fish populations on a long-term basis (as practiced in French
714 Mediterranean harbours which benefit from ecological restoration action) ; 2) a definition of the
715 physiological “quality” of juvenile fish (eco-physiological status of the recruits, established by
716 measuring the levels of thyroid hormones and baseline cortisol levels); 3) compensation solutions to
717 protect or restore the nursery function of harbours (*e.g.*, Bouchoucha et al., 2016; Mercader et al., 2017b;
718 Mercader 2018); and 4) proposals for good practices and communication with the general public about
719 possible ecological restoration solutions in and near harbours. The interactive and cumulative effects of
720 anthropogenic stressors on marine fishes in harbours remain largely unknown. These knowledge gaps
721 must be addressed and used along with precautionary principles to develop coherent environmental
722 protection plans. However, based on precautionary principles, the following guidelines can already be

723 formulated (Fig. 3): put in place structures to provide shelters for marine species; clean up and reduce
724 the inputs of plastics and chemical pollution (notably with nature-based methods, such as putting in
725 place wetlands that can filter water in addition to providing habitats; Wood 1995); avoid the discharge
726 of ballast water; reduce the speed of boats to lessen sound pollution; reduce light pollution at night.

Solutions



727

728 Fig. 3: Illustration of different precautionary measures to improve survival and health in marine
729 organisms that could be adopted in the port of Papeete, Tahiti, French Polynesia

730

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735

736 Declaration of competing interest

737 The authors declare that they have no known competing financial interests or personal
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739

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