

1 **How does eutrophication impact bundles of ecosystem services in multiple coastal habitats using**
2 **state-and-transition models.**

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23
24
25 **Abstract**

26
27 One of the current major scientific challenges to sustain social-ecological systems is to improve our
28 understanding of the spatial and temporal dynamics of the relationships between biodiversity,
29 ecosystem functioning and ecosystem services. Here, we analyze the bundles of ecosystem services
30 supplied by three coastal ecosystems (coastal lagoons, coral reefs and sandy beaches) along a gradient
31 of eutrophication. Based on a state-and-transition model, we analyses the dynamic responses of
32 ecological communities to environmental change and management actions. Although few exceptions
33 are highlighted, increasing eutrophication in the three ecosystem types leads to a degradation of the
34 ecosystem service bundles, particularly for nutrient and pathogen regulation/sequestration, or for the
35 support of recreational and leisure activities. Despite few obstacles to their [full](#) use, state-and-transition
36 models can be very powerful frameworks to integrate multiple functions and services delivered by
37 ecosystems while accounting for their temporal dynamics.

38

39 **Key-words**

40

41 Sandy beaches

42 Coral reefs

43 Coastal lagoons

44 Ecosystem service bundles

45 Temporal dynamics

46 Management

47 **1. Introduction**

48

49 The demographic and economic growth of societies is increasingly facing the ecological limits of the
50 planet (Meadows et al., 2004). This global ecological crisis, as illustrated by major changes in
51 ecosystem states with decreasing availability of natural resources, is accelerated by climate change. The
52 consequences of this crisis are already observable within societies and will most likely spread and
53 generalize in future decades (Cardinale et al., 2012 ; Isbell et al., 2017). One of the major scientific
54 challenges for biodiversity conservation is to improve the understanding of the [relationships](#) between
55 biodiversity, ecosystem functioning and ecosystem services (ES) to analyse the compatibility and the
56 interdependence between biodiversity conservation objectives and ES maintenance (Harrison et al.,
57 2014).

58

59 [The ES concept seeks](#) to account for the dependence of human societies on ecosystems, commonly
60 defined as the contributions of ecosystem structure and function to human well-being (MA, 2005).
61 Originally, ES and its monetary valuation (see Costanza et al., 1997) were primarily intended to alert
62 public opinion and governments about the importance of well-functioning ecosystem for societies and
63 the risks associated with the ecological crisis. Scientific developments of this concept, encouraged by
64 its institutionalization (Mongruel et al., 2016) i.e. the dissemination of the concept in the area of
65 environmental management decision-making, have gradually clarified its scope. It also defined multi-
66 criteria analysis as the most robust way to evaluate ES, seeking to inform decision-making processes
67 and the establishment of public policy and management policies (Keune and Dendoncker, 2013 ;
68 Saarikoski et al., 2016). However, 50% of ES studies focus on a single service, or on a limited number
69 of services, without considering interactions and feedback with other services ([Lee and Lautenbach,](#)
70 [2016](#)). This monofocal vision can lead to an operational ecosystem management based on the
71 maximization of a single ES and potentially to the detriment of the other ones (Couvet et al., 2016).

72

73 Indeed, ES [depend on](#) complex interactions among species and their abiotic environment, complex use
74 and utilization patterns and various perceptions by beneficiaries. ES bundles are defined as sets of ES
75 that repeatedly appear together across space or time (Raudsepp-Hearne et al., 2010). It is thus a useful
76 concept for improving the management of ecosystems and identifying common ES tradeoffs and
77 synergies: trade-offs arise when the provision of one service is enhanced at the cost of reducing the
78 provision of another service, and synergies arise when multiple services are enhanced simultaneously
79 (Raudsepp-Hearne et al., 2010). Bundle analysis seeks to inform management and decision-making for

80 reducing the cost of both tradeoffs and synergies. For example, the maximization of food produced by
81 agricultural ecosystems in the context of intensive agriculture has led to an erosion of supporting (e.g.
82 soil fertility), regulating (e.g. regulation of nutrients) and cultural (e.g. homogeneous landscapes) ES
83 (Power, 2010).

84

85 More recent scientific developments indicate that separating, *a minima*, the supply and demand of ES
86 helps to refine and clarify the bundle analysis (Villamagna et al., 2013 ; Burkhard et al., 2014 ; Levrel
87 et al., 2016 ; [Crouzat et al., 2016](#)). The supply represents the ecosystem capacity to provide ES (also
88 called potential), whereas the demand is the amount of services used, consumed but also desired by the
89 society (Villamagna et al., 2013). Different approaches can be used to analyze trade-offs and synergies
90 depending on whether the focus is on supply or demand for ES ([Mouchet et al., 2014](#)).

91

92 Coastal habitats are among the habitats the most exposed to current direct and indirect drivers of
93 change (Henson et al., 2017). Among them, sandy beaches, coastal lagoons and coral reefs are
94 particularly vulnerable (Defeo, 2009 ; Kennish and Paerl, 2010 ; Pendleton et al., 2016). Among these
95 drivers of change, eutrophication is particularly important, prevalent and at the origin of significant
96 ecological and social changes (Diaz and Rosenberg, 2008 ; Wilkinson, 2017). Although the ecological
97 impacts of eutrophication on these ecosystems are well studied today, its effects on ES bundles are little
98 explored. The ES approach can provide an interesting perspective to understand the ecological impacts
99 and associated risks of eutrophication to better inform decision-making processes and management
100 strategies. Here, we assess the effects of eutrophication in sandy beaches, coastal lagoons and coral
101 reefs on ES bundles. Our aim is to identify trade-offs and synergies between ES and the possible
102 societal benefits associated to the recovery of the ecological functions for these ecosystems.

103

104 **2. Materials and Methods**

105

106 2.1. State-and-transition model

107

108 State-and-transition models are an operational and conceptual framework for organizing and providing
109 information about ecosystem dynamics and management outcomes describing how communities
110 respond to pressures and management (Briske et al., 2005 ; Bestelmeyer, 2015). It has been developed
111 by [Westoby et al. \(1989\)](#) for rangeland ecological sites in southern Arizona. While its scientific
112 application is widespread for some terrestrial habitats (e.g. McIntyre and Lavorel, 2001 ; Quétier et al.,

113 2007 ; Tarrason et al., 2016), its application in the marine environment remains almost non-existent.

114

115 We apply here the two first steps of the operational framework described by Lavorel et al. (2015) - as
116 the aim of our paper is slightly different and isn't to identify and manage adaptation services - to three
117 marine ecosystems to explore the evolutions of communities and ES bundles supply along a gradient of
118 eutrophication. Eutrophication and management measures (e.g. nutrient flow, ecological restoration)
119 are seen as drivers determining the ecosystem state, i.e. specific biodiversity and functioning, at a
120 particular time and place. The first step aims to characterize the ecosystem dynamics under
121 eutrophication through state-and-transition models: alternative states may be represented by dominant
122 species and associated biodiversity based on empirical and prospective studies. For each ecosystem
123 state, i.e. eutrophication level, bundles of ecosystem services supplied are identified. The second step
124 aims to describe and, if possible, to quantify ecosystem responses to eutrophication levels. This
125 involves changes affecting ecosystem functions and supply of ES.

126

127 **We used** the classification of the Common International Classification of Ecosystem Services (CICES)
128 and the list of marine ES defined by Liqueste et al. (2013) **to defined the ES constituting bundles**
129 (TABLE 1). The main distinction between these classifications concerns supporting services or
130 ecological functions. These latter are the underpinning structures and processes that ultimately give rise
131 to ecosystem services - sometimes defined as 'intermediate services'. They are not covered in CICES
132 which seeks to only identify the final services that link to the goods and benefits that are valued by
133 people (i.e. demand). Since we focus here on the ES supply, main ecological functions are considered
134 as recommended by Liqueste et al. (2013).

135

136 Each step involved a literature review regarding ecosystem responses to eutrophication that **was**
137 supplemented with expert-knowledge. The literature review **encompassed** knowledge obtained and
138 disseminated on a global scale, while expert knowledge **focused** on data observed on a more local
139 scale, based on their field studies. However, experts **had** a good understanding of these ecosystems
140 which **allowed** them to pronounce in a qualitative way where data gaps **were** identified. All information
141 **were** compiled within a matrix. Information was then coded and analyzed to produce spider plots
142 summarizing the variation of ES supply between states. Five levels of ES supplied were considered :
143 "0: inexistent", "1: very low", "2: low", "3: medium", "4: high", "5: very high".

144

145 *TABLE 1: Correspondence between CICES and selected ES*

CICES		Liquete et al. (2013)	Selected ES for the study
Section	Division		
	Nutrition	Food provision	P1. Food through fisheries
Provisioning	Materials	Biotic materials and biofuels	P2. Material P3. Molecules
	Energy		-
Regulation & Maintenance	Mediation of waste, toxics and other nuisances		-
	Mediation of flows		R1. Coastal protection
	Maintenance of physical, chemical, biological conditions	Water purification Air quality regulation Coastal protection Climate regulation Weather regulation Biological regulation	R2. Nutrient regulation/sequestration R3. Pathogen regulation/sequestration R4. Climate regulation
	Physical and intellectual interactions with biota, ecosystems, and land-/seascapes [environmental settings]	Recreation and tourism Cognitive effects	C1. Support of recreational and leisure activities C2. Contribution to a pleasant landscape C3. Contribution to culture and territorial identity
	Spiritual, symbolic and other interactions with biota, ecosystems, and land-/seascapes [environmental settings]	Symbolic and aesthetic values	C4. Emblematic biodiversity
		Ocean nourishment Life cycle maintenance	F1. Habitat F2. Trophic networks F3. Recruitment

146

147 2.2. Driver of transition : eutrophication

148

149 Eutrophication occurs when the nutrient enrichment process (especially nitrogen and / or phosphorus
150 compounds) leads to an increase in primary production, growth and biomass of phytoplankton and / or
151 macroalgae, as well as a change in the equilibrium of organisms and a degradation of water quality
152 (Cloern, 2001; Ferreira et al., 2011). It is a natural phenomenon and ecosystems have a level of
153 resilience that allows them to resist against the high variability of nutrient enrichment. This resilience
154 may be insufficient when excessive nutrient enrichment occurs from human activities. In Europe, the
155 volume of nitrogen transported to the coastal areas is now four times higher than that of natural origin
156 (Voss et al., 2011). This eutrophication, with an anthropogenic origin is a real issue worldwide because
157 of its important socio-economic consequences: loss of tourist potential and water use for recreational
158 activities, unfit seafood or increased maintenance costs associated with algal removal (Lefebvre, 2011).
159 From a strictly ecological point of view, the eutrophication manifestations are classically distinguished
160 into two types, namely the development of opportunistic macroalgae and the development of
161 phytoplankton blooms. By modifying environmental conditions, these macroalgal and phytoplankton

162 developments will impact the entire ecosystem and ES.

163

164 2.3. Three coastal case studies: sandy beaches, Mediterranean coastal lagoons and coral reefs

165

166 The state-and-transition model is applied to sandy beaches, Mediterranean coastal lagoons and coral
167 reefs, three ecosystems with different biophysical characteristics related to contrasted ES supply.
168 Present at several latitudes, these ecosystems undergo changes proven in various parts of the world,
169 linked to a multitude of pressures among which eutrophication is particularly important. Beyond their
170 ecological functioning, these ecosystems underlie many uses and have important cultural and heritage
171 values. We believe that an increased awareness - by society - of the changes could favor the levers of
172 action to reverse the negative trend they are undergoing (Marzano et al., 2015).

173

174 Sandy beaches are defined as accumulations of non silty fine sediment along coastlines (Davis 2015)
175 including the entire foreshore since the level of the Mean High Water Springs until the level of the
176 Mean Low Water Springs. It constitutes a highly dynamic ecotone mainly influenced by its physical
177 environment. Indeed, the composition of species assemblages and the organism abundances are
178 correlated with physical factors such as wind, beach slope, tidal amplitude or sediment granulometry
179 (McLachlan and Dorvlo, 2005). Unfairly characterized as lifeless deserts (McDermott 1983), sandy
180 beach ecosystems harbor many organisms that are highly specialized and adapted to life in mobile
181 sediments leading to specific ecological functions (McLachlan and Brown 2006). Where conditions are
182 favorable to the development of opportunistic macroalgae, eutrophication will generate deposits on the
183 sandy beaches, the anaerobic decomposition will evolve toxic reducing substances, including hydrogen
184 sulfide. Sandy beaches are present worldwide constituting 70% of the ice-free coastline (McLachlan
185 and Brown 2006). Eutrophication occurs in many parts of the world (Smetacek and Zingone, 2013). In
186 France, green tides punctually occur along the Channel-Atlantic coast during spring and summer.

187

188 Mediterranean coastal lagoons are semi-enclosed ecosystems spread along the European coasts
189 (Fiandrino et al., 2017). They are expanses of shallow coastal water, of varying salinity and water
190 volume, partially separated from the sea by sand banks or shingle, or, less frequently, by rocks (Hill et
191 al., 2004). Salinity may vary from oligohaline to hyperhaline ranges depending on rainfall, freshwater
192 inland and underground water supplies, evaporation and through the addition of fresh seawater from
193 storms or tidal exchange. These ecosystems support habitats with or without macroalgae and
194 phanerogams vegetation. Eutrophication particularly occurs in many French mediteranean coastal

195 lagoons with a strong gradient from oligotrophic to hypertrophic states (Souchu et al., 2010 ; Bec et al.,
196 2011 ; Leruste et al., 2016 ; Le Fur et al., 2017). Where conditions are favorable to eutrophication, the
197 development of opportunistic macro- and micro-algae is observed with a marked change of primary
198 producers (Schramm, 1999 ; Leruste et al., 2016 ; Le Fur et al., 2017).

199

200 Coral reefs are developed on the immersed bottoms of volcanic islands in the intertropical zone. The
201 reefs are constructed from a mineral substrate (calcium carbonate) secreted primarily by the polyps of
202 scleractinian corals. This habitat is made of a reef surface and a non-reef surface (lagoon and
203 sedimentary terraces). Despite thriving in nutrient-poor waters, coral reefs belong to the most
204 productive ecosystems on Earth due to efficient retention and recycling of carbon and nutrients
205 (famously referred to as the "Darwin's Paradox"). Eutrophication has long-term negative impacts on the
206 structure and functioning of coral reef ecosystems. Increasing nutrient levels can: i) increase the
207 number and prevalence of coral diseases (Vega Thurber et al., 2013) and the susceptibility of corals to
208 temperature and light-induced bleaching (Wiedenmann et al., 2013), ii) reduce coral reproduction and
209 skeletal growth (Tomascik and Sander, 1987; Koop et al., 2001), iii) stimulate the growth of algae,
210 heterotrophic sponges and benthic cyanobacterial mats, which in turn can reduce coral recruitment,
211 alter the coral microbiome and drive reef decline further (Mumby and Steneck, 2008; Brocke et al.,
212 2015; Pawlik et al., 2016; Ford et al., 2018), iv) enhance periodic outbreaks of the corallivorous crown-
213 of-thorns starfish *Acanthaster planci* (Brodie et al., 2005), and v) promote higher bioerosion rates by
214 favouring the activity of filter-feeders such as endolithic bivalves and bioeroding sponges (Fabricius,
215 2005). Coral reefs are present worldwide in the intertropical zone. They are one of the most emblematic
216 tropical ecosystems because of its size, geomorphological diversity, biodiversity and high endemism
217 (Gardes and Salvat, 2008). In France, eutrophication occurs in coral reefs located along the most
218 inhabited volcanic islands (e.g. Martinique, Guadeloupe, La Réunion).

219

220

221 **3. Results**

222

223 3.1. State and transition description

224

225 For each ecosystem, ecological functioning is described by dominant species and associated
226 biodiversity for three to four levels of eutrophication (FIGURE 1).

227

228 3.1.1. Sandy beaches

229

230 First ecological state of sandy beaches is described by groups of species defined as reference species
231 living in a non-eutrophic ecosystem, where no green tides occur (state I). In some French Atlantic
232 sandy beaches, these reference species, for marine benthic macrofauna, are part of *Tellinidae*,
233 *Spionidae*, *Amphiuridae* and *Nephtyidae* families (Quillien et al., 2015). The continuous supply of
234 nutrients (exogenous inputs or release from sediments) (transition 1) causes a slight excess and leads to
235 the gradual development of green algae. As a response, dominant species change in this eutrophic
236 ecosystem (state II) with an appearance of new dominant species (*Donacidae*, *Oweniidae*,
237 *Magelonidae*) and the decrease, even the disappearance, of some reference species (*Tellinidae*,
238 *Spionidae*, *Amphiuridae*) (Quillien et al., 2015). Where hydrodynamic conditions are favorable, the
239 massive supply of nutrients (transition 2) leads to the massive and rapid development of green algae
240 forming green tides. Species of reference have disappeared in favor of species (*Donacidae*, *Oweniidae*)
241 better adapted to eutrophic conditions (state III). Abundance and biomass are higher in this new
242 eutrophic ecosystem, but the species richness is lower (Quillien et al., 2015).

243

244 3.1.2. Mediterranean coastal lagoons

245

246 First ecological state of primary production of Mediterranean coastal lagoon is characterized by a
247 dominance of reference species that are typical of a lagoon environment in oligotrophic conditions
248 (state I). For French Mediterranean coastal lagoons, the reference genus are the marine phanerogams
249 *Zostera* and *Ruppia* which form seagrass beds, and perennial benthic macroalgae (eg. *Cystoseira* sp.,
250 *Acetabularia* sp.). The continuous supply of nutrients (transition 1) causes a slight excess and leads to
251 the gradual disappearance of the reference species and the slow and sustainable development of algae
252 (Schramm, 1999). State II is dominated by a dominance of opportunistic and epiphytic macroalgae.
253 Most are red or brown algae, which can form drifting populations or seasonally bloom on substrates or
254 other macrophytes. The massive supply of nutrients (transition 2) leads to the massive and rapid
255 dominance of free-floating blooming opportunistic algae (state III). These algae have a shorter lifetime
256 and a higher growth rate than state II algae. Their ability to absorb nutrients is higher, making them
257 more competitive than other species in highly eutrophic environments. In case of proliferation, they can
258 cover and eliminate seagrass beds. In case of massive development of these species, they fill the whole
259 column of water and reach the surface, forming green tides. In the most eutrophicated systems,
260 phytoplankton community dominates the water column (transition 3, state IV). The proliferation of
261 macroalgae and phytoplankton can contribute to triggering the phenomenon of anoxic crisis.

262

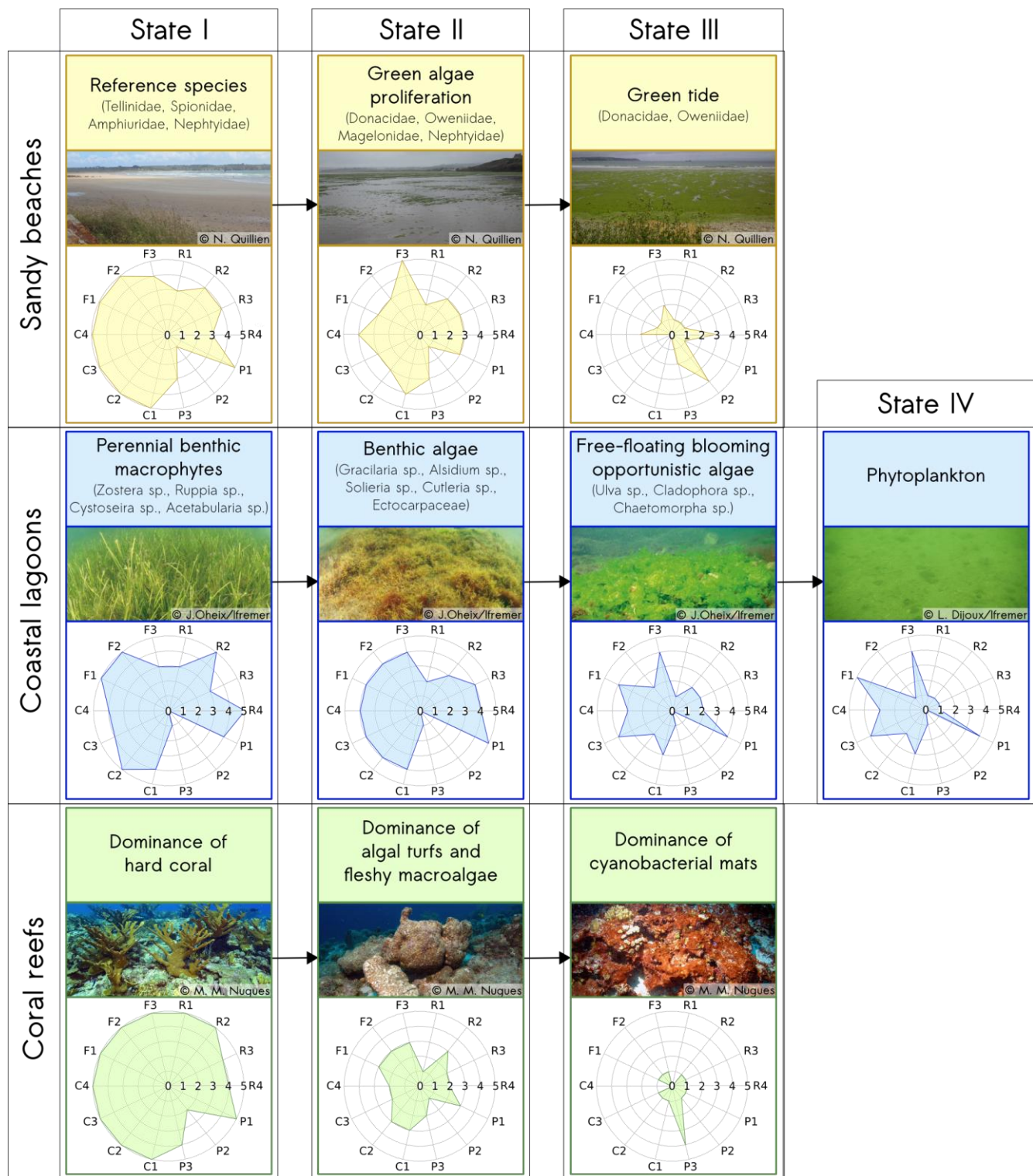
263 3.1.3. Coral reefs

264

265 Combining anthropogenic and natural stressors lead to changes in the ecological functioning of coral
266 reefs (Jackson et al., 2014; de Bakker et al., 2016). First ecological state of coral reefs is characterized
267 by the dominance of hard corals. In the Caribbean reefs of Curaçao and Bonaire, hard coral represented
268 two thirds of the benthic community cover in this initial state. Other benthic communities present were
269 algal turfs, crustose coralline algae, sponges and benthic cyanobacterial mats (de Bakker et al., 2017).
270 The increasing pressure (transition 1) leads to the development of algal turfs and fleshy macroalgae
271 which are fast-growing organisms and a gradual decline of coral cover (e.g. Hughes et al., 2018), in
272 particular from competitive losses against algae under conditions of reduced herbivory (Vermeij et al.,
273 2010) (state II). Algal turfs are multispecies assemblages of diminutive, mostly filamentous algae,
274 including cyanobacteria. Due to their opportunistic life-history characteristics, they are able to rapidly
275 occupy newly available substratum. Besides, they inhibit coral recruitment. Fleshy macroalgae are
276 commonly defined as more upright and anatomically complex algae with frond extension > 1 cm (e.g.,
277 *Dictyota* spp. and *Lobophora* spp.). They are frequently superior competitors against corals, inhibiting
278 coral growth, reproduction, and recruitment (Nugues and Bak, 2006). With a continuous and increasing
279 pressure (transition 2), benthic cyanobacterial mats increase and become dominant at the expense of
280 algal turfs and macroalgae while sponges showed a more limited but significant increase. Benthic
281 cyanobacteria mats benefit from increased levels of nutrient (Brocke et al., 2015) but also from high
282 grazing pressure and elevated water temperature (Bender et al., 2014). In the Caribbean reefs of
283 Curaçao and Bonaire, hard coral and algal turfs represented both around 10% of the benthic community
284 cover in this state III while benthic cyanobacterial mats represented more than 20% (de Bakker et al.,
285 2017).

286

287



288 **FIGURE 1: Main characteristics of the ecosystem states and transitions** (sources: Quillien et al. (2015)
 289 *for sandy beaches; Schramm (1999) for Mediterranean coastal lagoons; de Bakker et al. (2017) for*
 290 *coral reefs) and relative levels of ES supplied by the ecosystem in each state of eutrophication*
 291 *(0 = inexistent ; 1 = very low ; 2 = low ; 3 = medium ; 4 = high ; 5 = very high ; R1 = Coastal protection (vegetal or animal reef*

292 supplying a protection against erosion and submersion) ; R2 = Nutrient regulation/sequestration (ecosystem capacity to supply a "good
293 quality water", limiting the risk of eutrophication, encouraging shell fish farming...) ; R3 = Pathogen regulation/sequestration (ability of
294 ecosystems to purify the environment through hyperfiltration processes) ; R4 = Climate regulation (through GES sequestration/storage) ;
295 P1 = Human food through fisheries and aquaculture ; P2 = Material (Animal oil, sponges, algae... for domestic uses, industry,
296 agriculture, aquaculture...) ; P3 = Molecules (marine organisms from which are extracted molecules potentially useful for medicine) ; C1
297 = Support of recreational and leisure activities ; C2 = Contribution to a pleasant landscape ; C3 = Contribution to culture and territorial
298 identity ; C4 = Emblematic biodiversity (i.e. protected or rared species) ; F1 = Habitat (nursery, reproduction area...) ; F2 = Trophic
299 networks ; F3 = Recruitment)

301 3.2. ES bundle description (FIGURE 1)

303 3.2.1. Sandy beaches

305 Coastal protection is provided by both the physical structure of the beach and specific fauna and flora.
306 As ES only considers the roles played by biodiversity, coastal protection (R1) focuses on the latter,
307 ables to reduce the hydrodynamics or to stabilize the substrate. Indeed, bioturbating organisms
308 contribute to the stabilization of the substrate and the tide mark also limits the erosion phenomenon by
309 trapping the sand. But the presence of Ulva mats (states II and III) impacts the hydrodynamics
310 (Tambroni et al., 2016), thus affecting the sediment transport and ultimately the ES. Nutrient regulation
311 (R2) decreases along the gradient of eutrophication: beach ecosystems are important in processing
312 large quantities of organic material and recycling nutrients back to coastal waters (Schlacher et al.,
313 2008) but the release of excess nutrients and the presence of green macroalgae mats probably saturate
314 the filtering function and the ES as well. The capacity of beach ecosystems to provide a service of
315 pathogen regulation (R3) is not well-documented but in the same way as for nutrient regulation (R2)
316 the alteration of the filtering function can affect this ES. Climate regulation (R4) is constant between
317 state I to III as sequestration through the phytoplanktonic, microphytobenthic and green algae activity
318 is a short term function.

320 Human food (P1) is highly decreasing along the eutrophication gradient because of the changes in
321 species assemblages affecting the shellfish fishing activities. Indeed, sandy beaches support
322 professional fisheries of the bivalve *Donax trunculus*, which is of commercial importance (McLachlan
323 and Brown, 2006) but at eutrophication states (states II and III), a decrease in its density has been
324 shown (Quillien et al., 2015). Materials (P2) is slightly provided by driftwood and seashell which can
325 be collected but highly increase in state III because of the capacity of green algae to be collected and
326 used in industry (pet food, cosmetics...). Molecules (P3) is potentially provided in states I and II as the
327 diversity that is harboured by sandy beaches is high, specialized and unique and effectively provided

328 through *Arenicola marina*, which is collected and bred to get hemoglobin for medical uses. In state III,
329 molecules are effectively extracted from *Ulva* but the eutrophication impacts the other organisms, and
330 more specifically affects the overall diversity thus decreasing the potential pool of molecules.

331

332 Cultural ES (C1 to C4) decrease along the eutrophication gradient as the landscape, the leisure
333 activities, the territorial identity and the emblematic biodiversity are affected by green tides
334 (McLachlan and Brown, 2006 ; Schlacher, 2008 ; Levain, 2013).

335

336 The habitat function (F1) is altered as green tides affect nurseries of various species (McLachlan and
337 Brown, 2006 ; Quillien et al., 2016 ; Le Luherne et al., 2017). Trophic networks (F2) in state I is high
338 because the food web is complex, showing several potential carbon pathways and diverse trophic
339 niches while in eutrophication states, the trophic network is homogenized/simplified and shows less
340 niche differentiation (Quillien et al., 2016). Recruitment (F3) is high in state I for many species and
341 increases between states I and II as the presence of *Ulva* mats influence local hydrodynamics, which in
342 turn influence the recruitment of some species. For example, in Brittany, the presence of heterogenous
343 cover of *Ulva* enhances the recruitment of the bivalve *Donax vittatus* (Quillien et al., 2015). However
344 when the *Ulva* biomass is high, macroalgae affect the recruitment, community structure and production
345 of benthic fauna, including meiofauna, macrofauna and flatfish (Quillien, 2016).

346

347 3.2.2. Mediterranean coastal lagoons

348

349 On Mediterranean coastal lagoon ecosystems, coastal protection (R1) is estimated to decrease with the
350 alteration and decline of seagrass meadows which have the capacity to attenuate waves and to slow
351 down currents (Paquier et al., 2014). In a logical way, nutrient regulation (R2) decreases along the
352 gradient of eutrophication. Seagrass beds play an important role in regulating benthic nutrient fluxes in
353 lagoons as they increase the ability to store nutrients sustainably. The flow of nutrients from the
354 sediment to the water column and, at the same time, eutrophication levels are thus greater in lagoons
355 without seagrass (Viaroli et al., 2008 ; Ouisse et al., 2013). Pathogen regulation (R3) is more provided
356 in states I and II than in states III and IV because of the algicidal effects of *Zostera marina* L. and
357 *Zostera noltei* Hornem. on *Alexandrium catenella* (Laabir et al., 2013). More generally, seagrass
358 ecosystems reduce exposure to bacterial pathogens of humans, fishes, and invertebrates (Lamb et al.,
359 2017). However, emergence of toxic dinoflagellate is observed in oligotrophic conditions (Collos et al.,
360 2009) which leads to weighting the pathogen regulation service in state I. Climate regulation (R4) is

361 particularly high in state I and II because of the potential long-term capacity to sequester greenhouse
362 gases in the sediment through perennial macrophytes.

363

364 Human food (P1) is the most important provisioning service for Mediterranean coastal lagoons
365 (Newton et al., 2018) and is mainly based on shellfish farming. The quantity or the state of the suitable
366 areas for shellfish farming indicate the state of this ES. As shellfish farming needs a high rate of
367 primary productivity to feed shellfish, the state II meets the most optimal conditions. On the one hand,
368 oligotrophic conditions can lead to an under-capacity of production and on the other hand, a massive
369 supply of nutrients can lead to anoxic crisis and the death of shellfish stocks (Cloern, 2001). Molecules
370 (P3) exist as a potential but no successful example can be cited nowadays.

371

372 Emblematic biodiversity (C4) is varying along the eutrophication gradient. In states I and II, protected
373 and rare species like *Zostera sp.*, *Hippocampus sp.*, avifauna (e.g. *Anas penelope*, *Cygnus olor*, *Egretta*
374 *garzetta*, *Ardea cinerea*) are able to contribute to human well-being because of their mere existence, but
375 also because of their role in supporting of some recreational and leisure activities (C4) like scuba-
376 diving, snorkeling and nature watching. In states III and IV, the presence of these protected and rare
377 species decreases for the benefit of a more restrictive number of other protected species like flamingos
378 (de Wit et al., 2015). The contribution of Mediterranean coastal lagoon ecosystems to a pleasant
379 landscape (C2) is mainly based on avifauna, and in a lesser extent, on other living components
380 including underwater seascape (Chazée et al., 2017). Avifauna is present from state I to IV even if the
381 assemblage of species varies between them. However, the capacity of Mediterranean coastal lagoons to
382 provide pleasant underwater seascape can be considered altered with the degradation and decline of
383 *Zostera* meadows. Biodiversity of coastal lagoons also contributes to culture and territorial identity
384 (C3) as they are a socialization area, sometimes assimilated to a urban park (Chazée et al., 2017).

385

386 The habitat function (F1) is altered with degradation and decline of *Zostera* meadows since they are a
387 habitat for many species. Indeed, the leaf canopy and the network of rhizomes and roots create hiding
388 places to avoid predation. Mediterranean coastal lagoons also provide higher temperature during
389 growth and food to some fish species like *Sparus aurata*, which allow good lipid reserves, and large
390 sizes of juveniles, which may be very important to their survival over winter (Tournois et al., 2013 ;
391 Isnard et al., 2015). Trophic networks (F2) in state I is high because of its high complexity, which then
392 decreases along the eutrophication gradient until low complexity in degraded states (Pearson and
393 Rosenberg, 1978). As a consequence, if enrichment of food webs in lagoons is altered, the

394 consequences for fishery resources could be important with an impact on recruitment (F3). However,
395 the carrying capacity for juvenile oysters of oligotrophic lagoons is questioned (Lagarde et al., 2017)
396 and leads to weighting the recruitment function in state I.

397

398 3.2.3. Coral reefs

399

400 Coastal protection (R1) is an important service provided by coral reefs as they can dissipate 97% of the
401 wave energy that would otherwise impact shorelines (Ferrario et al., 2014). As eutrophication leads to
402 the loss of corals, water depth between the reef crest and the surface increases and should result in a
403 less effective, or even nonexistent, ES. Nutrient regulation (R2) decreases along the gradient of
404 eutrophication. This ES is intensively performed by zooxanthellae in living coral reefs (state I). The
405 risk of hyper-eutrophication is thus greater in altered or dead coral reefs. Moreover, cyanobacterial
406 mats and sponges who are also able to produce the ES in state III can be easily washed away by storms.
407 Pathogen regulation (R3) also decreases along from state I to III. Turf algae and macroalgae (state II)
408 alter the coral microbiome and elevate putative pathogen loads (Vega-Thurber et al., 2013 ; Zanefeld et
409 al., 2016 ; Pratte et al., 2018). Living coral reefs (state I) also widely contribute to climate regulation
410 (R4), stocking greenhouse gases through the production of carbonates (Roberts et al., 2017).

411

412 Human food (P1) is mainly based on reef fisheries. Coral-dominated reefs (state I) are the most
413 productive (Hughes et al., 2017). Depending on structural complexity, multi-species fisheries can shift
414 towards herbivorous fish species (state II). However, overfishing of herbivorous fishes prevents the
415 return to state I (Hicks et al., 2016). Bottoms lacking structural complexity (state III) become very poor
416 in target species. Coral ecosystems are particularly rich in molecules (P3) because of the wide
417 competition between species that leads to a diversity of chemical defense by organisms (Banaigs et al.,
418 2016). State I supports a high diversity of organisms and thus potential biomolecules. Cyanobacteria
419 and sponges (state III) are also chemically rich. However, chemical defense could lessen in absence of
420 consumers. For example, sponge communities have become dominated by fast-growing species that
421 lack chemical defenses on reefs where sponge-eating angelfishes and parrotfishes have been removed
422 by overfishing (Loh and Pawlik, 2014).

423

424 In many tropical societies, relations to nature are often very different from those related to the Western
425 lifestyle and the distinction between culture and nature is sometimes blurred. In these tropical contexts,
426 the difficult resilience and adaptive capacity to abrupt changes in coral reefs (eutrophication and other

427 pressures) can alter cultural ESs (C1 ; C2 ; C3) from state I to state III (Sterling et al., 2017).

428

429 Coral-dominated reefs (state I) are richer in habitat (F1), trophic networks (F2) and recruitment (F3)
430 than algal dominated reefs and cyanobacterial mats. Corals provide shelter and food for a large
431 diversity of benthic organisms and allow the creation of complex trophic networks. Algal-dominated
432 state can benefit some herbivorous fishes, but large fleshy macroalgae and cyanobacterial mats are
433 often unpalatable to fishes. Mesopredators can switch prey, shortening food chains, in response to coral
434 reef degradation (Hempson et al., 2017). The three dimensional structure of corals are important to fish
435 recruitment, which can, in turn, increase herbivory and favor coral dominance via positive feedback
436 mechanisms (Mumby and Steneck, 2008).

437

438 **4. Discussion**

439

440 4.1. Evolution of bundles of ecosystem services

441

442 ES bundles are very important in state I for each ecosystem, determined in part by their ability to
443 provide the three ecological functions (habitat, recruitment, food networks) that support the ES set. The
444 bundle is thus particularly strong for coral reefs but also very important for sandy beaches and coastal
445 lagoons. *Changes along the eutrophication gradient are essentially a shrinking of ES bundles. Indeed,*
446 *for all ecosystems, nearly all ES decrease, nutrients and pathogen regulation/sequestration or the*
447 *support of recreational and leisure activities being especially impacted. This contrasts with some results*
448 *published in terrestrial context regarding different drivers of change. For instance in floodplain*
449 *ecosystems, supply of provisioning ES decrease (e.g. water for irrigation) while regulating and cultural*
450 *ES increase (e.g. salinity control) between current situation and climate change (Colloff et al., 2016a).*
451 *In the same way, higher intensity fire in some forests can lead to increase several ES (e.g. groundwater*
452 *storage and erosion prevention) (Colloff et al., 2016b). In this study, only few ES increase. For*
453 *instance, the capacity of coral reefs to provide molecules for medicine decreases between the two first*
454 *states but increases again in state III, dominated by chemically rich cyanobacteria and sponges. The*
455 *capacity of sandy beaches to support recruitment function increases with the proliferation of green*
456 *algae as the latter can reduce hydrodynamics intensity allowing the fixation of larvae. When green tides*
457 *occur, sandy beaches also increase their capacity to provide material as algae might be collected and*
458 *used in industry for pet food and cosmetics. Finally, the capacity of Mediterranean coastal lagoon to*
459 *provide food through shellfish farming increases between states I and II as nutrient flows increase*

460 shellfish productivity. However, excessive nutrient flows occurring in states III to IV can lead to
461 shellfish mortality thus decreasing ES supply. Thus, for each of the three coastal ecosystems, ES
462 favored by eutrophication may be of interest for specific uses and industries (medicine, industry for pet
463 food and cosmetics, shellfish farming). However, there are some trade-offs between these few
464 increasing ES and all other decreasing ES supplied in eutrophicated states. Potentially, increasing ES
465 can be likened to “adaptation services” i.e. the *benefits to people from increased social ability to*
466 *respond to change, provided by the capacity of ecosystems to moderate and adapt to climate change*
467 *and variability* (Lavorel et al., 2015) but have to be explored through the concept of ES demand as it
468 refers to a societal choice.

469

470 4.2. Potential impacts on ES demand

471

472 ES demand is not explored here, but we can easily imagine that a deterioration of almost all ES in
473 increasing eutrophic would no longer meet the societal demand for use and consumption of these ES,
474 thus turning into an expression of a societal demand for the conservation of these ecosystems. For
475 example, in Brittany (France), local environmental protection associations have been created and
476 mobilized against green algae after the the deaths of a horse, dogs and wild boar linked to gas
477 emissions generated by green tides was broadcasted into local and national medias (Levain, 2013).
478 Another example is the French NGO Coral Guardian, created in 2012 in response to the multiple
479 pressures these ecosystems are undergoing and their impacts on local communities.

480

481 In the few cases where increased eutrophication can favor a given ES, some stakeholders can express a
482 new demand, positioning themselves in favor of a slight or a significant eutrophication because an
483 economic activity could result of it. This could be the case for shellfish farmers in Mediterranean
484 lagoons, for companies cleaning and transforming green algae along the French Atlantic coast, or for
485 pharmaceutical industries towards molecules of cyanobacterial mats and sponges in tropical
486 environments. *Cyanobacteria and macroalgae can also potentially generate research and development*
487 *interest in bioenergy production due to increasing and contextual demand for bioenergy* (Mohan et al.,
488 2016). *Otherwise*, even if the cleaning process of macroalgae is still costly (Morand and Merceron,
489 2005), industrial utilization of this macroalgal biomass is in full growth worldwide (Abd El-Baky et al.,
490 2009 ; Khan et al., 2016 ; Qiu et al., 2017) and could bear these costs for economic purposes which
491 would not solve the problem of eutrophication at source. Hence the interest of communicating at the
492 scale of the ES bundles so that society and decision-makers can make their own trade-offs, balancing

493 the gains obtained from enhancing a specific ES with the loss of other ES of the bundle. Another
494 example: in the case of the Water Framework Directive, cost-benefit analysis of achieving the good
495 environmental status can lead to the argument that costs to restore ecological functions and ES are
496 disproportionate regarding the benefits associated to this restoration. This is due to methodological and
497 conceptual issues regarding the assessment of benefits focusing on few ES (Feuillette et al., 2016). To
498 avoid this situation, decision-makers could really use state-and-transition models to better understand
499 the consequences of eutrophication on the ES bundle as a whole and better analyse the cost and
500 benefits.

501

502 4.3. State-and-transition models : pros and cons

503

504 The use of state-and-transition models to explore the dynamics of ecosystems and ES is slightly
505 growing (Briske et al., 2005 ; Bestelmeyer, 2015), but its application to marine and coastal ecosystems
506 remained almost non-existent. The lessons learned from this exploratory application are multiple. State-
507 and-transition model can be a very powerful framework to work in an interdisciplinary perspective
508 taking into account all functions and services delivered by the ecosystem and avoiding the conclusions
509 focused on single service. [It meets the challenge of strengthening the links between biodiversity, ecological functioning and ecosystem services \(Harrison et al., 2014\).](#) It is also relevant to take into
510 account the temporal dynamics of ES ([Colloff et al., 2016b](#)) which are too often ignored . [Otherwise, it could help identify knowledge and data gaps. In this study,](#) a significant heterogeneity [thus remains regarding](#) the available [knowledge and data](#) according to the considered ecosystems, ecosystem
511 services, states and transitions : (i) there are more quantitative data on coral reefs than on sandy
512 beaches as the former are much more explored ; (ii) there is thus a lack of studies exploring the climate
513 regulation function of sandy beaches, as well as their role in pathogen sequestration, or in harboring
514 species showing interesting molecules for medicine ; (iii) there are more data concerning the supply of
515 provisioning ES than cultural ES since the latter is more studied in the light of the societal demand,
516 based on socio-economic indicators ; (iv) the transition from coral-dominated to algae-dominated reefs
517 and its associated states are much more documented than the state and transition to cyanobacterial
518 mats. [To fulfill these gaps, state-and-transition approach can be used as a mean to structure study designs and sampling strategies. The latter would provide new eutrophication response indicators and would validate or not the expected ES changes. This would ultimately improve understanding of the trade-offs in ecosystem values \(McIntyre, 2008\).](#)

525

526 The most difficult and challenging step for experts involved in state-and-transition models is to
527 quantify each ES based on qualitative and heterogeneous quantitative data. To create a consensus
528 regarding the level of supply granted to each ES, the analytical framework could be complemented by
529 the use of focus groups or by expanding the size of the panel of experts complemented by the use of the
530 Delphi method for example (Filyushkina et al., 2018).

531

532 4.4. How to reverse the situation?

533

534 The transition from eutrophic states to initial states depends on the ecosystem resilience. While
535 Mediterranean coastal lagoons have already proved a resilience after years of efforts to reduce nutrient
536 inputs (Leruste et al., 2016), reef recovery to a coral-dominated state is rare (but see Adjeroud et al.,
537 2018). The transition from coral-dominated to macro-algal dominated reefs can be a regime shift,
538 making it difficult to reverse to the previous state because of strong feedback processes (Hugues et al.,
539 2017). In addition, the eutrophication management must be carried out taking into account also the
540 multiple stressors context (global change, overfishing, urbanization, etc.).

541

542 In 2016, the eutrophication management costed € 272 million in metropolitan France distributed as
543 follows: € 6.6 million of monitoring and information costs; € 262 million of avoidance costs targeting
544 both reduction of agricultural inputs (41%) and domestic inputs (59%); € 2.5 million of restoration and
545 mitigation costs (Henry et al., 2018). Specifically, the eutrophication management can be carried out at
546 two levels: upstream by focusing on the causes (control of pollution flows from domestic, agricultural
547 or industrial sources) in order to restore the ecosystem; or downstream by tackling these symptoms
548 (dilution action via mixing water, water reoxygenation, green algae cleaning...) (Charlier et al., 2006).
549 The latter does not orient the ecosystem towards an initial state so we believe that upstream strategies
550 for the restoration of eutrophic ecosystems are essential, before any other remedial measures. However,
551 depending on the source type of pollution it may be challenging to control the pollution flows. Since
552 they are easily identifiable, point sources of pollution (e.g. domestic pollution) are easier to control, to
553 monitor and to effectively regulate than non-point source or diffuse pollution (e.g. agricultural
554 pollution) characterized by random and intermittent occurrence, and influenced by different drivers
555 (e.g. land use, soil type, management practices) (Duncan, 2017). For example, the considerable efforts
556 made to water depuration systems on the watershed have induced a significant decrease of nutrient
557 pollution since the 1970s and the late 2000s and have gradually led to a good environmental status of
558 the Thau lagoon according to the Water Framework Directive (WFD) (Derolez et al., 2017). On the

559 other hand, even if agricultural pollution has been identified as the main source of eutrophication since
560 several decades, green tides are still occurring in Brittany since effective tools are more difficult to
561 implement and should be more based on a redesigned agricultural practices (Molénat et al., 2002). Thus
562 a strong political will is needed to effectively regulate the sources of pollution and needs to better
563 interconnect the management of coastal ecosystems with the management of terrestrial ecosystems. [For
564 example, the creation of protected areas implemented in conciliation with pre-existing uses \(Donia et
565 al., 2017\) could be strengthened.](#)

566

567 An alternative would be the establishment of hybrid markets to regulate eutrophication such as water
568 quality trading in which participants can voluntarily exchange their water pollution rights taking into
569 account the respect of certain biophysical criteria related to the water quality. Even if they are still
570 facing obstacles to be effective (Heberling, 2010), these markets are expected to act as win-win
571 solutions as they reduce the costly regulatory burden on the state while mobilizing new sources of
572 private funding to address water quality problems. They can also provide new sources of revenue to
573 farmers through direct payments for nutrient credit offsets and offer greater flexibility to the farmers in
574 how to achieve environmental goals (Ribaud et Gottlieb, 2011).

575

576 In addition to these management strategies, supra-local and supra-national actions are needed scales.
577 For example, land use and climate change in northern Africa can influence the seasonal deposition of
578 dust in the Caribbean, adding other types of nutrients (e.g. iron) and potential coral pathogens, with
579 negative effects on Caribbean corals. Thus, local mitigation efforts need to be coupled with actions
580 from nations far from the coastal areas where reefs are found. This eutrophication management can also
581 mitigate the effects of global warming and climate change by decreasing coral susceptibility to disease
582 and bleaching.

583

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585

586 C.K., D.B. and R.M. designed the research and developed the analytical framework. C.K. developed
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588 authors significantly contributed to the writing of the paper as well. Six co-authors, identified as
589 experts of specific ecosystems, performed the research collecting the data and reviewing the existing
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592 discussion regarding ecological data. As economist and social scientist, P.S. and D.V. contributed to the
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594

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