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1   **Species range shifts along multi-stressor mosaics in estuarine environments under**

2   **future climate**

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9

10   **Abstract**

11   Range shifts are a key mechanism that species employ in response to climate change. Increasing

12   global temperatures are driving species redistributions to cooler areas along three main spatial axes:

13   increasing latitudes, altitudes, and water depths. Climate-mediated range shift theory focuses on

14   temperature as the primary ecological driver, but global change alters other environmental factors as

15   well, and these rarely work in isolation. Ecosystems are often characterised as mosaics of overlapping

16   environmental stressors, resulting in temporal and spatial heterogeneity which differs between stable,

17   low complexity mosaics (e.g. open ocean) and highly variable, highly complex mosaic environments

18   (e.g. estuaries). We propose a multi-stressor mosaic of climate-mediated species range shift across

19   abiotic environmental gradients, typical for mobile species (e.g. fish) in variable coastal

20   environments. We conceptualise how climate-driven changes in salinity, temperature, dissolved

21   oxygen, and pH can drive redistribution of estuarine species in a future world. Non-thermal drivers

22   are a critical component of species range shifts and when not considered, underestimate the impact of

23   global change on species populations and ecosystem services.

24

25   *Keywords:* Climate change, fish, global stressors, ocean acidification, salinity, species distributions

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Introduction

45   Our global climate is changing rapidly, and species are typically observed responding by

46   shifting, contracting, or extending their current ranges to: i) greater depths (Dulvy et al., 2008, Pinsky

47   et al., 2013), ii) increasing altitudes (Lenoir et al., 2008, Comte and Grenouillet, 2013), and iii) higher

48   latitudes (Hickling et al., 2005, Chen et al., 2011, Sunday et al., 2012). These range shifts are

49   occurring in response to rising air and ocean temperatures. However, global change is altering other

50   key environmental variables, such as precipitation and CO_2, which are known to regulate present-day

51   species distributions (Maestre and Reynolds, 2006, VanDerWal et al., 2013, Gibson-Reinemer and

52   Rahel, 2015). Currently, species range shift studies in the ocean predominately model the effects of

53   elevated temperature as a key ecological driver, without putting much emphasis on the interaction

54   with other global change stressors. Here we conceptualise species range shifts along multi-stressor

55   mosaics, created by overlapping abiotic environmental gradients of salinity, temperature, oxygen

56   content and pH.

57   Understanding how species fill their realised, fundamental, and tolerance niches is vital for

58   accurate species distribution modelling, by identifying how suitable an environment is for a specific

59   species or population (Sunday et al., 2012, Sax et al., 2013, Wetz and Yoskowitz, 2013). The realised

60   niche describes the conditions that a species currently persists in, which is impacted by the interplay

61   of both abiotic and biotic variables (Sax et al., 2013). The fundamental niche describes the abiotic

62   conditions in which a species can persist but may not currently exist in, and the tolerance niche

63   describes the abiotic and biotic conditions in which a species can exist, but is unable to maintain a

64   self-sustaining population (Sax et al., 2013). While niche theory is often looked at from the

65   perspective of abiotic factors, species interactions (both positive and negative) also play an important

66   role in shaping the realised and tolerance niches (Lauchlan et al., 2019), particularly when abiotic

67   stress is low (Louthan et al., 2015). The capacity of a species to fill the different niches is largely

68   dependent on the breadth of its niche, defined here as the area along environmental axes in which a

69   species currently resides as a result of both abiotic and biotic interactions, and can vary substantially

70   between species. For example, ectotherms at higher latitudes have been observed to have a broader

71   thermal tolerance than those nearer the equator, and marine ectotherms have been observed to

72   fulfilling more of their fundamental niche than their terrestrial counterparts (Sunday et al., 2011,

73   Sunday et al., 2012).

74   Current theory on niche utilisation and climate-mediated range shifts is largely based on

75   ecosystems comprised of more homogenous environmental mosaics, such as oceans, which are

76   relatively stable with little within-day variability. Estuaries, however, are subjected to regular

77   predictable semidiurnal, diurnal, seasonal and decadal variations in physical and chemical conditions,

78   which also differ at various spatial scales, creating large spatiotemporal variability within these

79   systems (O'Boyle et al., 2012, Amann et al., 2015). Due to the high variability with estuaries,

80   estuarine species have been observed to have a broader fundamental and realised niche than their

81   marine counterparts do, although they occupy more of their niche, making them more vulnerable to

82   climate change stressors (Davis and Wing, 2012, Madeira et al., 2012). Climate change will not only

83   alter the predictable long-term changes in mean and maximum temperatures, but will also alter

84   unpredictable variation, such as that caused by the increased frequency and duration of extreme

85   events, that results in short but extreme increases/decreases in means and magnitude of temperature

86   and other global change stressors. How current range shift theory will apply to environments with

87   more complex mosaics that experience high predictable and unpredictable variability, such as

88   estuaries, ocean upwelling margins, and the savannas and grasslands of the semi-arid zone, is still

89   largely unknown (Cai et al., 2011, VanDerWal et al., 2013, Sperling et al., 2016).

90

91   **Global Change Alters Multiple Climate Stressors**

92

93   With increasing global temperatures come a myriad of environmental changes that impact

94   ecosystems and their associated species (Nagelkerken et al., 2019). In aquatic systems there are

95   changes in the solubility and production of oxygen (O_2) (Altieri and Gedan, 2015) and carbon dioxide

96   (CO_2) (Feely et al., 2010). Additionally, aquatic systems are also facing decreases in pH due to ocean

97   acidification, as the ocean continues to absorb CO_2 from the atmosphere as a result of increased

98   human carbon emissions. As the planet warms it is also experiencing changes in climatic patterns,

99   with associated shifts in precipitation (and therefore seawater salinity) and intensification of extreme

100   weather events (IPCC, 2014, Moore et al., 2015). In ecosystems with lower mosaic complexity, the

101   velocity of latitudinal temperature shifts and associated species range shifts in response to climate

102   change has explained non-linear shifts, and forms the basis for recent climate change modelling

103   (Loarie et al., 2009, Burrows et al., 2011, IPCC, 2014). However, ecosystems with more complex

104   environmental mosaics, such as estuaries and areas of upwelling, experience larger natural

105 fluctuations in environmental conditions (Fig. 1) as a result of complex interactions between biotic

106 and abiotic factors (Geawhari et al., 2014, Baumann et al., 2015). The amplitude of these fluctuations

107 in variable environments under present-day conditions regularly surpasses far beyond end of the

108 century projections for stable environments such as the open ocean. Nevertheless, climate change may

109 still have an impact by raising the mean values of these stressors rather than their amplitudes per se

110 (Duarte et al., 2013, Baumann et al., 2015). How species in dynamic, highly variable environments

111 that form complex mosaics will respond to these abiotic changes as a result of climate change is still

112 largely unknown.

113   Concurrent alterations to multiple abiotic factors as a consequence of global change means

114 that range shifts of coastal species will be driven by multi-stressor mosaics (Gibson-Reinemer and

115 Rahel, 2015). The direction of such range shifts is dependent on the sensitivity and responsiveness of

116 species to environmental change, their biological interactions and adaptive capabilities, and where

117 these changes fall in relation to their realised, fundamental and tolerance niches (Bates et al., 2014,

118 Sunday et al., 2015). Furthermore, species responses to co-occurring stressors frequently differ from

119 those of individual stressors due to their interactive effects (Ban et al., 2014, Fey et al., 2015). Current

120 species range shift theory does not adequately account for multi-stressor responses, that likely result

121 in range shifts inconsistent with the direction of thermal change (Gibson-Reinemer and Rahel, 2015).

122 As such, current research on biological responses to thermal shifts is only capturing a fraction of

123 potential climate-mediated species responses and is insufficient for the development of more holistic

124 models that better predict biological responses under future climate scenarios. Hence, we propose the

125 consideration of species range shift in response to multi-stressor environmental mosaics under future

126 climate conditions.

127

128 Model Ecosystem - Estuaries

129   Estuaries are an ideal model ecosystem to test our proposed concept due to the multiple

130 strong, overlapping environmental gradients that naturally exist in these systems. Compared to the

131 more stable and typically homogenous conditions of the open ocean, estuaries have strong gradients

of salinity, temperature, dissolved oxygen and pH, at fine to system-wide spatial scales, forming

complex environmental mosaics. Fluctuations of these variables differ both within and among

estuaries, with changes often occurring rapidly, up to two-fold in one tidal cycle (O'Boyle et al., 2012,

Baumann et al., 2015). Despite both ocean and estuarine conditions being largely influenced by

climate, the inherent buffering capacity of estuaries is not as robust as that of the open ocean (Wetz

and Yoskowitz, 2013). As such, the extremes and amplitude of variation experienced within estuaries

is much greater than the open ocean (Fig. 1), resulting in differing physiology and life history

strategies among resident species. Because of the high variation in when and how species use

estuarine systems, we have here defined range as any area that a species utilises, including as part of

seasonal and ontogenetic movements.

Due to their positioning at the interface between land and sea, and between fresh and marine

waters, estuaries are subjected to a range of naturally co-occurring factors that can act as stressors, as

well as an array of anthropogenic modifications, such as river regulation, that often mimic and

intensify stressors (Fig. 2). Due to their close proximity to human population centres, high biological

productivity, and significant economic value, estuaries have been widely studied providing a wealth

of knowledge on how estuarine species respond to environmental change (Blaber et al., 2000,

Costanza et al., 2014). Previous studies have considered non-climate stressor effects on estuaries in

detail (Matthiessen, 2000, Cloern, 2001, Lotze et al., 2006, Worm et al., 2017). To develop a

conceptual framework of how species range shifts or extensions might be mediated by changes to

multiple climate stressors in a future world, we here used published long-term studies, which show

how species distributions are already changing in response to current climatic and anthropogenic

modifications of estuaries.

Potential Species Range Shifts in Response to Key Environmental Gradients

Salinity

158   Salinity gradients are the primary driver for species distribution within estuaries (Peterson and

159   Ross, 1991, Thiel et al., 1995, Neves et al., 2011). Salinity determines the distribution of freshwater,

160   estuarine, and marine species due to its ability to act as a barrier to dispersal and movement (Neves et

161   al., 2011, Igulu et al., 2014). The salinity gradient of an estuary is determined by several factors,

162   including precipitation, stream flow, tidal range, estuary topography, evaporation and sea-level, all of

163   which are anticipated to change in the future as a response to anthropogenic influences, notably

164   climate change (Wetz and Yoskowitz, 2013, IPCC, 2014, Ross et al., 2015) (Fig. 2).

165   Increasing estuarine salinity can drive an increase in the relative abundance of marine and

166   estuarine species as they extend their ranges upstream, and a simultaneous relative decrease in

167   freshwater species abundance as they undergo a range contraction (Thiel et al., 1995, Pasquaud et al.,

168   2012, Baptista et al., 2015) (Table 1, Fig. 3a). Typically, the lower portions of an estuary where

169   salinity is highest have greater species richness than the less saline upper reaches of the estuary (Thiel

170   et al., 1995, Neves et al., 2011). However, when estuary-wide salinity gradients change an inverse

171   relationship with species richness often occurs, whereby species richness decreases with increasing

172   salinity (due to loss of freshwater species), but increases with decreasing salinity (Poizat et al., 2004,

173   Baptista et al., 2015). The latter is explained by the fact that when the salt front shifts and salinity

174   decreases, this allows freshwater species not previously found in the estuary to extend their range,

175   while most estuarine and marine inhabitants can maintain their ranges under decreased salinity (Poizat

176   et al., 2004, Baptista et al., 2015) (Fig. 3b). Nevertheless, whilst estuarine and marine species have

177   some resilience to increased freshwater inputs, after prolonged exposure they eventually will suffer

178   from range contractions, with concomitant decreases in their relative abundances and species richness

179   (Garcia et al., 2003, Poizat et al., 2004) .

180

181   **Temperature**

182   Temperature is an important secondary driver of species distributions within estuarine

183   systems and is heavily influenced by local, regional and global climate, and seasonality (Marshall and

184   Elliott, 1998, Neves et al., 2011). Temperature confines species ranges through altering metabolism,

185 thereby imposing species-specific thermal limits. This is particularly important in habitats that contain

186 predominantly ectothermic organisms, such as estuaries. In addition to climatic conditions,

187 temperature within estuaries is determined by topography, stream flow, water residency time, mixing,

188 and latitude, resulting in high spatial variation within and among estuaries (Ding and Elmore, 2015)

189 (Fig. 2). The impacts of increasing global temperature is already evident in our oceans, with coastal

190 areas and estuaries shown to be regions of rapid warming (Lima and Wethey, 2012, Fulweiler et al.,

191 2015, Oczkowski et al., 2015). Modelled projections indicate increased risk to some species and life

192 stages, such as the suitable habitat for juvenile Atlantic Sturgeon (*Acipenser oxyrinchus*) in

193 Chesapeake Bay projected to be reduced by up to 65% with a future temperature increase of just 1°C

194 (Niklitschek and Secor, 2005, Najjar et al., 2010).

195 As seawater temperature increases, estuarine species shift or contract their range (Table 1) as

196 they approach or exceed their thermal tolerance limits, retreating to deeper, cooler water, or further

197 upstream to cooler mountainous waters at increasing altitudes (Niklitschek and Secor, 2005,

198 Grenouillet and Comte, 2014). Freshwater species frequently reside in shallower habitats than their

199 marine and estuarine counterparts, increasing their vulnerability to rising temperatures. As such, we

200 anticipate seeing range contractions over a greater spatial scale in freshwater species and the estuarine

201 species that typically occur in those shallower regions (Fig. 3c). In addition to localised thermal

202 changes, changes in global temperatures are resulting in poleward species range extensions, with

203 some temperate and subtropical estuaries already experiencing increased invasions of tropical, warm

204 water species (Baptista et al., 2015). This range extension of tropical species can initially lead to an

205 overall increase in species richness in the lower reaches of the estuary (Pasquaud et al., 2012) (Fig.

206 3d).

207

208 **Oxygen**

209 Dissolved oxygen (DO) concentration is a key driver of life in aquatic environments, with

210 prolonged low DO resulting in dead zones, areas where dissolved oxygen is too low to support

211 extensive life. Aquatic species typically have a strong positive relationship with DO, resulting in

212 decreasing abundance or complete absence at low concentrations as mobile species actively avoid

213 hypoxic water, even when exposure time is short (Thiel et al., 1995, Campbell and Rice, 2014). Low

214 DO can have significant effects on estuarine community composition and fishery yields, particularly

215 when it results in severe fish kills or dead zones (Mallin et al., 2002, Stevens et al., 2006, Diaz and

216 Rosenberg, 2008). Concentrations of DO are primarily controlled by the balance between solubility of

217 oxygen from the atmosphere, and the rates of photosynthesis and respiration within the water column

218 (Diaz and Rosenberg, 2008, Li et al., 2015). Increasing global temperatures reduces the solubility of

219 oxygen into water, promotes stratification that in turn reduces mixing between surface and bottom

220 waters, alters rates of both photosynthesis and respiration, and facilitates eutrophication-induced algal

221 and microbial blooms, thus increasing the frequency, magnitude, and duration of hypoxic and anoxic

222 events particularly in coastal regions (Diaz and Rosenberg, 2008, Gilbert et al., 2010, Altieri and

223 Gedan, 2015) (Fig. 2).

224   In a future climate where low DO events increase in frequency and magnitude, estuarine taxa

225 are likely to undertake range contractions as their tolerance threshold is exceeded, with individuals

226 restricting themselves to areas with higher DO concentrations. During these events we expect fish and

227 other mobile taxa to shift from deeper stratified channel waters and the fresh-brackish water interface,

228 where low DO is more prevalent, to shallower, well mixed areas where oxygen solubility is high

229 (Table 1, Fig. 3e). While low DO events are typically seasonal, short-lived and usually followed by

230 complete recolonisation, fish have restricted habitat use for the duration of these events leading to

231 compression of the population resulting in pockets of extremely high densities, reduced feeding, and

232 potential for reduced growth rate (Campbell and Rice, 2014, Kraus et al., 2015). The winners in these

233 events are taxa highly adapted to low DO concentrations, typically non-indigenous species, that are

234 able to reach their maximum abundance and biomass in low DO conditions due to the reduction in

235 competitive and predatory pressures (Thiel et al., 1995, Stevens et al., 2006). In estuaries experiencing

236 frequent hypoxia these species are expected to increase in relative abundance (Thiel et al., 1995,

237 Stevens et al., 2006, Altieri and Gedan, 2015).

238

239 **Carbon Dioxide and pH**

240   Increasing atmospheric anthropogenic CO_2 and the concomitant pH decreases in the ocean are

241   threatening the functioning of important oceanic ecosystems (Nagelkerken and Connell, 2015), yet

242   how this translates to estuarine ecosystems has largely been unaddressed. In the open ocean, the

243   partial pressure of CO_2 (pCO_2) is in equilibrium with the atmosphere; in contrast, coastal systems,

244   such as estuaries, are particularly complex to model as they are more heavily influenced by local

245   processes (Hofmann et al., 2011, Duarte et al., 2013). Estuaries are subject to a variety of natural and

246   anthropogenic processes that control both pCO_2 and pH either directly or indirectly, thus resulting in

247   spatially and temporally different patterns, scales and habitat specificity (Feely et al., 2010, Duarte et

248   al., 2013). The key processes that determine pCO_2 and pH levels in estuarine environments are

249   respiration, photosynthesis, upwelling, mixing, and river alkalinity (Fig. 2). Currently, respiration is

250   the primary driver of estuarine pCO_2 and pH, resulting in high diel variation, in many instances

251   exceeding levels projected for the open ocean at the end of the century (Duarte et al., 2013, Baumann

252   et al., 2015). Highly alkaline rivers and mixing currently buffer most high pCO_2 estuarine waters,

253   however, highly acidic rivers, future changes in land use, sea level rise, and increasing ocean

254   acidification can reduce the efficiency of these buffering mechanisms, and in some cases exacerbate

255   them, resulting in a baseline increase whereby the upper limits of variation are likely to exceed the

256   physiological tolerance of many organisms (Hofmann et al., 2011, Ianson et al., 2016).

257   While range shifts have not yet been identified as a result of ocean acidification, behavioural

258   changes have been observed in both freshwater and marine systems in response to changes in pCO_2

259   and pH (Briffa et al., 2012, Leduc et al., 2013). These behavioural changes include decreased predator

260   avoidance (Nagelkerken et al., 2016), decreased response to food stimuli (Caprio et al., 2014, Pistevos

261   et al., 2015), unsuitable settlement behaviour (Munday et al., 2009, Rossi et al., 2015), and changes in

262   sexual selection preferences (Leduc et al., 2013) . Not surprisingly, some fish show significant

263   avoidance behaviour towards water with high pCO_2 or low pH levels (Jutfelt and Hedgärde, 2013).

264   Importantly, behavioural responses and tolerance are not uniform across all species, with some fish

265   showing behavioural shifts with pH changes as little as 0.1 unit (Leduc et al., 2013, Walden et al.,

266   2019), with others demonstrating little to no behavioural change when subjected to greater change

267   (Jutfelt and Hedgärde, 2013, Caprio et al., 2014). Although estuarine species are predicted to be more

268 resilient to high pCO$_2$ (Jutfelt and Hedgärde, 2015), several common estuarine species are sensitive to

269 ocean acidification (DePasquale et al., 2015, Pistevos et al., 2016, Rodriguez-Dominguez et al.,

270 2019). Due to the high *in situ* variability and lack of long-term studies measuring pCO$_2$,

271 understanding how the distribution and abundance of estuarine species will change in response to

272 ocean acidification is difficult to predict. Future climate scenarios project that increasing oceanic

273 pCO$_2$ will result in oceanic pH decreasing by ~0.33 units under RCP8.5, with a likely shift from

274 respiration to ocean acidification as the primary driver of high pCO$_2$ and low pH within estuaries

275 (Feely et al., 2010, Duarte et al., 2013, IPCC, 2014)ʼ. Areas most likely to be impacted by increasing

276 basal pCO$_2$ are the portions of the estuary that currently have already high pCO$_2$ levels relative to the

277 rest of the estuary, as mobile species are likely to avoid these areas, much like they avoid areas of low

278 DO. These hotspots of elevated estuarine pCO$_2$ include salt marsh habitat, bottom sediment, and areas

279 affected by algal blooms (Cai et al., 2011, Amann et al., 2015, Baumann et al., 2015).

280

281 **Multi-stressor physiology and adaptation**

282 When gradients of environmental factors are superimposed, they can result in a diverse range

283 of multi-stressor interactions and associated physiological responses in organisms (Table 1b).

284 Stressors can interact either synergistically, additively, or antagonistically, whereby some

285 physiological processes are more adversely affected than others (Przeslawski et al., 2015). The direct

286 physiological impacts on species of changing abiotic variables primarily depend on; i) the specific co-

287 occurring stressors and their intensity, ii) the tolerance of the individual, species or population, and iii)

288 life stage. The impacts of physiological change on the individual can also manifest at the population

289 or species level resulting in ecological impacts, such as changes in recruitment, reduced size at

290 maturity, and reduced fecundity (Koenigstein et al., 2016).

291 Phenotypic plasticity is a proxy of the extent of acclimation capacity, which can be species-

292 or population-specific and therefore difficult to anticipate. Aquatic taxa have shown consistent trends

293 towards greater thermal acclimation responses than terrestrial taxa (Gunderson and Stillman, 2015).

294 Species communities that show no response to changing ecosystem pressures are likely to be a good

295   indication of plasticity at work (Reusch, 2014). While plasticity provides buffering to climate change,

296   adaptation through evolutionary processes will be required to ensure the long-term success of species

297   and populations. Adaptation is highly dependent on life history strategy, diversity of genotypes and

298   the degree of polymorphism within the species, and the rate of environmental change experienced

299   (Sih et al., 2004, Donelson et al., 2016, Henson et al., 2017). Transgenerational exposure to climate

300   stressors promotes adaptation within offspring, with some populations better suited to adaptation than

301   others (Goncalves et al., 2016). How species and populations respond to climate change, be it through

302   range shifts, phenotypic plasticity, adaptation or a combination of the three, will largely depend on

303   localised rates of change (Henson et al., 2017).

304

305   **Multi-stressor mosaics**

306   In estuaries, the most detrimental interactions between multiple climate-mediated stressors are

307   likely to be between salinity and temperature. This is due to rapid global increases in temperature, the

308   importance of salinity as the primary driver of species distribution along estuarine gradients, and the

309   predominately synergistic interaction between these two stressors across many phyla and life stages

310   (IPCC, 2014, Przeslawski et al., 2015). This will likely result in whole-system responses, whereas the

311   impact of changes in DO, pH and pCO$_2$ are likely to be more localised (Figs. 4a, 4b). Importantly,

312   interactive effects among stressors may lead to loss of habitat connectivity between different portions

313   of the estuary, particularly between freshwater and estuarine habitats, leaving only a small number of

314   highly tolerant taxa (e.g. invasive and generalist species) to inhabit these areas (Figs. 3f, 4a, 4b). Not

315   all species will be able to promptly respond to rapid stressor changes through movement, particularly

316   highly territorial species, or those with limited to no mobility. These species will rely more heavily on

317   their larval dispersal abilities, particularly those with greater dispersal ranges, for population and

318   species survival in these regions.

319   Habitat fragmentation within estuaries, particularly at the interface between fresh and

320   brackish waters, would have significant implications for waterway and fisheries management,

321   particularly for migratory species (including important fishery species such as eels, salmon,

322   barramundi) that rely on this habitat connectivity for reproduction and population replenishment

323   (Crook et al., 2015, Altieri and Gedan, 2015). For these type of species, non-climatic pressures (e.g.

324   river regulation, and intensive commercial and recreational fishing) also result in decreased

325   abundances and will compound the impact of multi-stressor interactions with possible collapses in

326   stocks.

327   Besides habitat fragmentation, loss of suitable habitat is an additional driver of range shifts.

328   Climate-mediated phenomena such as sea level rise and increased sedimentation have the potential to

329   change the distribution and/or composition of habitat forming species. Fully submerged habitats, such

330   as seagrass meadows and coral reefs, are vulnerable to changes in sunlight due to sea level rise, be it

331   from increasing water depth, or from increased turbidity. Partially and periodically submerged

332   habitats, such as mangrove forests and salt marshes, are highly susceptible to increased inundation

333   and sedimentation (Gilman et al., 2008, Torio and Chmura, 2015). Loss of suitable habitat will occur

334   when habitat forming species are unable to relocate to areas with tolerable environmental conditions

335   or are not replaced with functional equivalents, thereby limiting or increasing the suitable habitat

336   available for mobile species.

337   Comparable to environmental stressors, species interactions can delimit a species realised

338   niche through indirect (i.e. trophic cascades) and direct (i.e. competition, predation) interactions.

339   Climate change will create novel species interactions, through range shifts and facilitated invasions, as

340   well as potentially changing the strength and/or the direction of existing interactions (Van de Waal et

341   al., 2011, Lurgi et al., 2012). Competitive release has been shown in some species, where the

342   previously dominant species is more negatively affected by climate-mediate abiotic changes

343   (McCormick et al., 2013, Lauchlan et al., 2019), while in other species interactions there has been a

344   strengthening of existing dominance (Milazzo et al., 2013). While our understanding of how species

345   interactions will affect climate-mediated range shifts is still in its infancy, concerns have been raised

346   about the potential loss of biodiversity and localised extinctions (Cahill et al., 2013, Magurran et al.,

347   2015).

348

349   **Moving forward**

350   We have here conceptualised potential climate-driven range shifts, extensions, and

351   contractions of species in highly variable coastal environments along multi-stressor mosaics (Fig. 4),

352   contrasting the more commonly considered single-stressor gradients in more stable environments.

353   Multi-stressor mosaics are already important in constraining and promoting changes in species

354   distributions within highly variable environments, with the gradients that form these mosaics expected

355   to further intensify under the combined pressures of climate change and increasing human coastal

356   populations. Our understanding of how species and communities will respond to climate change is

357   still rudimentary and largely focused on thermal gradients within environments with lower mosaic

358   complexity, such as the open ocean. In environments with more highly complex mosaics (e.g.

359   estuaries and shallow coastal areas), the magnitude of variation of abiotic factors can differ

360   considerably within and among habitats and regions, whereby climate-mediated changes will increase

361   the environmental mosaic complexity. In addition to long term predictable variation, species will also

362   be exposed to an increase in the frequency and duration of short unpredictable variation, such as

363   extreme weather events, whereby the magnitude of environmental stressors can rapidly exceed

364   tolerance thresholds (Wetz and Yoskowitz, 2013, Moore et al., 2015). The impact of both predictable

365   and unpredictable variation on communities will be highly dependent on the resilience and

366   adaptability of its inhabitants, and the types and intensity of multi-stressor interactions that occur.

367   Climate change further poses a serious threat to coastal habitat connectivity. Changes in key

368   environmental factors that fall outside a species tolerance niche may diminish connectivity, giving

369   rise to distinct populations or resulting in population collapses where connectivity is required for

370   survival or population replenishment. In ecosystems such as estuaries, where seascape connectivity

371   pathways are spatially restricted, increased complexity in multi-stressor mosaics may exclude species

372   from sections of that pathway, hampering the ability of diadromous species to undertake essential

373   migrations or access nursery habitats (Cloern et al., 2016). Seascape connectivity plays a vital role in

374   the life history strategies of many commercially important fisheries species, changes to which may

375   have significant population and economic ramifications (Nagelkerken et al., 2015).

376   Our ability to identify and forecast climate-mediated species range shifts is limited by our

377   knowledge of physiological and behavioural responses to interacting climate stressors across species.

378 Long-term field studies or manipulative experiments in areas with natural environmental gradients,

379 combined with multi-stressor laboratory or mesocosm experiments on species communities are key in

380 identifying niche boundaries and the drivers of distributional change. Typically, empirical data is

381 based on a restricted collection of moments in time or on short exposure of one species to a single

382 climate stressor, thereby ignoring the effect of natural cyclic or decadal trends, under or

383 overestimating plasticity and adaptation due to inadequate exposure time, and not accounting for

384 multi-stressor and species interactions. The quality of empirical data available limits the accuracy of

385 species distribution models, which are becoming increasingly popular for projecting future

386 community responses under a changing climate. Yet, by collecting basic environmental data at

387 appropriate spatial and temporal scales, the areas where hotspots or cold spots of overlapping

388 environmental stressor are likely to occur can already be predicted or modelled. This can aid mangers

389 in starting to identify potential coastal areas that need further consideration, protection, or study,

390 because these could emerge as critical species refugia under future climates.

391 Based on the postulated strengthening of multi-stressor mosaics in coastal environments

392 under future climates, we make several testable predictions to aid future research agendas and climate

393 change adaptation approaches (Box 1). Overall, we predict that estuaries will ultimately become less

394 diverse, both in terms of number of individuals, species, and functional groups, with future climate

395 projections favouring invasive as well as short-lived generalist species with broad environmental

396 niches. This will be to the detriment to rare and endemic species, driving regional homogenisation of

397 species communities consisting increasingly of similar species or functional species group.

398

Conclusions

399

400 (1) Range shift theory currently focuses on species redistributing in response to global

401 increases in temperature, with little acknowledgment of the important range-limiting role that

402 mosaics of co-occurring abiotic stressors can have in coastal marine environments. While some

403 studies have examined the impact of inconsistent temperature changes, often referred to as climate

404   velocity, few have considered the impacts of interacting stressors and the ability of the resulting

405   mosaics to act as both barriers and facilitators to movement of species.

406   (2)   Climate change is altering various key non-thermal abiotic factors, either directly or

407   indirectly, as well as the interactions between them. This is increasing the complexity of multi-

408   stressor environmental mosaics, presenting new challenges to the species that reside there, and

409   ultimately see many undertaking range shifts that do not correlate with future temperature

410   increases alone.

411   (3)   Short-term species and habitat-specific sampling and experiments have provided

412   insight into how species can respond to increasing temperatures and stressor interactions. By

413   using a combination of consistent long-term sampling along natural gradients of environmental

414   factors and multi-stressor community experiments, we can test our postulated predictions to

415   identify species sensitivities, spatial refugia, and future species distributions. Such insights and

416   empirical data are important for improved species distribution modelling that can support

417   management initiatives.

418

419   **Acknowledgements**

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721   Pollutant. *Annual Review of Environment and Resources* **42,** 1-26.

Table 1| Case studies that demonstrate effects of single abiotic stressor changes on present-day and future estuarine fish communities (a) and the effects of abiotic stressor interactions on marine and estuarine fishes and invertebrates (b).

a

Stressor	Species community response	Examples
Salinity ↑	↓ Species richness ↓ Functional richness (↑ generalists) ↑ Estuarine & marine species ↓ Freshwater species	Baptista et al. (2015), Leitao et al. (2007) Baptista et al. (2015) Baptista et al. (2015), Leitao et al. (2007) Leitao et al. (2007)
Salinity ↓	↑ Species richness ↑ Freshwater species ↓ Marine species	Garcia et al. (2003) Poizat et al. (2004), Garcia et al. (2003) Garcia et al. (2003)
Temperature ↑	↑ Overall abundance Shift in community composition ↓ Suitable habitat[†]	Genner et al. (2004) Genner et al. (2004) Niklitschek and Secor (2005)
Dissolved oxygen ↓	↓ Overall abundance ↑ Abundance highly tolerant species Avoidance of affected waters Habitat compression	Thiel et al. (1995), Campbell and Rice (2014), Stevens et al. (2006) Thiel et al. (1995), Campbell and Rice (2014), Stevens et al. (2006) Campbell and Rice (2014) Campbell and Rice (2014)
pCO_2 ↑ /pH ↓	Avoidance of affected waters Altered food webs	Jutfelt and Hedgärde (2013) Pistevos et al. (2015), Nagelkerken and Munday (2015)

b

Interacting stressors	Community, behavioural and physiological responses	Interactive effects	Examples
Salinity ↑ + Temperature ↑	↑ Abundance marine species Altered early development	Antagonistic Not reported	Delorme and Sewell (2014) Pasquaud et al. (2012)
Salinity ↓ + DO ↓	↓ Overall abundance ↓ Species richness	Not reported	Stevens et al. (2006)
Salinity ↓ + pCO_2 ↑	↑ Metabolic rate ↓ Growth	Not reported	Dickinson et al. (2013)
Temperature ↑ + DO ↓	↑ Avoidance of affected waters ↑ Habitat compression Preference for cooler normoxic conditions	Antagonistic	Kraus et al. (2015)
Temperature ↑ + pCO_2 ↑/pH ↓	↔ Biomass (dependent on functional group[†]) ↔ Community structure ↓ Growth ↑ Metabolic rate	Additive Antagonistic Synergistic No effect Not reported	Griffith et al. (2012) Miller et al. (2012) Meadows et al. (2015), Sheppard Brennand et al. (2010), Enzor et al. (2013), Clements and Hunt (2015) Clements and Hunt (2015) Kroeker et al. (2016)
DO ↓ + pCO_2 ↑ /pH ↓	↓ Survival & growth	Additive Synergistic Not reported	Gobler et al. (2014), DePasquale et al. (2015) Gobler et al. (2014) Altieri and Gedan (2015)
Temperature ↑ + pCO_2 ↑ + Fishing pressure	↓ Biomass[†]	Synergistic	Griffith et al. (2012)

↑ represents an increase, ↓ represents a decrease, and ↔ represents change (either increase or decrease). DO = dissolved oxygen, and [†] indicates modelled data. Stressor effects, particularly interactive effects, can vary dramatically for different species, tropic levels, life stages and life strategies. The direction of the responses – positive or negative – is often dependent on the extent of stressor change and where that lies within the species' realised, fundamental and tolerance niches.

722

Box 1: How will estuarine species respond to climate change?

These predictions centre around how species in estuaries, separated into 13 common functional groups, might respond in a future climate where water temperature increases, pH decreases as a result of increasing pCO$_2$, and the frequency and duration of hypoxic events increases. Salinity will either increase or decrease depending on the estuary, with some regions of the world anticipating increases in precipitation, others decreases, thereby strongly influencing the amount of freshwater runoff and salinity. The predictions are as follows:

1. **Freshwater species** will likely experience range contractions at the downstream edge of their range as a result of increasing salinity (Garcia et al., 2003, Poizat et al., 2004). Long term this will likely result in a decreased abundance of freshwater species. Downstream range contractions may also increase population fragmentation within freshwater species by preventing migration between catchment areas, reducing gene flow. Alternatively, if salinity was to decrease, we expect that overall abundance of freshwater species would increase as their range extends downstream (Garcia et al., 2003, Poizat et al., 2004). Range extensions may also increase gene flow and population diversity, by increasing connectivity of catchments.

2. **Estuarine species** will experience both range extensions and contractions as the extent of the salinity intrusion increases. Where salinity increases there will likely be a range shift upstream as species follow their ideal salinity range (Garcia et al., 2003, Baptista et al., 2015). Similarly, if estuarine salinity decreases, we can expect a range shift downstream.

3. **Saltwater species** will experience a range extension at the upstream edge of their range if salinity increases (Thiel et al., 1995, Baptista et al., 2015). Long term an increased abundance of saltwater species is expected in the upper reaches of the estuary. Alternatively, if there was to be a decrease in salinity saltwater species would experience an overall decrease in abundance in estuaries as their range contracts (Thiel et al., 1995).

4. Populations of **benthic species** are expected to become increasingly fragmented. Hypoxic events disproportionally affect bottom waters, creating barriers to movement. Highly tolerant species, such as eels, may flourish due to decreased competition, particularly where hypoxia is persistent (Thiel et al., 1995, Stevens et al., 2006).

5. Populations of **water column species** are also expected to become increasingly fragmented. As surface temperatures, and the frequency and duration of hypoxic episodes in bottom waters increases, there may be a reduction in the extent of suitable habitat available in the water column (Campbell and Rice, 2014, Kraus et al., 2015). This 'squeeze' will likely result in patches of favourable conditions where abundances will be high, which are separated by areas that are unfavourable or even intolerable, where abundances will be low (Niklitschek and Secor, 2005).

6. Due to their broad fundamental and tolerance niches, **generalists** have a greater tolerance to extremes than specialists do. It is anticipated that they will become more widespread throughout the estuary, increasing their abundance, as competition by specialists declines (Baptista et al., 2015).

7. **Specialists** often have a narrower breadth of tolerance to environmental conditions than generalists and will likely respond to climate change with declines in abundance and in extreme circumstances, population collapses in some estuaries.

8. The number and abundance of **invasive species** is likely to increase due to their broad fundamental and tolerance niches, their typically short life spans, increasing the likelihood of adaptation, and the likely decrease in competition by native species due to decreased fitness and/or range contractions and extensions (Stevens et al., 2006).

9. **Territorial** and **sessile species** will be at greatest risk of population decline due to their small home ranges and typically limited dispersal distance. If territorial species are unable to find suitable refugia, fast adaptation will be essential to keep pace with changing conditions.

10. As warm-water marine and estuarine species extend their ranges poleward under climate change, commonly referred to as **tropicalisation**, to stay within their thermal niches, an increase in the number and abundance of these species is expected within estuaries, particularly larval and juvenile stages that may use this habitat as nursery grounds or initial settlement areas (Baptista et al., 2015).

11. **Short-lived species** will thrive under future climate conditions. Due to their smaller size, younger age at maturity, and short generation time, they have the greatest opportunity for adaptation to climate impacts and intensifying environmental mosaics.

12. **Long-lived species** will be disadvantaged under future climate conditions due to their larger size at maturity and long generation times, restricting their ability for transgenerational adaptation. As they are typically larger, physiological processes to maintain homeostasis require greater amounts of energy making them more susceptible to decreases in fitness.

13. **Diadromous species**, such salmonoids, will experience an increase in barriers to movement. In addition to physical anthropogenic barriers, they will experience many chemical barriers, such as hypoxia and temperature hotspots that will make travel between fresh and saltwater more difficult. The abundance of diadromous species is likely to decrease as some estuaries become inaccessible, while others become more difficult to navigate (Pasquaud et al., 2012). As diadromous migrations are already physiologically strenuous, the addition or increase of estuarine stressor hotspots will likely decrease species survival and fitness and pose a threat to populations of diadromous species.

Figure legends

724

725 **Figure 1| A comparison of the variation of climate-driven environmental stressors experienced by some**

726 **estuaries as a proportion relative to values for the open ocean** where the solid line is the mean, and the

727 shading represents the amplitude of variation. Data was compiled from Matear and Hirst (2003), Dore et al.

728 (2009), Morais et al. (2011), Neves et al. (2013).

729

730 **Figure 2| A simplified diagram of the major processes responsible for species distributions within**

731 **estuarine systems and how they are affected through direct and indirect biotic and abiotic drivers.**

732 Global change alters key environmental drivers responsible for species distributions both directly and indirectly.

733 Here we provide a simplified overview of how these drivers could interact to determine future species ranges.

734 A) Increasing atmospheric CO_2 gets trapped in the atmosphere thereby increasing global air temperatures

735 (IPCC, 2014). B) Increasing temperatures alter weather patterns resulting in the increasing frequency,

736 magnitude and duration of extreme weather events and intensify global climatic patterns such as ENSO, thereby

737 altering precipitation (Wetz and Yoskowitz, 2013, Moore et al., 2015). The increase in temperature also leads to

738 the melting of glaciers, resulting in sea level rise. C) Large changes in precipitation, such as magnitude, timing

739 or nature of precipitation (i.e. snow, rain) can have a significant impact on river discharge. Precipitation is also a

740 primary driver for terrestrial runoff and the associated pollutants that enter our waterways. D) Changes to river

741 discharge, particularly extreme changes such as flood and drought events, can impact salinity immediately,

742 while subtler long-term changes to river discharge can lead to less abrupt, but equally disruptive salinity changes

743 (Baptista et al., 2015). River discharge has the ability buffer or intensify pH if the water chemistry is alkaline or

744 acidic, respectively (Ianson et al., 2016). E) Terrestrial runoff contains pollutants, such as fertilisers that contain

745 high levels of nitrogen and phosphorus, which promote biological activity in waterways, particularly

746 eutrophication (Diaz and Rosenberg, 2008). F) Biological processes within the estuary alter the oxygen and

747 pCO_2 levels through respiration and photosynthesis (Baumann et al., 2015). Algal and microbial blooms, such as

748 those caused by eutrophication, can result in high levels of oxygen consumption leading to low dissolved

749 oxygen and high pCO_2 (Altieri and Gedan, 2015). Habitat changes, such as a shift from oyster reefs to algal-

750 dominated habitats, also have the ability to alter the topography of the estuary, as well as a suite of other

751 biological processes. G) Estuary topography directly affects temperature, as deep channels are typically cooler

752 than shallow channels. Depth and width of the estuary indirectly affects habitat type and their use by species,

753 water column mixing, and the extent of the tidal forcing. H) The extent of mixing directly affects temperature by

754 determining residency time of the waterbody, where low mixing can lead to stratification between the hotter

755 surface waters and the cooler bottom waters. The stratification of the water column also promotes hypoxia as

756 oxygenated surface waters are unable to mix with deoxygenated bottom waters, directly impacting oxygen and

757 pCO_2 concentrations (Ianson et al., 2016). I) The upstream distance that saltwater intrudes to from the mouth of

758 the estuary directly influences the salinity gradient. Regions with greater tidal ranges often see the salinity

759 gradient extend much further up the estuary than those with a small tidal range. J) Sea level is also an important

760 direct driver of estuarine salinity, as rising sea levels will result in saltwater intruding further into most estuaries

761 (Ross et al., 2015). It can also affect the tidal range of the estuary, by increasing tidal amplitude, thereby

762   indirectly altering the salinity gradient. Aspects of this image are courtesy of the Integration and Application

763   Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/)

764

765   **Figure 3| Six conceptual diagrams representing species range contractions, expansions and shifts along**

766   **environmental gradients, anticipated for multi-stressor environments such as estuaries under future**

767   **climate scenarios.** Solid lines represent the current distribution and abundance of species along the freshwater–

768   estuarine–marine gradient, with broken lines representing the anticipated change in species ranges under future

769   climate conditions, identified as either extensions or contractions by their fill as per the legend. In addition to

770   changes to range limits we have also included potential changes in abundance. When a species, or functional

771   group, extends their range their abundance automatically increases in their new range. Concomitant contractions

772   by other species or functional groups can also allow them to simultaneously increase their abundance in their

773   existing range due to increased availability of limiting factors, such as food or habitat. In all scenarios, both

774   marine and freshwater species are depicted as maintaining decreased abundances as they respectively approach

775   the marine or freshwater ends of the estuary. For marine species this is due to the nursery role that most

776   estuarine systems have, resulting in a typically higher abundances near the mouth of the estuary. Moving

777   offshore, the abundance of marine species that use estuaries decreases due to lower survival rates. For

778   freshwater species, the river will often widen downstream to include flood plains and wetlands. This increased

779   surface area and the associated nutrients can support increased species abundances in downstream parts of the

780   river. Furthermore, the lower reaches of the river, as opposed to tributaries, are less likely to experience river

781   desiccation.

782   Changes in salinity most greatly affect the estuarine zone when it increases (a) resulting in an increase in

783   abundance and range extension of marine and estuarine species, and concomitant decreases in freshwater

784   species as a result of range contractions. Decreases in salinity (b) result in an increase in abundance of

785   freshwater and estuarine species as they extend their range, and a decrease in marine species as their range in the

786   estuary contracts. Globally, air and sea temperatures are increasing (c), resulting in range contractions away

787   from areas with shallow habitats, such as the brackish-freshwater interface, into deeper cooler waters. The

788   shallow habitats of the brackish-freshwater interface experience a greater residency time of water compared to

789   the lower reaches of an estuary. These combine to increase the likelihood of higher than tolerable temperatures,

790   which would cause range contractions of freshwater and estuarine species in opposite directions. For some

791   species increasing temperatures lead to latitudinal changes (d) that can result in the addition of marine species

792   from warmer or tropical environments entering the estuarine system. Low dissolved oxygen and/or hypoxia (e)

793   results in compression of habitat to areas of higher dissolved oxygen (DO), typically shallow, well-mixed areas.

794   The interface between freshwater and estuarine water, and estuarine and marine waters are more likely to

795   experience low dissolved oxygen due to stratification that can occur when two waterbodies of different salinities

796   meet. When multiple stressors are combined, there are several interactive effects to account for. Currently, these

797   multi-stressor interactions are poorly understood; however, based on the paired interactive effects between

798   increased salinity, temperature and pCO$_2$ and decreased dissolved oxygen (Table 1b) we postulate one possible

799   outcome of future climate change within estuaries (f). In this scenario, marine and more tropical species thrive at

800   the expense of estuarine and freshwater species. Multi-stressor conditions also enhance the establishment of

801   invasive species and promote greater success within highly tolerant species, both of which generally perform

802   well in response to the individual climate stressors shown but are expected to perform even better relative to

803   specialist species under future multi-stressor scenarios.

804

805   **Figure 4| Conceptual diagram illustrating potential differences between a current and future estuary**

806   **under the influence of climate change.** The coloured lines represent different environmental stressors, where

807   red indicates increased water temperatures, green shows areas of hypoxia, blue represents high salinity, and

808   yellow depicts high pCO$_2$/low pH. Each scenario is illustrated from both an elevated and a cross-sectional view.

809   Examples of potential current (**a**) and future (**b**) abiotic conditions in estuaries are depicted. In the future climate

810   scenario, there is an increase in the mosaic complexity of the estuary as the number of areas experiencing

811   increased temperatures grows, the salinity front extends further upstream, there is an increase in the extent of

812   high pCO$_2$ waters, and there is the addition of hypoxia. The outline of the spatial extent of the abiotic stressors in

813   the current climate has also been overlayed with the distribution of six major functional groups to represent

814   possible current species distributions (**a**). The same has been done for the future climate scenario (**b**), where the

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816   tropical species into the estuary. The increased complexity of the mosaic allows for novel environments to form
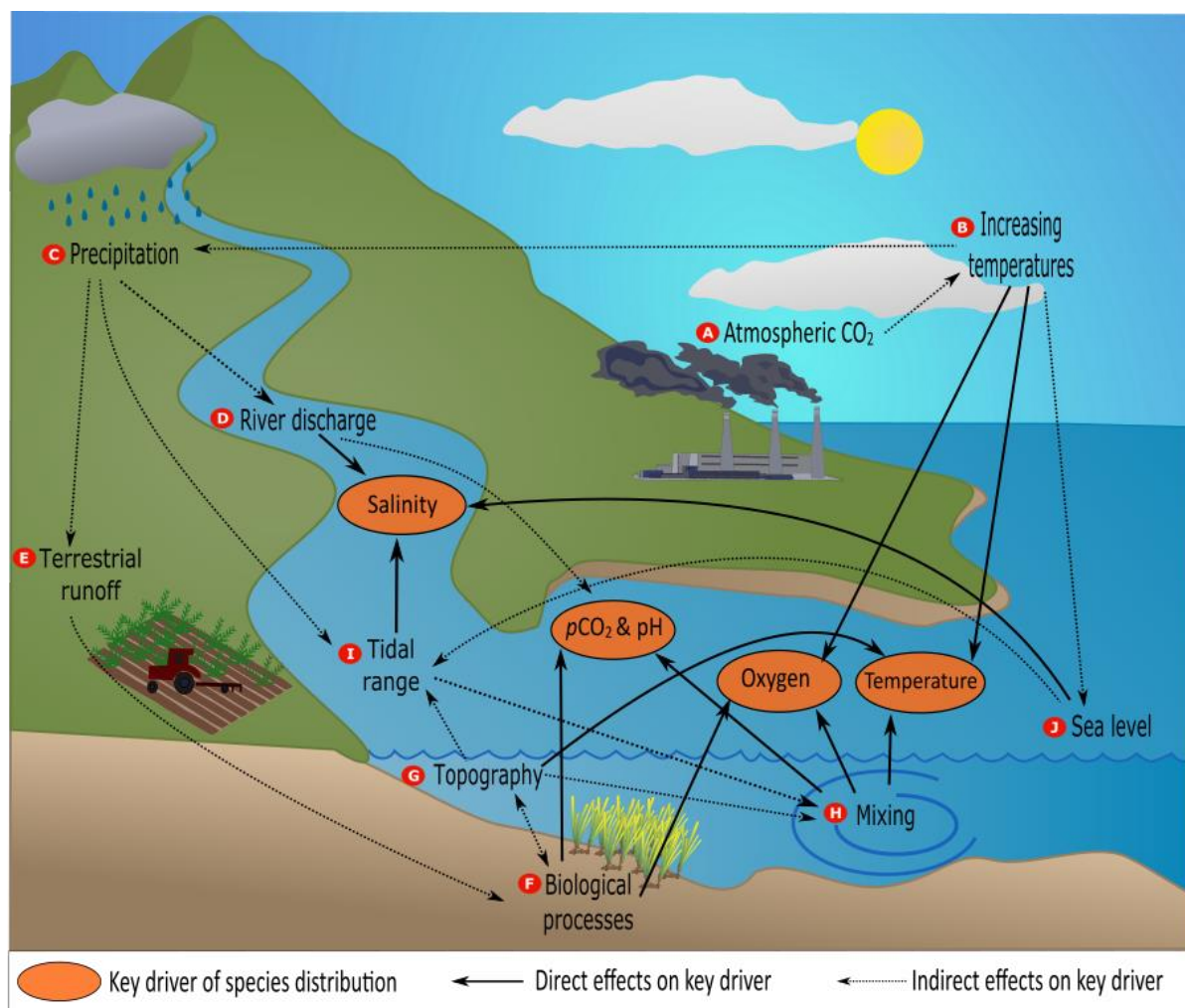
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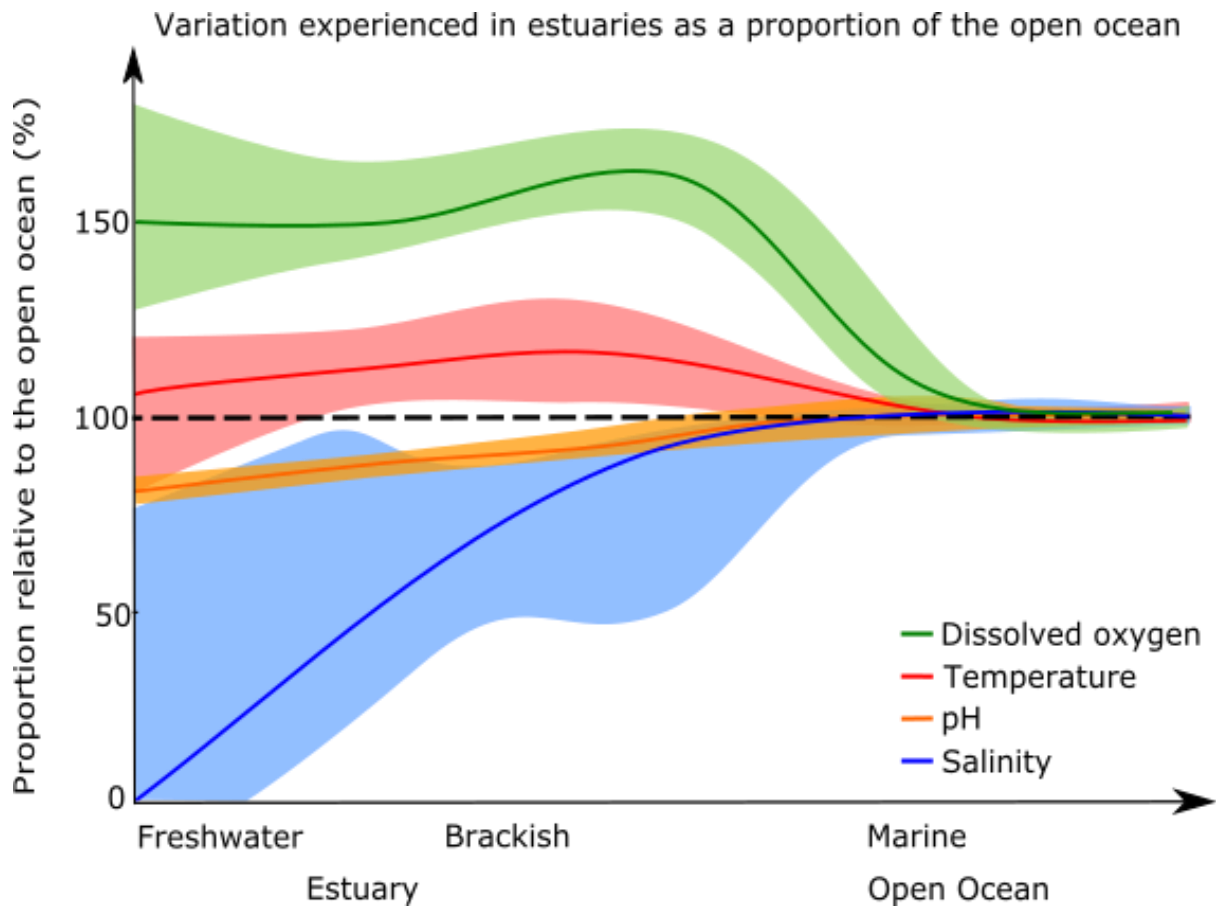
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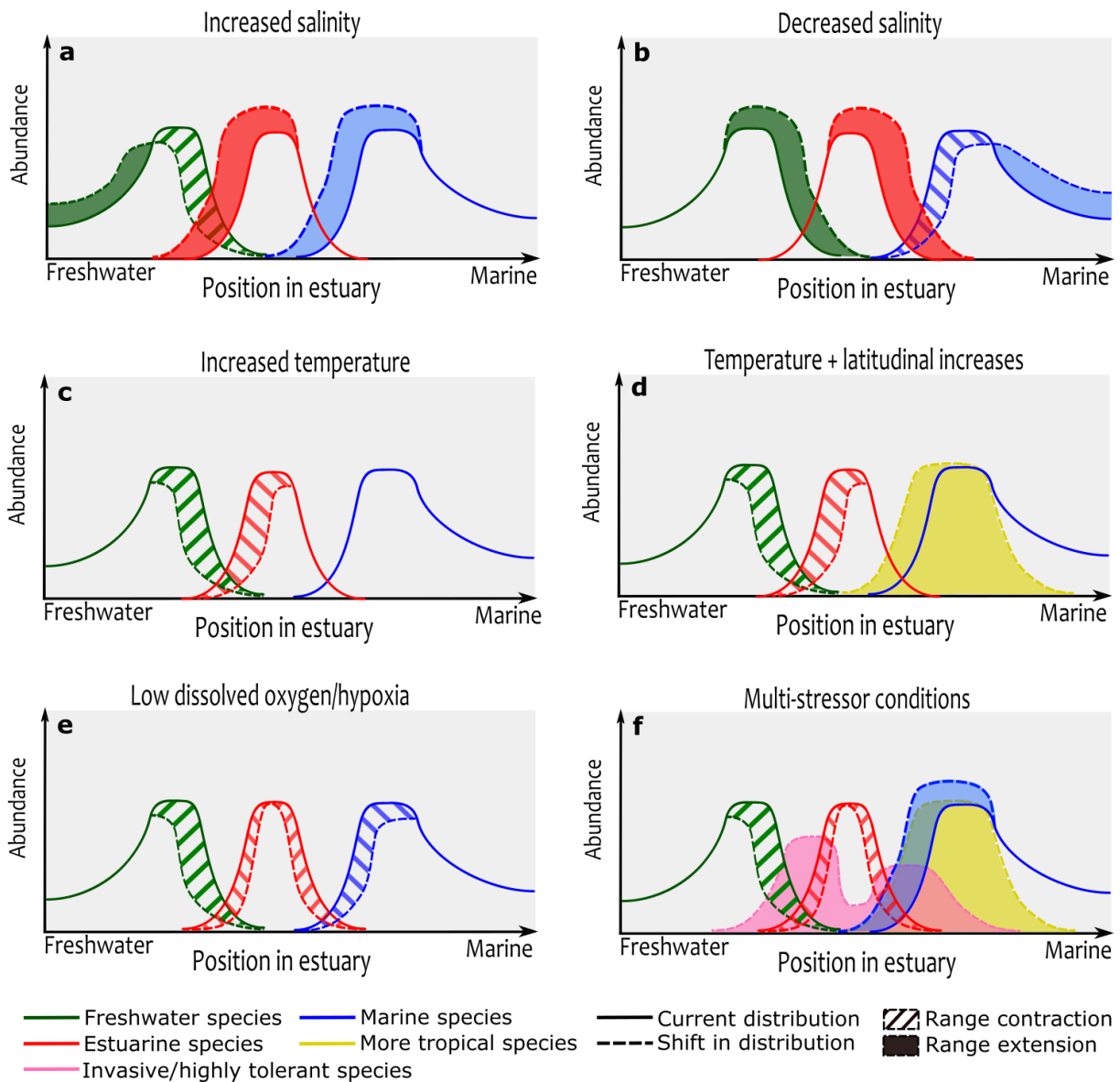
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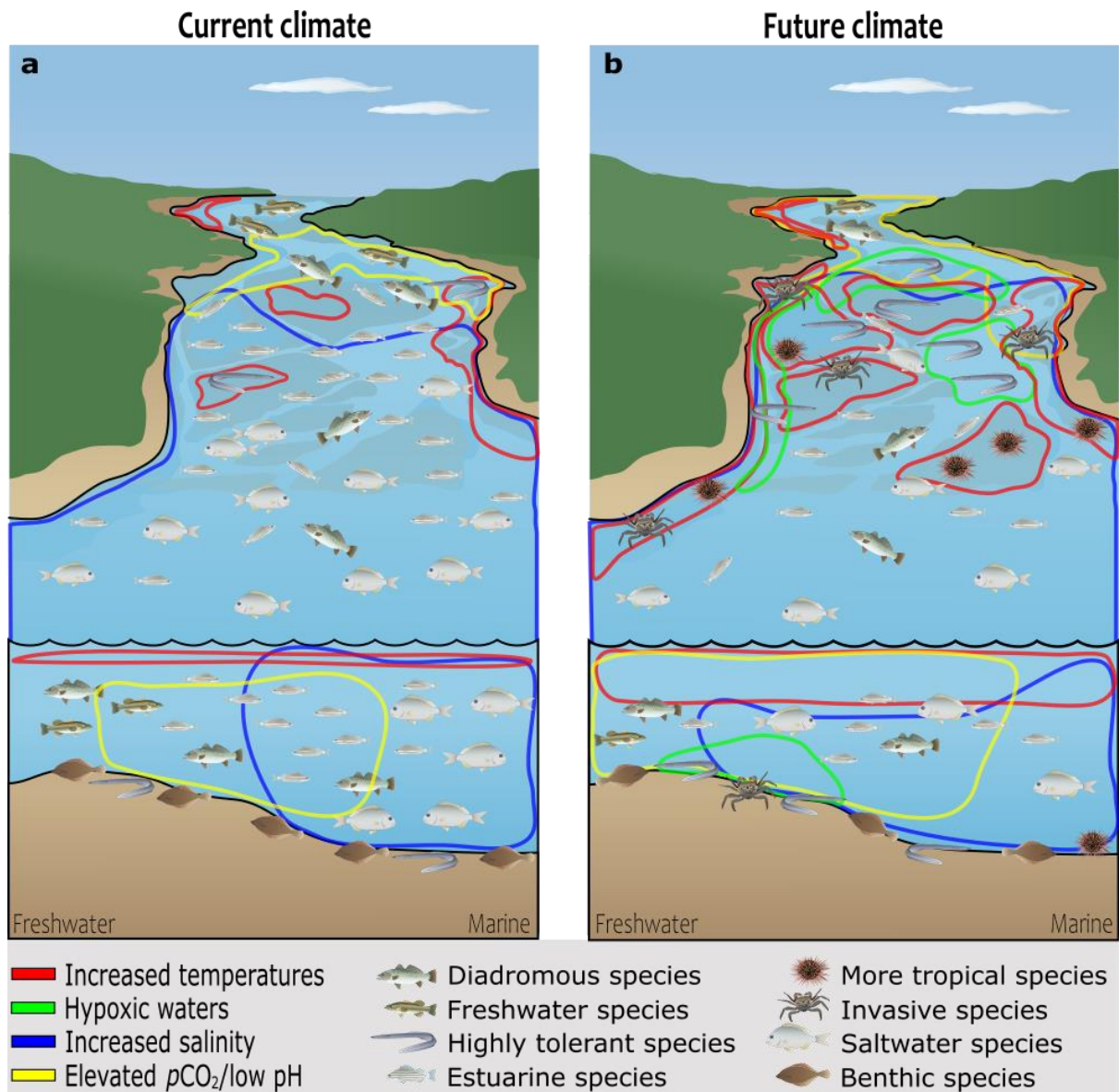Climate-mediated species range shifts along multi-stressor mosaics in coastal environments figures

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