- 1 Title: Spatial connectivity and marine disease dispersal: missing links in aquaculture
- 2 carrying capacity debates
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- 13

14 Summary

The concept of aquaculture carrying capacity (CC) aims at defining sustainable limits to 15 16 aquaculture growth in order to ensure ocean health. Usually, estimations are based on locally defined regions and on the farm-scale. However, interactions of aquaculture with 17 18 the ocean can have far-reaching effects, such as introduction and spread of invasive 19 species and marine diseases. The ocean is a fluid environment, subject to large- and 20 small-scale dynamics that introduce spatial connectivity between aguaculture sites and 21 more distant ecosystems than considered in current CC estimates. We, therefore, suggest to embrace spatial ocean connectivity into the CC concept by using 22 23 hydrodynamic modelling and dispersal simulations as high-throughput methods to 24 estimate potential impact areas and provide risk assessments. Here, we focus on the 25 example of dispersing infectious diseases in bivalve farming and discuss ecological as 26 well as social consequences of spatial connectivity. Both are applicable to a wide range 27 of organisms and marine aquaculture systems internationally.

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29 Abstract

One major societal challenge is meeting the constantly increasing demand for (sea)food in a sustainable way. With marine aquaculture on the rise, it is crucial to define limits to aquaculture growth in order to ensure ocean health. Along these lines, the concept of aquaculture carrying capacity (CC) is increasingly intersected with the principles of the ecosystem approach to aquaculture. Its primary aims are to estimate sustainable production potential and limits of locally defined regions. However, the ocean is a fluid

environment, subject to large- and small-scale dynamics, including ocean currents, tidal 36 fluctuations, and human action. These dynamics introduce spatial connectivity between 37 38 aquaculture sites and more distant ecosystems than considered in current CC estimates. 39 We argue that far-reaching effects of aquaculture on the ocean, such as introduction and 40 spread of invasive species and marine diseases, are thus underestimated when providing recommendations. Marine diseases can impact biodiversity, society, and overall ocean 41 health and it is imperative to guide aguaculture development to reduce the risk of marine 42 disease dispersal. We, therefore, suggest to embrace spatial ocean connectivity into the 43 CC concept by using hydrodynamic modelling and dispersal simulations as high-44 45 throughput methods to estimate potential impact areas and provide risk assessments. In this work, we focus on the example of dispersing infectious diseases in bivalve farming 46 47 and discuss ecological as well as social consequences of spatial connectivity. Both are 48 applicable to a wide range of organisms and marine aquaculture systems internationally. 49

50 **Definitions**

51 We aim to examine the topic of aquaculture carrying capacity from an interdisciplinary 52 perspective and use terms that can have differing meanings depending on context and 53 discipline. Therefore, we provide definitions of key terms according to the use in this 54 perspective article (marked in text in bold at first mention).

Marine aquaculture: The breeding, rearing, and harvesting of marine plants and animals.
Though this typically takes place in the ocean directly, the ocean-land interface is crossed
when aquaculture input is received from specific facilities on land (e.g., hatcheries).
Marine aquaculture is sometimes also referred to as mariculture.

59 **Ocean health**¹: Integrity, functionality, and resilience of the ocean ecosystem from a 60 transdisciplinary perspective. Human societies are dependent on various ocean 61 ecosystem services, and a sustainable use of, and interaction with the ocean must aim 62 to secure ocean health.

Aquaculture carrying capacity (CC): Maximum level of aquaculture that a social ecological system of a defined size can sustain before experiencing unacceptable
 changes to a state indicator.

66 **State indicator:** State indicators are used to measure carrying capacity. They are 67 variables to define maximum tolerable change induced by aquaculture before a system 68 may experience undesirable impacts. Common state indicators are e.g., chlorophyll or 69 oxygen concentration, or biomass of a non-cultured species. Dispersal (in the ocean): The passive spreading of biotic or abiotic entities with water
 masses through ocean currents, or anthropogenic processes like ship transport, here
 termed "anthropogenic dispersal".

Spatial connectivity (in the ocean): The connection and interaction between nonneighboring marine habitats or organisms through water movement. Water can move both naturally by ocean currents and anthropogenically, e.g., through ballast water transport.

Marine diseases: In this context, we refer to infectious diseases of marine organisms
 caused by disease agents (such as bacteria, viruses, or protists) that can be transmitted
 directly between hosts, or via seawater.

80 **Wild and farmed organisms:** Populations of organisms that occur naturally in the marine 81 habitat, and populations of organisms that are intentionally cultured by humans for 82 aquaculture purposes, respectively.

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84 Marine aquaculture and the carrying capacity concept

85 With declining wild fish and shellfish stocks and a simultaneously increasing demand for seafood, marine aquaculture is on the rise. The sector currently produces about 86 88 million tons of aquatic animals annually, which amounts to about 50% of the global 87 production². However, the aquaculture industry is criticized for its growth regardless of 88 the consequences for **ocean health** (FAO 2022² p. 18). The effects of aquaculture on 89 90 surrounding ecosystems can take many forms, of which are depending on the farmed species, the environmental setting, and additional anthropogenic stressors^{3–5}. The 91 alteration of the physical-environmental space may have been most prominently 92 93 discussed: be it through resource depletion⁶, changes in ocean currents^{7,8}, release of waste products and nutrients⁹, shifts in the gene pool of wild organisms¹⁰, the 94 95 introduction of potentially invasive species¹¹, or erosion¹².

All of these, and similar interactions of aquaculture with the ocean ecosystem may threaten biodiversity and ultimately what can be covered under the umbrella term "ocean health": ecosystem integrity, functioning and resilience¹. In turn, compromised ecosystem services affect human communities who are depending on the ocean for food supply or economy^{1,13}. In overall, the aquaculture sector is challenged to find sustainable solutions as to not compromise ocean nor human health.

102 The concept of **aquaculture carrying capacity (CC)** has created much attention for 103 debates on sustainable aquaculture growth. It aims at defining limits to production in order to create a "safe"¹⁴ operating space for aquaculture management^{15,16}. The application of the ecological concept of CC to aquaculture settings emerged in the 1990s¹⁷. It is based on the assumption that an ecosystem can only sustain a certain level of biomass grown in culture, before unacceptable changes to the ecosystem occur, e.g., a decrease in biodiversity or physical space^{15,16,18}.

109 Yet, what represents an unacceptable change to a system is easier defined 110 theoretically, than put into practice. Different state indicators and the change thereof 111 have been used to define thresholds for unacceptable change to a specific system as 112 induced by aquaculture operations within that same setting¹⁹. Some approaches focus 113 on physical production constraints of aquaculture: the location of farm sites and the 114 availability of space (i.e. *physical* CC^{20,21}), or the maximization of stocking density 115 without compromising individual growth and oxygen concentrations (i.e. production 116 CC²²). Others discuss ecological concerns which acknowledge that marine 117 aquaculture does not take place in an enclosed box but is embedded in a complex and 118 dynamic ecosystem. Farms may, for example, cause aquaculture-external species to decline (i.e. *ecological CC*^{23–26}), ecosystem integrity to be compromised²⁷, or exceed 119 120 the system's capacity to deal with organic matter, nutrient and contaminant input (i.e., assimilative CC^{14,28–30}). Fewer studies have looked at socio-economic considerations, 121 122 such as social acceptance or willingness to pay, for guiding aguaculture expansion (i.e., social $CC^{31,32}$). In the end, any limiting value for aquaculture expansion should 123 124 necessarily be shaped by social debates, and processes to estimate CC should be 125 multidimensional, iterative, inclusive and just³³. Importantly, they should be backed on the governmental level^{18,34,35}. 126

As such, the CC concept has found consideration in the ecosystem approach to aquaculture (EAA) that aims at guiding aquaculture development sustainably within social-ecological systems^{36,37}, and to foster the "ecological well-being"³⁸. Yet, few studies have combined CC and EAA principles in their modelling^{24–26} or decisionmaking processes^{39–41}. In the following, we will discuss potentially far-reaching effects of marine aquaculture that are currently underrepresented in the CC debate but crucial to ocean health.

134 Moving ahead: embracing spatial ocean connectivity

135 CC estimates and state indicator assessments have often been based on box system 136 models and applied to small-scale ecosystems well below 500 km² (i.e. estimating CC 137 at bay scale; **Table 1**). This focus on particular settings has its methodological-

conceptual reasoning. Further, place-based boundary values are easier to apply in 138 139 decision-making processes. Nevertheless, the fluidity of space in the ocean allows for 140 passive dispersal of organisms and their developmental stages and other aquaculture related output over hundreds of kilometers⁴² (Figure 1). As a result of natural spatial 141 142 **connectivity**, biotic and abiotic entities on which state indicators are based, may ultimately leave areas conventionally considered to estimate CC or even cross 143 144 international borders (Figure 1). 145 While spatial connectivity in the ocean might seem obvious, the extend of its 146 implications may currently not be fully acknowledged. Also in conservation planning, connectivity has been recently highlighted as a necessary factor^{43,44}, importantly on 147

the management and governance level⁴⁵. Few studies so far have considered connectivity in the CC context as the inflow or replenishment of oxygen or seston into the aquaculture area^{46,47}. Still, the dispersal away from aquaculture sites is currently largely overlooked. Therefore, the sustainable management of ecosystem services requires a more holistic approach⁴⁸.

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Table 1: Examples of state indicators used in different case studies aiming to define physical, production, ecological, assimilative or social aquaculture carrying capacity (CC) for systems of different sizes (following Inglis et al. 2000¹⁶ in their CC categories, adding *assimilative CC sensu* Chamberlain et al. 2006²⁸ and Tett et al. 2011¹⁴).

System carrying capacity (CC)	State indicator	Case study reference	Considered area (size)
Physical CC	Availability of space considering distance from shore and water depth	Yigit et al. 2021 ²¹	Sigacik Bay, Turkey (0.389 km²)
Production CC	Depletion of phytoplankton and oxygen	Uribe & Blanco 2001 ²²	Tongoy Bay, Chile (55.86 km²)
Ecological CC	Change of major energy fluxes or structure of the food web	Jiang & Gibbs 2005 ²³	Golden and Tasman Bays, New Zealand (4500 km²)
	Change in biomass of non-farmed species	Byron et al. 2011 ²⁶	Narragansett Bay, USA (355 km ²)
	Change in biomass of non-farmed species	Byron et al. 2011 ²⁵	Rhode Island, USA (lagoons from 1.5 to 7.8 km ²)
	Change in biomass of non-farmed species	Kluger et al. 2016 ²⁴	Sechura Bay, Peru (400 km²)
	Depletion of seston	Filgueira et al. 2021 ⁴⁷	Sober Island, Wine Harbour and Whitehead, Canada (0.9-14.2 km ²)
Assimilative CC	Organic matter, nutrient and contaminant levels	Chamberlain et al. 2006 ²⁸	Great Entry Lagoon, Magdalen Islands, Canada (2.5 km ²)

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Figure 1: Interactions of marine aquaculture with the surrounding ecosystem and anthropogenic activities that become relevant as state indicators for different aquaculture CC categories (letters). Here the focus is on the example of coastal bivalve aquaculture as one of the first systems to which the concept of aquaculture CC was applied. Almost all state indicators are potentially affected by spatial connectivity within the ocean and hence have effects beyond the typical area considered for CC (highlighted in yellow).

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170 Applying the lens of marine diseases to the carrying capacity debate

In some cases, the dispersal of organisms from aquaculture to the surrounding ecosystem is especially problematic for ocean health and we want to highlight two cases here, which are (i) the dispersal of invasive species and (ii) the dispersal of pathogens or organisms carrying **infectious diseases**. There are several examples of species introduced for economic purposes to a non-native region that have established populations far exceeding their initial point of cultivation with substantial impact on the ecosystem and competition with native species⁴⁹. For example, the Pacific oyster *Magallana gigas* (previously *Crassostrea gigas*) was introduced to Europe in the 1980s for aquaculture due to their high growth and reproduction rate⁵⁰. Up to now it has established populations all across the North-West European shelf including in places where no oyster aquaculture is pursued^{51,52}. Populations continue to expand even against their preferred temperature regime⁵³ and most recently into the low saline Baltic Sea⁵⁴. The implications for the environment range from displacement of native species to habitat transformation⁵⁵.

185 Another highly topical example for the unregulated introduction of non-native species 186 is the seaweed industry⁵⁶ which is at exceptional growth rates in recent years^{2,57}. Dispersal of reproductive seaweed material from the initial point of introduction can 187 188 introduce shifts in the gene pool of spatially connected **wild populations**¹⁰. Even 189 though numerous cases of non-native species introduction for cultivation are known⁵⁸. 190 translocations and introductions are continuing but urgently need governance and 191 biosecurity regulations to control the translocation of non-native cultivates⁵⁶ as well as 192 the associated diseases⁵⁹.

Together with cultured organisms, also pathogens can escape from aquaculture and 193 194 disperse to the surrounding environment. Disease outbreaks in aquaculture can greatly 195 affect mortality and growth of farmed animals as well as seafood product quality^{30,35}, 196 all of which compromise economic returns. Infection risk is highly dependent on population density^{60,61} with increasing density resulting in an increasing risk of disease 197 198 transmission. Beyond the economic impact, disease outbreaks and reoccurring mass 199 mortality events are increasingly recognized as a threat to ocean health and expected 200 to intensify in frequency and magnitude under progressing climate change and 201 monoculture practices^{62,63}.

202 Surprisingly, only 24 marine infectious diseases are currently listed by the World 203 Organization for Animal Health (in comparison to 172 terrestrial diseases, March 2023) 204 with major diseases such as the ostreid herpesvirus Os-HV-1 missing. In oyster 205 aquaculture, Os-HV-1 can cause a loss of up to 100% and mass mortalities have 206 already been recorded worldwide^{64,65}. However, infections keep recurring due to a 207 limited understanding of the biology of the diseases as well as insufficient management 208 and governance⁶⁶. This fragmentation of both knowledge on and documentation of 209 diseases highlights the challenges imposed to correctly document diseases in the 210 marine realm.

Beyond disease outbreaks within aquaculture farms and the costs involved, there is a high risk for disease spill-over to the surrounding ecosystem (**Figure 1**). Dense

213 populations kept in aquaculture farms can turn into a hub for disease outbreaks transmitted to wild populations^{67,68}. The spillover of sea lice from salmon farms, for 214 example, was identified as a reason for wild population declines and local extinction of 215 216 pink salmon on the Westcoast of Canada⁶⁹. Disease transmission can happen by direct 217 contact to infected organisms or via pathogens shed into seawater where they remain infectious for usually for a short time. Sea lice were shown to cross-infect even distant 218 219 salmon farms via dispersal by ocean currents^{70–72}. Infection of neighboring wild populations is a likely consequence especially in open aquaculture systems, where 220 221 water exchange between farm and environment is continuous and unavoidable. 222 However, there are also ways to reduce the risk of disease dispersal by considering 223 epidemiology⁷³. For example, it was predicted that harvesting oysters prior to the peak 224 disease release season would limit the impact on surrounding organisms⁷⁴. Overall, 225 wild populations are often much less monitored for disease outbreaks than farmed 226 animals due to inaccessibility and hence costs and effort involved, or simply because 227 monitoring of the natural environment is not prioritized by management. Even if infected wild animals are detected, the extend of related mortality events are often 228 229 unknown and the impact of spill-over from and to aquaculture is not yet fully understood for most systems⁷⁵. 230

231 What we do know, is that there are multiple dispersal pathways between farms and the 232 direct and distant environment that are relevant for connectivity and potentially for 233 disease transmission. Farmed bivalves and wild populations are connected via ocean 234 currents (#1 in Figure 2) where wild bivalves can potentially act as stepping stones in-235 between farms (#2) or enhance disease transmission when being in close proximity to 236 farms through spill-over and spill-back of diseases (#3). Human action may have an 237 even bigger impact on spatial connectivity through anthropogenic dispersal: 238 transport and relocation of bivalves (and their diseases) (#4,#5), as well as introduction 239 from hatcheries (#6) are vectors for dispersal, even if produced bivalves are consumed 240 locally (#7). Ship transport and ballast water (#8) are additional routes for disease 241 dispersal in the ocean and increase spatial connectivity in the ocean where they can 242 act against direction of ocean currents. Thereby, even very distant locations can in theory be at risk through combined natural and anthropogenic dispersal processes 243 244 (#9). Considering various dispersal routes and their potential impact on close-by and 245 distant ecosystems, we call to take the resulting multidimensional spatial connectivity 246 into account when providing CC estimates. For example, when applying the lens of 247 marine diseases to CC, options to predict but more importantly reduce the spreading

of diseases introduced and amplified by aquaculture should necessarily be developed as to correctly assess the impact of aquaculture on ocean health. Our ocean's health is, in the end, a combinate product of all ocean's – and its subsystems – health and the sustainable use of ocean resources inevitably depends thereof.

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254 Figure 2: Long-distance dispersal of pathogens as well as farmed organisms introducing connectivity. Dispersal can be passive with ocean currents (in yellow), or 255 256 via anthropogenic transport (in blue) from hatcheries to different field sites or relocation 257 between sites. Scenarios depicted in the graphic: 1. Connectivity between wild 258 population and farmed bivalves via ocean currents and potential way of disease 259 dispersal. 2. Transport of bivalves (and disease) from production to consumption site. 260 3. Relocation between different farms. 4. Bivalves (and disease) transported from hatchery to different farms. 5. Local bivalve production and consumption. 6. Wild 261 262 bivalve population as stepping stone between farms, connected via ocean currents, 7. Wild bivalve population in close proximity to farm. Site of disease spill-over and spill-263 back. 8. Dispersal of bivalves (and disease) with ship ballast water, also against 264 265 direction of ocean currents. 9. Bivalves that are only produced and consumed locally 266 are still at risk of infection by the combination of anthropogenic and natural dispersal 267 routes. 268

269 **Opportunities for holistic carrying capacity estimates**

In the EAA, it is differentiated between several spatial levels to which considerations should apply: farms, watersheds and the global level, emphasizing CC is mostly applied to the farm level³⁷. As a first step towards the integration of spatial connectivity in future CC estimates, system boundaries should be carefully rethought. The aim would be to continue providing CC recommendations for the immediately affected and well characterized local area around an aquaculture farm as was done so far, to then predict the potential maximum impact area that is spatially connected. 277 The strength of connectivity between sites depends on farm size and number of farmed individuals, but also ocean currents and anthropogenic activities such as distance to 278 279 the next harbor. Continuing with the bivalve aquaculture example (Figure 1 and 2). 280 guiding questions for defining system boundaries could be: How many farms are 281 located in that physical space? Where and how large are wild populations of the farmed 282 organisms? Where do seeds come from? Are animals relocated during the growth 283 period? Is there shipping traffic (ballast water exchange) in close proximity? How is the 284 local current regime? Does it change with season? How do ocean currents and their 285 physical-chemical parameters shape connectivity relevant to CC estimates?

286 Providing quantitative and comprehensive CC estimates is already a complex 287 endeavor at a local scale and valid concerns and constraints have been discussed previously^{15,18,35,76,77}. However, especially with respect to governance and international 288 289 legislation, there should be an interest to consider the potential far-reaching impact of 290 marine aquaculture including those across international boundaries. One potential 291 method to embrace the natural spatial connectivity by ocean currents are 292 hydrodynamic modelling approaches and Lagrangian particle dispersal 293 simulations^{78,79}. This toolkit from physical oceanography has been successfully applied to biologically motivated questions, among them the dispersal of passively drifting 294 295 larvae of various organisms^{80,81} (see **Figure 3 A+B** for more details on the method).

296 Few studies, however, have yet applied dispersal modelling to the spreading of 297 pathogens from aquaculture with ocean currents. One of the few examples is a case 298 study on the infection on sea lice infections in salmon aquaculture farms that 299 demonstrated that increasing the distance between farms would lower the risk of cross-300 infections^{71,72,82}. Although the importance of diseases has been discussed for the context of aquaculture CC earlier³⁵, it has only been recently used as a tool to inform 301 302 CC decisions⁸³. In a specific case study, dispersal models were used to assess 303 connectivity and risk of disease dispersal between in- and offshore aquaculture³⁰. And 304 while this is a very relevant start to discuss effects of cultures across farm-system-305 boundaries, the connectivity was pre-defined (in-offshore aquaculture facilities) and 306 other dimensions of spatial connectivity as discussed in the present work were 307 consequently not included.

Here, we demonstrate for the example of bivalve aquaculture, the potential impact area of oyster farms at the North West European shelf (**Figure 3 C**, locations of a small subset of farms extracted from EMODnet, accessed January 2023). The simulated entities in this example are infected oyster larvae that pose a risk for disease spread

312 between farms and spill-over to wild populations. On average, infected ovster larvae are predicted to spread over 70 km from aquaculture farms which exceeds most of the 313 314 areas used to calculate CC (Table 1). Depending on the exact location of farms, their 315 proximity to the coast and exposure to the open ocean, dispersal distances can vary 316 greatly. Even in this rather small dataset, average dispersal varies between 21 and 317 over 200 km, demonstrating the need and benefit of applying dispersal simulations to 318 each specific case. An advantage over, for example, genetic methods of assessing 319 spatial connectivity between populations, is the potential for high-throughput and fast 320 application to several locations at a time. Further, simulations are non-invasive and 321 can be applied without much a priori knowledge of a region if a hydrodynamic model 322 is available (e.g., Copernicus Marine Service provides an open access platform for 323 various hydrodynamic models of the global ocean⁸⁴).

324 In order to integrate this method into CC assessments, thresholds of acceptable 325 connectivity would need to be assessed and defined. This might be achieved by setting 326 a limit to a "maximum impact area" or "maximum impact distance" depending on the 327 epidemiology of a disease. Beyond the use for site selection for aquaculture, 328 connectivity could be re-assessed regularly, since it depends not only on local current 329 conditions but also on weather and other environmental variables and can vary 330 between years. As such, simulations might be used to determine annual production 331 limits or harvesting times. Even in the event of a disease outbreak within a farm, 332 simulations could be used to inform potentially affected farms or protected areas to 333 increase monitoring efforts. Especially farms close to international borders or other 334 legislative districts are expected to benefit from early warning systems (Figure 3 B).

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337 Figure 3: Hydrodynamic ocean models and particle dispersal analysis can provide insights into the potential impact of aquaculture farms through simulation of passive 338 339 dispersal of farmed organisms and/or associated pathogens. In total, 10,000 virtual 340 particles representing infected ovster larvae were released from an aquaculture farm 341 site on the French North Atlantic coast (red square) during the reproductive season 342 (on 01.07. for the years 2019-2022) in 4 m water depth. The position of virtual particles 343 was tracked every 12 h for 28 days using a km-scale operational ocean model from Copernicus Marine Service⁸⁵. (A) Ten representative dispersal trajectories of virtual 344 345 particles are displayed for the year 2019 (points represent position every 12 h). (B) 346 The particle density from day 14-28 after particle release represents the most likely 347 distribution of larvae during the time window for settlement. Larval development time depends on the species but also environmental conditions, and 28 days are within the 348 range of Pacific oyster development⁸⁶. The example shows that ocean currents can 349 disperse infected larvae into different directions along the coast, but also transport 350 351 them offshore. On average, in 28 days larvae are transported 66.5 km from this 352 example source site in France with a maximum distance of 134.8 km (**Table 2**). 353 Interannual variability of dispersal ranges from 40.1-85.0 km. (C) On a larger scale, 354 different locations of farms can be explored as shown here for randomly chosen oyster 355 farms across the North-West European shelf (locations exported from EMODnet⁵² and marked as red X's. The square marks the example site from panels A and B). 356 357

Table 2: Average dispersal distance of simulated oyster larvae over 28 days in July 2019-2022 from aquaculture farms across the North-West European shelf (**Figure 3**).

360 Example station from Figure 3 A+B is highlighted in bold.

Farm ID	Country	Latitude	Longitude	Average dispersal distance (km)	Standard- deviation (km)
DK_0044	Denmark	56.7228554	8.19900009	114.30	6.15
FR_0015	France	49.877171	0.7817767	36.75	4.30
FR_0073	France	48.8850522	-1.8093268	50.23	6.99
FR_0083	France	51.0044913	1.99148109	66.49	16.54
FR_0090	France	49.6947215	-1.4528919	65.04	32.95
FR_0172	France	48.695011	-3.9342667	89.90	17.97
FR_0206	France	48.0407095	-4.8642537	74.13	6.55
IE_0659	Ireland	51.9011809	-7.8894274	58.49	7.97
IE_0928	Ireland	52.7501887	-6.132192	25.31	4.80
IE_0982	Ireland	51.7852591	-10.193842	88.21	20.96
IE_1052	Ireland	55.322142	-7.353343	50.70	5.84
NL_0005	Netherlands	53.350908	4.93342326	112.49	37.05
NL_0006	Netherlands	51.7866845	3.80923335	43.76	19.04
NW_0159	Norway	58.399811	8.75663328	212.36	15.35
NW_0168	Norway	59.5085182	5.22214721	55.37	0.00
NW_0179	Norway	58.013203	6.9467395	161.68	32.42
UK_0012	United Kingdom	54.1212819	-3.2470733	27.46	8.70
UK_0013	United Kingdom	50.8045756	-1.036354	36.01	15.45
UK_0014	United Kingdom	53.3024457	-4.5826485	55.81	15.01
UK_0018	United Kingdom	50.6540275	-3.1967017	85.32	26.86
UK_0019	United Kingdom	55.6579133	-1.8346828	155.73	26.30
UK_0022	United Kingdom	50.0719985	-5.0687273	60.60	7.70
UK_0036	United Kingdom	51.066977	-4.204715	22.13	2.74
UK_0052	United Kingdom	51.8648432	1.26074314	21.27	1.82
UK_0074	United Kingdom	52.9693518	0.98433588	25.35	6.60
UK_0214	United Kingdom	60.4953089	-1.1118026	68.32	21.47
UK_0224	United Kingdom	55.7484707	-4.871023	39.54	15.43
UK_0237	United Kingdom	56.8853686	-6.1270371	55.37	23.22
UK_0245	United Kingdom	58.8665972	-2.85647	90.97	30.97
UK_0285	United Kingdom	57.6219784	-7.1290903	51.39	34.66
UK_0428	United Kingdom	57.8661349	-5.6597361	88.62	21.29
UK 0461	United Kingdom	56.3456584	-2.7502096	95.01	38.51

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We can only predict, not change ocean currents and thus have to embrace their flow and the spatial connectivity they introduce into our considerations. However, we can certainly influence anthropogenic dispersal of farmed organisms and their pathogens and reducing the latter should always be a priority. In ecological terms: the less

anthropogenic transport the better, though not always avoidable. Further, a well-367 documented disease screening of both native and non-native organisms before 368 369 introduction to aquaculture sites is absolutely crucial to reduce pathogen loading and 370 spill-over of diseases. Similarly, a regular disease screening of already cultivated 371 organisms ensures early detection before mortality events occur and thus stable 372 biomass production and profit. Optimizing the timing of harvest of farmed oysters as to 373 reduce the pathogen loading of the environment may be a management option, though 374 the costs for producers has to be priced in. Lastly, any recorded and guantified disease 375 breakouts should be publicly available, best in an international database, providing a 376 resource for early detection and warning system before disease spread occurs. 377 Overall, the design and implementation of meaningful regulations is the most important 378 measure to control unwanted introductions of non-native species and their potential 379 pathogens for aquaculture purposes.

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381 Summary

Aquaculture CC calculations need to embrace spatial connectivity in the ocean and
 the potential far reaching effects through dispersal by ocean currents.

2. Embracing spatial connectivity in CC calculations allows to improve estimations of aquaculture impact on the environment and ocean health that currently might be underestimated.

387 3. Spatial connectivity touches several impacts of aquaculture on ecosystems, while
 388 the introduction and dispersal of invasive species and marine diseases are of highest
 389 concern.

4. Hydrodynamic modelling and Lagrangian particle dispersal simulations provide tools

to assess the potential area affected by marine aquaculture and predict connectivity to

392 distant ecosystems and other farms including those across international boundaries.

393 5. Importantly, simulations are suggested as part of a multicriteria approach and not to394 replace current ecological or social CC frameworks.

395 6. Understanding dispersal from aquaculture farms is a first step towards limiting it396 actively to a minimum.

397 7. Including connectivity and the focus on ocean health into the CC concept has
398 implications for natural, social, political and economic sciences as well as governance.
399 It provides a crucial step towards sustainably promoting aquaculture as to feed the

- 400 ever-growing human population, while maintaining and protecting ocean health.
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