

## SEAGRASS POPULATION CONNECTIVITY IN THE SOUTH CHINA SEA

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### ABSTRACT

Seagrass plays important ecological roles and ecosystem services, yet degrading alarmingly in the South China Sea (SCS), one of the largest marginal seas of the Western Pacific. As connectivity is a vital component in population persistence, understanding of connectivity is of importance for effective seagrass conservation management. In the South China Sea, our understanding of connectivity is mainly based on studies in fishes and invertebrates. Connectivity in seagrass populations, on the other hand, is still poorly investigated. In this review, I predict that genetically structured population of seagrass is likely to occur in the SCS. Future research on seagrass connectivity should include (i) investigation on the pattern of connectivity at a local and broader-regional scale, and (ii) investigation on processes involved in the seagrass connectivity. These investigations are aimed to improve our knowledge of seagrass connectivity and to contribute in providing a solid framework for seagrass restoration/transplantation and spatial planning of seagrass management.

**Keywords:** seagrass, connectivity, conservation, South China Sea, resilience

### INTRODUCTION

In the marine environment, most populations are not randomly distributed in space and they are geographically separated from each other. These populations are often linked to each other to some degree by the exchange of organisms, genes, and materials (*e.g.*, nutrients, pollutants). Connectivity is basically described as the degree of which exchange of materials links populations and encompasses three main aspects, 1) genetic or evolutionary connectivity (the exchange of genes), 2) demographic connectivity (individual exchanges among populations through dispersal), and 3) oceanographic connectivity (flow of materials, mostly by water circulation and currents) (Kool *et al.*, 2013; Lowe & Allendorf, 2010).

In the face of climate change and increasing anthropogenic pressures on marine ecosystems, there has been growing interest among conservationists and ecologists in understanding

connectivity and its impact on the persistence of metapopulation. Studies in connectivity link with many subjects in ecology and conservation, including source-sink population dynamics (Bode *et al.*, 2006), dispersal and migration (Cowen & Sponaugle, 2009), and potential resilience to climate changes (Bernhardt & Leslie, 2013). Importantly, understanding connectivity also provides practical insights on a broad range of conservation management, for example, designation of marine protected areas and unit to conserve/UTC (Green *et al.*, 2014; Magris *et al.*, 2014) restoration/transplantation program (Lipcius *et al.*, 2008) and predicting/controlling outbreaks of diseases or invasive species (Hock *et al.*, 2014).

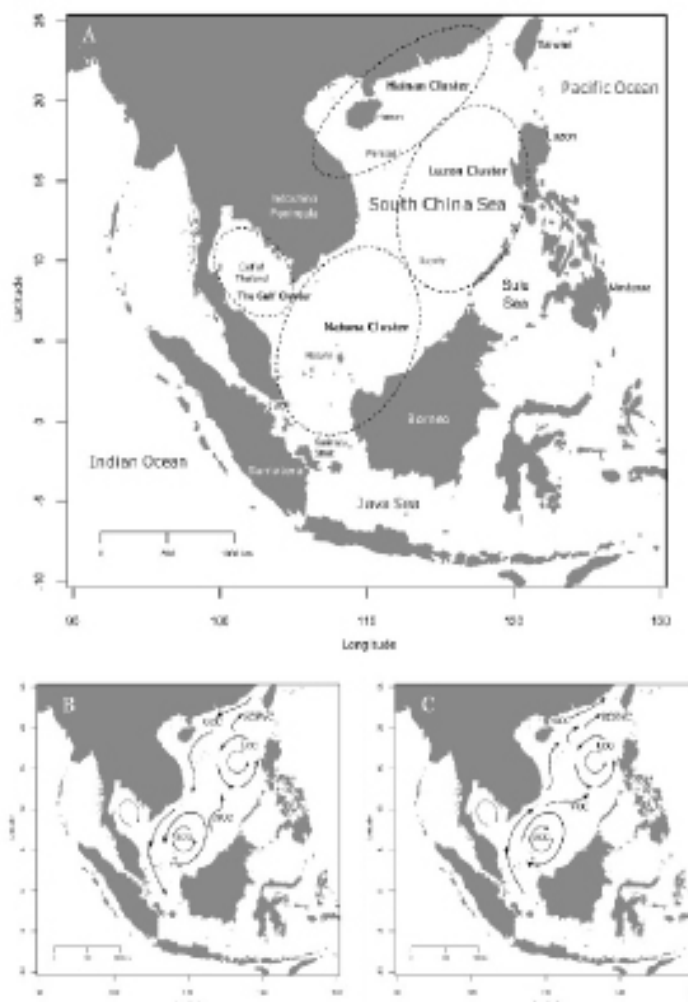
Seagrasses, angiosperms living in the marine environment, are foundation species that form ecologically critical coastal ecosystems, yet they are globally degrading. In the coastal ecosystems, they play significant roles in food web dynamics (Duffy 2006, Vonk *et al.*, 2008),

nutrient recycling (McGlathery *et al.*, 2007), carbon sink (Duarte, 2016), and habitat provision for numerous organisms, many of which are commercially important species (Ávila *et al.*, 2015; Gartner *et al.*, 2013; Hutchinson *et al.*, 2014). While providing important functions and services, seagrasses are declining in many parts of the world, including the South China Sea; calling for urgent, effective management actions (Short *et al.*, 2014; Vo *et al.*, 2013; Waycott *et al.*, 2009). With regards to effective management, studies in population connectivity may provide a significant contribution in formulating conservation management of seagrasses, especially in the South China Sea.

The review firstly presents the findings of a literature review of the extent of seagrass conservation status in the South China Sea. Secondly, focusses on the knowledge gaps of seagrass connectivity in the South China Sea and how to measure connectivity. Lastly, provides an outline of a direction for future research needed to fill the knowledge gaps and how conservation managers could benefit from the research.

### THE SOUTH CHINA SEA

The South China Sea (SCS) is a semi-enclosed sea surrounded by most ASEAN countries (*i.e.*, Singapore, Brunei, Indonesia, Malaysia, Cambodia, Vietnam, and the Philippines) and



**Figure 1.** The South China Sea situated in Southeast Asia. Dashed circles show hypothetical genetic clusters of seagrass population: Hainan Cluster, Luzon Cluster, Natuna Cluster, and the Gulf Cluster (Panel A). The seasonally changing pattern of water circulation in winter (December-February, Panel B) and in summer (June-August, Panel C). Arrowed lines indicate water current and its directions. SCWS: South China Sea Warm Current; GCC: Guangdong Coastal Current; LCG: Luzon Cyclonic Gyre; NOC: Natuna Offshore Current; SCG: South China Sea Cyclonic Gyre; VOC: Vietnam Offshore Current (modified from Hu *et al.*, 2000).

China (Figure 1). It is one of the largest marginal seas of the Western Pacific Ocean, spanning the tropical to subtropical zones and covering about 3.5 million square kilometers with an average depth of 1,212 m. The southern limit of the SCS is adjoined with the Java Sea, while the northern limit borders with the East China Sea. On the eastern side, the SCS neighbors with the Sulu Sea and the Pacific Ocean. The SCS connects with the Indian Ocean through the Malacca Strait and the Karimata Strait (Liu, 2013). The coastal borders of the SCS are home to 270 million people, many of whom are dependent on the ecosystem services provided by the sea, *e.g.*, food and livelihood (Vo *et al.*, 2013).

The SCS is generally characterized by eddies and seasonal circulation which reverses its direction in winter (cyclonic) and summer (anti-cyclonic) (Figure 1). The circulation pattern at the surface layer is mostly driven by the combination of monsoon winds and water exchange between the SCS, the Kuroshio (through the Luzon Strait), and the East China Sea (through the Taiwan Strait). Seabed topography could also contribute to the pattern. Those factors result in at least two prominent eddies: the Luzon Cyclonic Gyre (LCG) in the west side on Luzon and the South China Sea (Anti-) Cyclonic Gyre (SCG) in the Southern part of the SCS (Hu *et al.*, 2000).

Although it occupies less than 2% of Earth's surface covered by oceans, the SCS harbors diverse assemblages of ecosystems ranging from coral reefs, rocky and sandy shores, seagrasses, mangroves, estuaries, and mudflats to open waters, and has rich reserves of marine biodiversity supporting millions of livelihoods. Species richness in this region averaged 247 species per 100km coastline (Liu, 2013; Ng & Tan, 2000). Being at the western border of the Coral Triangle, the center of maximum marine biodiversity, at least 3,365 species of fishes have been recorded from this region (Arai, 2015; Randall & Lim, 2000). With only 4.7% of the world's total reef surface area, the SCS is home to 571 species of coral reef, rivaling the Coral Triangle that has 605 species (Huang *et al.*, 2015). Of the 60 seagrass species found worldwide, 18 species were reported to occur in the South China Sea. Mangrove forests (45 mangrove species out of a global total of 51) were estimated

to cover about 1,770,000 ha (11.4% of the world's mangrove forests) in the coastal region of the SCS (Morton & Blackmore, 2001; Vo *et al.*, 2013). Further, in the context of ecosystem services, the SCS has contributed significantly to global fisheries production where about 10 % of the global annual fisheries catch was reported from the SCS, and countries bordering the SCS are among the top producers of shrimps and tunas (Song, 2011; UNEP, 2007).

## SEAGRASS CONSERVATION IN THE SOUTH CHINA SEA

With rapid development and industrialization, the SCS is one of the world's most over-exploited and degraded ecosystem. Seagrass habitats have been experiencing degradation with decadal loss rates (30% in 2006). More than half of the original mangrove habitats had been lost during the last century. However, coral reefs, a biologically diverse ecosystem, is degrading (16% in 2007) (Vo *et al.*, 2013). Stocks of many economically important species have been reported to be depleted or collapsed due to over-fishing. Illegal, unreported, and unregulated (IUU) fishing is common in the region (Li & Amer, 2015; Vo *et al.*, 2013). Main threats identified on these ecosystems are anthropogenic activities, such as coastal development, pollution, destructive fishing, coastal aquaculture and mariculture, unsustainable tourism, coastal construction, and deforestation upland (Vo *et al.*, 2013). Ecosystem degradation requires more effective measures in fisheries management and marine biodiversity conservation as these interventions are yet to eliminate the threats and to improve the ecosystem status (Zou, 2015).

Despite their important ecosystem services and critical roles in coastal ecosystems, seagrasses have been degrading increasingly at both a global (Waycott *et al.*, 2009) and regional scale: such as the South China Sea (Vo *et al.*, 2013). Vietnam had lost 50% of seagrass meadows within the last decade (Luong *et al.*, 2012). The status of seagrass beds in Indonesia is poorly known, but one source (UNEP, 2008) reported at least 30% of habitat loss in Indonesian seagrass since 1966. About 45% of seagrass habitats have been lost within the last five decades in Singapore (Yaakub *et al.*, 2014). In Thailand, seagrass habitat

had degraded 20-30%, and in the Philippines, the habitat loss is about 30-50%. Seagrass degradation is mainly driven by anthropogenic factors, particularly destructive fishing, over-fishing, sedimentation from coastal development, wastewater effluent, nutrients inputs, severe coastal storms and coastal infrastructure (UNEP, 2008; Vo *et al.*, 2013).

The decline of seagrass ecosystems has necessitated implementation of effective management practices for seagrass restoration and conservation. About 16.5% of the total known area of seagrass in the South China Sea is currently under some form of management, yet most of the management sites do not have any specific legal status. Further, the effectiveness of the conservation management was generally medium to low (Vo *et al.*, 2013). This low success rate of seagrass management was also experienced in many parts of the world (Cunha *et al.*, 2012). Although factors responsible for the management failure vary spatially and temporally at multiple scales, two important factors were highlighted: (i) understanding of population connectivity so that the appropriate spatial scales of the conservation management are considered, and (ii) the critical roles of selecting appropriate donor and restoration sites (Cunha *et al.*, 2012; van Katwijk *et al.*, 2009).

## MEASURING POPULATION CONNECTIVITY

Connectivity can have profound consequences in metapopulation dynamics and population persistence. In the context of genetic connectivity, movement of individuals allows gene flow to occur. However, a certain level of gene flow (immigrant) is required to spread advantageous alleles and to avoid harmful effect local inbreeding (Lowe & Allendorf, 2010). Furthermore, as populations need to adapt to environmental changes (*e.g.*, climate change), connectivity ensures species' adaptive potential to be spread across a metapopulation (Frankham, 2005).

In the context of demographic connectivity, in which population growth (or specific vital rate, *e.g.*, survival) is affected by immigration or emigration, a population can benefit from the supply of immigrants from other populations as a

subsidy to compensate low survival or birth rates. In source-sink dynamics, immigrants from source populations can be critical for the persistence of sink populations that have low local recruitment. If sink populations are strongly dependent on the source populations, the diminished supply of immigrants due to, for example, extinction in the sources and changes in the pattern of oceanographic connectivity resulting in dispersal limitation, may pose a risk of extinction for the sink populations (Lowe & Allendorf, 2010).

## Measuring Connectivity with the Genetic Approach

Direct tracking may be the most powerful tool to examine connectivity over demographic time-scales, yet this tool is not representative over longer timescales (*e.g.*, evolutionary) (Kool *et al.*, 2013). Furthermore, given the vast size of the ocean and the minute size of seagrass propagules (fruit, seeds, and pollen), examining patterns of connectivity by direct tracking is not feasible; thus a different approach is needed. Here, the genetic approach can be used to estimate connectivity indirectly. As successful migrants carry genetic traits of their natal site, the pattern of connectivity over a broad range of spatial and temporal scale can be inferred from the gene flow among populations. Varying levels of gene flow among populations leads in spatially distributed genetic variation that reflects the structure of the metapopulation (Lowe & Allendorf, 2010).

Depending on the objectives and scales of various genetic markers (*e.g.*, microsatellites, single nucleotide polymorphisms/SNP, mitochondrial DNA, etc.) these can be used for estimating connectivity. Microsatellite can be used to assess contemporary connectivity as the mutation rate is relatively high (10<sup>-2</sup> to 10<sup>-6</sup> mutations per locus per generation). The microsatellite is characterized by highly polymorphic loci, thus very informative to detect change at both the finer spatial scale and the more recent time scale (Selkoe & Toonen, 2006). Sequences of mitochondrial or chloroplastic DNA might be used for examining historical connectivity; however these markers are known to have small variations, thus might not be able to detect changes among populations (Aires *et al.*, 2011; Olsen *et al.*, 2004). In case of failing to detect variation using the sequence markers,

phylogeographic reconstruction is still possible using SNP. This marker is abundant and widely spread across the genome, thus offering a high resolution of historical connectivity among populations (Brumfield *et al.*, 2003; Procaccini *et al.*, 2007).

### The Pattern of Seagrass Connectivity

Our understanding of seagrass population connectivity in the SCS is yet to develop as connectivity studies in the region are still limited. Studies have mostly focused on marine animals (fishes and invertebrates) using a broader spatial context that includes the neighboring regions, for example, the Coral Triangle and the western Pacific Ocean. Several patterns emerged from these studies. For example, a genetic study on the big eye tuna (*Thunnus obesus*) showed strong connectivity among the tuna populations in the SCS, Philippine Sea, and the western Pacific Ocean, suggesting that the fish populations over the sampling regions constitute a single panmictic population (Chiang *et al.*, 2006). Furthermore, sub-population structure within the SCS was revealed on other fish species, for example, the six bar wrasse (*Thalassoma hardwicki*) (Chen *et al.*, 2004) and the mottled spinefoot *Siganus fuscescens* (Ravago-Gotanco & Juinio-Meñez, 2010). Fine-scale population structure within the SCS system was also revealed in the blue starfish *Linckia laevigata* and the giant clam *Tridacna crocea* (Juinio-Meñez *et al.*, 2003). By contrast, the sea urchin (*Tripneustes gratilla*) did not show any significant genetic differentiation in this region (Casilagan *et al.*, 2013).

Our knowledge of seagrass connectivity in the SCS may be limited and based on *Cymodocea rotundata* (Arriesegado *et al.*, 2016), *C. serrulata* (Arriesegado *et al.*, 2015), *Enhalus acoroides* (Nakajima *et al.*, 2014), and *Thalassia hemprichii* (Hernawan *et al.*, 2017). The pattern of seagrass connectivity varies among species, and population may be genetically structured at different spatial scales, from a few meters (within meadows) to hundreds of kilometers (among regions). Seagrass panmictic populations can be spatially very large in size, from hundreds to thousands of kilometers as indicated in *C. rotundata*, *C. serrulata*, *E. acoroides*, and *Thalassia hemprichii* (Arriesegado *et al.*, 2015, 2016; Hernawan *et al.*, 2017; Nakajima *et al.*, 2014). However, the

structured population may also occur at finer scales (tens of kilometers; within meadows and among meadows), for example in *E. acoroides* in the Guimaras Strait, Philippines (Nakajima *et al.*, 2017).

Although the spatial context of those studies was not necessarily located in the SCS, the studies suggested that a single panmictic seagrass population may not occur in the SCS. The seagrass *E. acoroides* showed limited seagrass connectivity between the Hainan island populations (northern SCS) and the Philippine populations (Nakajima *et al.*, 2014), while the seagrass *C. serrulata* in the western seaboard of Luzon (on the SCS coast) were genetically clustered with the other populations in the Philippines (Arriesegado *et al.*, 2015). On the other hand, *C. rotundata* showed limited connectivity among populations in the Hainan island, the Philippine, and Ryukyu island (Arriesegado *et al.*, 2016). In addition, seagrass in Natuna islands, particularly *T. hemprichii*, was reported to be genetically connected with other populations in the Java Sea and Karimata Strait (Hernawan *et al.*, 2017).

The pattern of population connectivity in seagrass can be significantly influenced by abiotic factors, such as water currents (Hernawan *et al.*, 2017; McMahon *et al.*, 2014). Based on the water circulation pattern (Figure 1B and 1C), it is predicted that seagrass populations in the SCS are structured into four genetic clusters (Figure 1A). Seagrass around the Hainan islands and the Vietnamese coast would be clustered into a single genetic population (Hainan Cluster). The Guangdong Coastal Current (GCC) may facilitate connectivity among seagrass meadows within this genetic population. The LCG that occurs on the western side of Luzon would likely form a connectivity barrier between the Hainan Cluster and the Luzon Cluster. These two clusters were evidently indicated in *C. rotundata* (Arriesegado *et al.*, 2016). Seagrass around Natuna islands would form single a single genetic cluster (Natuna Cluster) since the SCG might prevent seagrass dispersal beyond the region affected by that gyre. Additionally, seasonal eddies occurring in the Gulf of Thailand might drive seagrasses in the gulf forming the Gulf Cluster separated from populations in the other regions. It is important to note that the patterns mentioned above are hypothetical, and empirical studies are needed to test this prediction.

## RESEARCH DIRECTION

As data are insufficient to draw complete patterns of seagrass connectivity at any spatial and temporal scale in the SCS, future research should aim to address the following topics:

### The Pattern of Connectivity

The general prediction of a pattern of seagrass connectivity in the SCS has been highlighted (Figure 1) and can be used as a framework to investigate seagrass connectivity in the region empirically. In the observed patterns of connectivity of most marine mammals, these are partially driven by their dispersal potential mainly associated with the species mobility characteristic and the larval duration (Bradbury *et al.*, 2008; Cowen & Sponaugle, 2009). Because seagrasses passively disperse via: (i) propagules (seeds or fruits), (ii) clonal propagation, and (iii) vegetative fragment (unrooted shoots), ranging from a few meters to several hundreds of kilometers over different time scale (days to millennia) (McMahon *et al.*, 2014), different patterns of connectivity might be expected in seagrass populations.

Investigation on this topic encompasses many relevant research questions. Is there any population structure? How many panmictic populations are there? If there is any pattern of population structure, to what extent are the populations connected to each other? Considering the connectivity strength and directionality, is the connectivity among populations symmetrical or asymmetrical? Which populations do act as the sources or sinks? Is there any barrier to connectivity?

Examining connectivity at a broader spatial scale, are seagrass populations within the SCS clustered together and connected with the other populations of the neighboring regions, *for example*, the Coral Triangle? If so, what proportion of seagrass recruits is originated from the local meadows, and what proportion comes from outside the SCS? As recent biophysical studies showed a strong connection between the SCS (particularly the Spratly Islands) with the Coral Triangle (Treml *et al.*, 2015) and the SCS acts as important sources of larvae and genetic diversity for the Coral Triangle (Kool *et al.*, 2011), can we expect the same pattern in

seagrass population? To what degree the regional connectivity is supporting population recovery of degraded meadows within the SCS and the neighboring regions?

### Processes Controlling Connectivity

There are gaps of knowledge in understanding processes that control connectivity in the SCS. Conceptually, connectivity in seagrass population occurs via dispersal of pollen, sexual propagules, and vegetative fragments, mainly by the water current. Seagrasses also expand and colonize available habitat by the individual spread of clonal growth (McMahon *et al.*, 2014). Previous studies have indicated the potential dispersal distance of *E. acoroides* and *T. hemprichii* (Lacap *et al.*, 2002) and the influence of the Kuroshio Current in determining the pattern of seagrass connectivity. Several populations show strong genetic connectivity although they have geographically separated far away (>1000 km) (Arriegado *et al.*, 2015; Hernawan *et al.*, 2017; Nakajima *et al.*, 2014).

To improve our understanding of seagrass connectivity in the SCS, we need to investigate how the interaction between the plants, dispersal vectors (*e.g.*, water current) and the local environmental state determines the seagrass connectivity. How far can the local water current disperse seagrass propagules? What is the probability of successful movement (migrants settle and contribute to the local recruitment) for sexual and vegetative propagules? What is the significance of successful movement to the local population? What is the extent of clonal growth and its significance? Are there any biotic vectors for moving seagrass in the SCS?

## SEAGRASS CONSERVATION MANAGEMENT

Comprehensive understanding of connectivity contributes in providing a solid framework for seagrass restoration, transplantation and spatial planning of seagrass management. In a rapidly changing environment, one of the major conservation goals is to maintain species population resilience by representatively protecting the population. Connectivity is crucial in population resilience as it enhances ecosystem capacity for recovery and self-organization after

disturbances. The exchange of propagules, larvae and adults among populations may maintain genetic diversity and also reduce the risk of local extinction because it allows continuous recruitment from outside sites (Bernhardt & Leslie, 2013; Lowe & Allendorf, 2010). For this reason, research on seagrass connectivity provides insight about: (i) the spatial size of management unit, (ii) design of marine reserve network, (iii) which population should be prioritized for the management (based on source-sink populations), and (iv) which population should be selected as a donor population in the case of seagrass transplantation.

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### REFERENCES

- Aires, T., Marbà, N., Cunha, R., Kendrick, G., Walker, D., Serrão, E., ... Arnaud-Haond, S. (2011). Evolutionary history of the seagrass genus *Posidonia*. *Marine Ecology Progress Series*, 421, 117–130. <https://doi.org/10.3354/meps08879>.
- Arai, T. (2015). Diversity and conservation of coral reef fishes in the Malaysian South China Sea. *Reviews in Fish Biology and Fisheries*, 25(1), 85–101. <https://doi.org/10.1007/s11160-014-9371-9>.
- Arriegasdo, D. M., Kurokochi, H., Nakajima, Y., Matsuki, Y., Uy, W. H., Fortes, M. D., ... Lian, C. (2015). Genetic diversity and structure of the tropical seagrass *Cymodocea serrulata* spanning its central diversity hotspot and range edge. *Aquatic Ecology*, 49(3), 357–372. <https://doi.org/10.1007/s10452-015-9529-0>.
- Arriegasdo, D. M., Kurokochi, H., Nakajima, Y., Matsuki, Y., Uy, W. H., Fortes, M. D., Lian, C. (2016). Population genetic diversity and structure of a dominant tropical seagrass, *Cymodocea rotundata*, in the Western Pacific region. *Marine Ecology*, 37(4), 786–800. <https://doi.org/10.1111/maec.12350>.
- Ávila, E., Yáñez, B., and Vazquez-Maldonado, L. E. (2015). Influence of habitat structure and environmental regime on spatial distribution patterns of macroinvertebrate assemblages associated with seagrass beds in a southern Gulf of Mexico coastal lagoon. *Marine Biology Research*, (April), DOI: 10.1080/17451000.2015.1007875. <https://doi.org/10.1080/17451000.2015.1007875>.
- Bernhardt, J. R., and Leslie, H. M. (2013). Resilience to climate change in coastal marine ecosystems. *Annual Review of Marine Science*, 5, 371–92. <https://doi.org/10.1146/annurev-marine-121211-172411>.
- Bode, M., Bode, L., and Armsworth, P. R. (2006). Larval dispersal reveals regional sources and sinks in the Great Barrier Reef. *Marine Ecology Progress Series*, 308(2002), 17–25. <https://doi.org/10.3354/meps308017>.
- Bradbury, I. R., Laurel, B., Snelgrove, P. V. R., Bentzen, P., and Campana, S. E. (2008). Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. *Proceedings of the Royal Society B Biological Sciences*, 275(1644), 1803–9. <https://doi.org/10.1098/rspb.2008.0216>.
- Brumfield, R. T., Beerli, P., Nickerson, D. a., and Edwards, S. V. (2003). The utility of single nucleotide polymorphisms in inferences of population history. *Trends in Ecology and Evolution*, 18(5), 249–256. [https://doi.org/10.1016/S0169-5347\(03\)00018-1](https://doi.org/10.1016/S0169-5347(03)00018-1).
- Casilagan, I. L. N., Juinio-Meñez, M. A., and Crandall, E. D. (2013). Genetic diversity, population structure, and demographic history of exploited sea urchin populations (*Tripneustes gratilla*) in the Philippines. *Journal of Experimental Marine Biology and Ecology*, 449, 284–293. <https://doi.org/10.1016/j.jembe.2013.09.012>.
- Chen, C. A., Ablan, M. C. A., McManus, J. W., Bell, J. D., Tuan, V. S., Cabanban, A. S., and Shao, K.-T. (2004). Population structure and genetic variability of six bar wrasse (*Thalassoma hardwicki*) in northern South China Sea revealed by mitochondrial control

- region sequences. *Marine Biotechnology*, 6, 312–326. <https://doi.org/10.1007/s10126-003-0028-2>.
- Chiang, H.-C., Hsu, C.-C., Lin, H.-D., Ma, G. C., Chiang, T.-Y., and Yang, H.-Y. (2006). Population structure of bigeye tuna (*Thunnus obesus*) in the South China Sea, Philippine Sea and western Pacific Ocean inferred from mitochondrial DNA. *Fisheries Research*, 79, 219–225. <https://doi.org/10.1016/j.fishres.2005.11.026>.
- Cowen, R. K., and Sponaugle, S. (2009). Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, 1, 443–466. <https://doi.org/10.1146/annurev.marine.010908.163757>.
- Cunha, A., Marbá, N., van Katwijk, M., Pickerell, C., Henriques, M., Bernard, G., Manent, P. (2012). Changing paradigms in seagrass restoration. *Restoration Ecology*, 20(4), 427–430. <https://doi.org/10.1111/j.1526-100X.2012.00878.x>.
- Duarte, C. M. (2017). Reviews and syntheses: Hidden Forests, the role of vegetated coastal habitats on the ocean carbon budget. *Biogeosciences Discussions*, 14, 301–310. <https://doi.org/10.5194/bg-2016-339>.
- Duffy, J. E. (2006). Biodiversity and the functioning of seagrass ecosystems. *Marine Ecology Progress Series*, 233, 233–250. <https://doi.org/10.3354/meps311233>.
- Frankham, R. (2005). Stress and adaptation in conservation genetics. *Journal of Evolutionary Biology*, 18(4), 750–755. <https://doi.org/10.1111/j.1420-9101.2005.00885.x>.
- Gartner, A., Tuya, F., Lavery, P. S., and McMahon, K. (2013). Habitat preferences of macroinvertebrate fauna among seagrasses with varying structural forms. *Journal of Experimental Marine Biology and Ecology*, 439, 143–151. <https://doi.org/10.1016/j.jembe.2012.11.009>.
- Green, A. L., Maypa, A. P., Almany, G. R., Rhodes, K. L., Weeks, R., Abesamis, R. a., ... White, A. T. (2014). Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews*, n/a-n/a. <https://doi.org/10.1111/brv.12155>.
- Hernawan, U. E., Dijk, K. van, Kendrick, G. A., Feng, M., Biffin, E., Lavery, P. E., and McMahon, K. (2017). Historical processes and contemporary ocean currents drive genetic structure in the seagrass *Thalassia hemprichii* in the Indo-Australian Archipelago. *Molecular Ecology*, 26, 1008–1021. <https://doi.org/10.1111/mec.13966>.
- Hock, K., Wolff, N. H., Condie, S. A., Anthony, K. R. N., and Mumby, P. J. (2014). Connectivity networks reveal the risks of crown-of-thorns starfish outbreaks on the Great Barrier Reef. *Journal of Applied Ecology*, 51, 1188–1196. <https://doi.org/10.1111/1365-2664.12320>.
- Hu, J., Kawamura, H., Hong, H., and Qi, Y. (2000). A review on the currents in the South China Sea: Seasonal circulation, South China Sea Warm Current and Kuroshio Intrusion. *Journal of Oceanography*, 56, 607–624. <https://doi.org/10.1023/A>.
- Huang, D., Licuanan, W. Y., Hoeksema, B. W., Chen, C. A., Ang, P. O., Huang, H., ... Chou, L. M. (2015). Extraordinary diversity of reef corals in the South China Sea. *Marine Biodiversity*, 45(2), 157–168. <https://doi.org/10.1007/s12526-014-0236-1>.
- Hutchinson, N., Jenkins, G. P., Brown, A., and Smith, T. M. (2014). Variation with depth in temperate seagrass-associated fish assemblages in Southern Victoria, Australia. *Estuaries and Coasts*, 37(4), 801–814. <https://doi.org/10.1007/s12237-013-9742-9>.
- Juinio-Meñez, M. A., Magsino, R. M., Ravago-Gotanco, R. G., and Yu, E. T. (2003). Genetic structure of *Linckia laevigata* and *Tridacna crocea* populations in the Palawan shelf and shoal reefs. *Marine Biology*, 142, 717–726. <https://doi.org/10.1007/s00227-002-0998-z>.
- van Katwijk, M. M., Bos, A. R., de Jonge, V. N., Hanssen, L. S. A. M., Hermus, D. C. R., and de Jong, D. J. (2009). Guidelines for seagrass restoration: Importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. *Marine Pollution Bulletin*, 58(2), 179–188. <https://doi.org/10.1016/j.marpolbul.2008.09.028>.
- Kool, J. T., Paris, C. B., Barber, P. H., and Cowen, R. K. (2011). Connectivity and the development of population genetic structure in Indo-West Pacific coral reef communities.

- Global Ecology and Biogeography*, 20(5), 695–706. <https://doi.org/10.1111/j.1466-8238.2010.00637.x>.
- Kool, J. T., Moilanen, A., and Treml, E. A. (2013). Population connectivity: recent advances and new perspectives. *Landscape Ecology*, 28(2), 165–185. <https://doi.org/10.1007/s10980-012-9819-z>.
- Lacap, C. D. A., Vermaat, J. E., Rollon, R. N., and Nacorda, H. M. (2002). Propagule dispersal of the SE Asian seagrasses *Enhalus acoroides* and *Thalassia hemprichii*. *Marine Ecology Progress Series*, 235, 75–80. <https://doi.org/10.3354/meps235075>.
- Li, J., and Amer, R. (2015). Closing the net against IUU fishing in the South China Sea: China's practice and way forward. *Journal of International Wildlife Law & Policy*, 18(2), 139–164. <https://doi.org/10.1080/13880292.2015.1044799>.
- Lipcius, R. N., Eggleston, D. B., Schreiber, S. J., Seitz, R. D., Shen, J., Sisson, M., ... Wang, H. V. (2008). Importance of metapopulation connectivity to restocking and restoration of marine species. *Reviews in Fisheries Science*, 16(1–3), 101–110. <https://doi.org/10.1080/10641260701812574>.
- Liu, J. Y. (2013). Status of marine biodiversity of the China seas. *PLoS ONE*, 8(1), e50719. <https://doi.org/10.1371/journal.pone.0050719>.
- Lowe, W. H., and Allendorf, F. W. (2010). What can genetics tell us about population connectivity? *Molecular Ecology*, 19(15), 3038–51. <https://doi.org/10.1111/j.1365-294X.2010.04688.x>.
- Luong, C. Van, Thao, N. Van, Komatsu, T., Ve, N. D., and Tien, D. D. (2012). Status and threats on seagrass beds using GIS in Vietnam. In *The International Society for Optical Engineering* (p. 852512). <https://doi.org/10.1117/12.977277>.
- Magris, R. A., Pressey, R. L., Weeks, R., and Ban, N. C. (2014). Integrating connectivity and climate change into marine conservation planning. *Biological Conservation*, 170, 207–221. <https://doi.org/10.1016/j.biocon.2013.12.032>.
- McGlathery, K. J., Sundbäck, K., and Anderson, I. C. (2007). Eutrophication in shallow coastal bays and lagoons: The role of plants in the coastal filter. *Marine Ecology Progress Series*, 348(Table 1), 1–18. <https://doi.org/10.3354/meps07132>.
- McMahon, K., Dijk, K. van, Ruiz-Montoya, L., Kendrick, G. A., Krauss, S. L., Waycott, M., ... Duarte, C. (2014). The movement ecology of seagrasses. *Proceedings of the Royal Society B Biological Sciences*, 281, 20140878.
- Morton, B., and Blackmore, G. (2001). South China Sea. *Marine Pollution Bulletin*, 42(12), 1236–1263. [https://doi.org/10.1016/S0025-326X\(01\)00240-5](https://doi.org/10.1016/S0025-326X(01)00240-5).
- Nakajima, Y., Matsuki, Y., Arriesegado, D. M., Campos, W. L., Nadaoka, K., and Lian, C. (2017). Population genetics information for the regional conservation of a tropical seagrass, *Enhalus acoroides*, around the Guimaras Strait, Philippines. *Conservation Genetics*, 18(4), 789–798. <https://doi.org/10.1007/s10592-017-0927-9>.
- Nakajima, Y., Matsuki, Y., Lian, C., Fortes, M. D., Uy, W. H., Campos, W. L., ... Nadaoka, K. (2014). The Kuroshio Current influences genetic diversity and population genetic structure of a tropical seagrass, *Enhalus acoroides*. *Molecular Ecology*, 23(24), 6029–6044. <https://doi.org/10.1111/mec.12996>.
- Ng, P. K. L., and Tan, K. S. (2000). The state of marine biodiversity in the South China Sea. *The Raffles Bulletin of Zoology*. Supplement, 8, 3–7.
- Olsen, J. L., Stam, W. T., Coyer, J. a, Reusch, T. B. H., Billingham, M., Boström, C., ... Wyllie-Echeverria, S. (2004). North Atlantic phylogeography and large-scale population differentiation of the seagrass *Zostera marina* L. *Molecular Ecology*, 13(7), 1923–41. <https://doi.org/10.1111/j.1365-294X.2004.02205.x>.
- Procaccini, G., Olsen, J. L., and Reusch, T. B. H. (2007). Contribution of genetics and genomics to seagrass biology and conservation. *Journal of Experimental Marine Biology and Ecology*, 350(1–2), 234–259. <https://doi.org/10.1016/j.jembe.2007.05.035>.
- Randall, J. E., and Lim, K. K. P. (2000). A checklist of the fishes of the south china sea.

- Raffles Bulletin of Zoology*, (8), 569–667.
- Ravago-Gotanco, R. G., and Juinio-Meñez, M. A. (2010). Phylogeography of the mottled spinefoot *Siganus fuscescens*: Pleistocene divergence and limited genetic connectivity across the Philippine archipelago. *Molecular Ecology*, 19(20), 4520–4534. <https://doi.org/10.1111/j.1365-294X.2010.04803.x>.
- Selkoe, K. A., and Toonen, R. J. (2006). Microsatellites for ecologists: a practical guide to using and evaluating microsatellite markers. *Ecology Letters*, 9(5), 615–29. <https://doi.org/10.1111/j.1461-0248.2006.00889.x>.
- Short, F. T., Coles, R., Fortes, M. D., Victor, S., Salik, M., Isnain, I., ... Seno, A. (2014). Monitoring in the Western Pacific region shows evidence of seagrass decline in line with global trends. *Marine Pollution Bulletin*, 83(2), 408–416. <https://doi.org/10.1016/j.marpolbul.2014.03.036>.
- Song, Y. (2011). A marine biodiversity project in the South China Sea: Joint efforts made in the SCS workshop process. *The International Journal of Marine and Coastal Law*, 26(1), 119–149. <https://doi.org/10.1163/157180811X541413>.
- Treml, E. A., Roberts, J., Halpin, P. N., Possingham, H. P., and Riginos, C. (2015). The emergent geography of biophysical dispersal barriers across the Indo-West Pacific. *Diversity and Distributions*, 21, 456–476. <https://doi.org/10.1111/ddi.12307>.
- UNEP. (2007). *National Reports on Coral Reefs in the Coastal Waters of the South China Sea*. UNEP/GEF/SCS Technical Publication No. 11.
- UNEP. (2008). *National reports on seagrass in the South China Sea*. UNEP/GEF/SCS Technical Publication No. 12.
- Vo, S. T., Pernetta, J. C., and Paterson, C. J. (2013). Status and trends in coastal habitats of the South China Sea. *Ocean and Coastal Management*, 85, 153–163. <https://doi.org/10.1016/j.ocecoaman.2013.02.018>.
- Vonk, J. A., Christianen, M. J. A., and Stapel, J. (2008). Redefining the trophic importance of seagrasses for fauna in tropical Indo-Pacific meadows. *Estuarine, Coastal and Shelf Science*, 79(4), 653–660. <https://doi.org/10.1016/j.ecss.2008.06.002>.
- Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 106(30), 12377–12381. <https://doi.org/10.1073/pnas.0905620106>.
- Yaakub, S. M., McKenzie, L. J., Erfteimeijer, P. L. A., Bouma, T., and Todd, P. A. (2014). Courage under fire: Seagrass persistence adjacent to a highly urbanised city-state. *Marine Pollution Bulletin*, 83(2), 417–424. <https://doi.org/10.1016/j.marpolbul.2014.01.012>.
- Zou, K. (2015). Managing biodiversity conservation in the disputed maritime areas: The case of the South China Sea. *Journal of International Wildlife Law and Policy*, 18(2), 97–109. <https://doi.org/10.1080/13880292.2015.1044810>.