

Allochthonous dissolved organic carbon in river, lake and coastal systems: transport, function and ecological role

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Introduction to special issue

Dissolved organic carbon (DOC) in aquatic systems derives from two distinct sources; either autochthonous primary production within the system or from allochthonous organic carbon entering the system from the catchment. Allochthonous DOC is one of the largest organic carbon fluxes from catchments to aquatic systems (Hinton *et al.* 1997, 1998). Allochthonous DOC through its effects on microbial processes, plays an important role in driving metabolism, decomposition and food web dynamics at the ecosystem scale. Interestingly, the importance of allochthonous DOC in aquatic systems is debated in the literature. Models of aquatic ecosystem function such as the Riverine Continuum Concept (Vannote *et al.* 1980) and the Riverine Productivity Model (Thorp and Delong 1994) generally do not consider allochthonous sources of carbon as very important to the productivity of lowland rivers. The early work of Cole and co-authors (Cole *et al.* 2002, 2006) in lakes suggested that inputs of terrestrial DOC are often biologically recalcitrant, contributing little to the productivity of higher trophic levels relative to autochthonous carbon sources. Alternatively, other theories such as the Flood Pulse Concept (FPC) of Junk *et al.* (1989) suggest that the movement of terrestrial resources from the floodplain and catchments during flooding and rainfall events may be a significant source of energy to aquatic systems. More recently, paradigms about autochthonous carbon dominating lakes are being questioned (Cole *et al.* 2011). The significance of allochthonous DOC to aquatic ecosystems is being further recognised with the understanding that terrestrial subsidies are playing a much greater role in some systems than previously thought (Tanentzap *et al.* 2014).

Understanding where and when allochthonous DOC supports aquatic ecosystems remains challenging to quantify (Wiegner *et al.* 2015) and an area of contention between researchers (Cole *et al.* 2006). This suggests that there may be

no one universal theory about the dominance of autochthonous or allochthonous dissolved organic carbon in aquatic systems and which source dominates may vary between different systems both spatially and temporally. Consequently there is a need to better understand allochthonous DOC transport to aquatic systems, and its function and incorporation into food webs in different aquatic environments. Such information is important for our theoretical understanding of how aquatic systems function (Cole *et al.* 2006).

In this special issue we have brought together studies from a range of different aquatic systems from locations around the world that examine the transport and ecological role of allochthonous DOC. We hope this will improve the knowledge base on allochthonous DOC and stimulate discussion on the role of allochthonous DOC in management of aquatic systems.

Transport of allochthonous DOC

Allochthonous DOC is one of the largest organic carbon fluxes from catchments to aquatic systems and is influenced by many factors including rainfall, hydrologic flow paths, catchment land use, flooding, leaching and presence of wetlands (Hinton *et al.* 1998; Westhorpe and Mitrovic 2012). Understanding the processes controlling the transfer of DOC from terrestrial to aquatic environments is of fundamental importance to aquatic sciences (Wilson *et al.* 2016). Our current understanding of DOC transport was developed in unmodified, upland temperate streams, where precipitation events dissolve soil DOC and transport it to the water column (Hinton *et al.* 1998). Although there is a good understanding of DOC transport in such systems, the driving factors for DOC transport in other types of systems, such as in lowland and modified river networks are still being developed.

Some of the papers in this special issue highlight the importance of floodplain inundation and precipitation and runoff as

important mechanisms of DOC transport to rivers, estuaries and coastal zones. [Robertson *et al.* \(2016\)](#) in a lowland river system, estimated the magnitude and direction of exchanges of particulate organic carbon (POC) and DOC between the river channel and four floodplain wetlands (billabongs) during a managed high flow experiment. There was a large net transport of organic carbon from the river to billabongs during connection, ranging from 87–525 kg POC per billabong and 36–4357 kg DOC. At the whole reach scale there was a net input of 821 Mg DOC to the river channel. The DOC entering the river was derived from litter and soils in riverbank habitats or from abraded biofilms in the river channel. [Nielsen *et al.* \(2016\)](#) also showed the contribution that floodplains make to the main river channel during different sized floods in a lowland river. A large flood contributed 300 Mg DOC, 7 Mg of zooplankton, whereas a smaller flood contributed much less. They suggested that the magnitude of flow and area of floodplain wetted may be very important in determining the subsidies of terrestrial matter to river systems.

Even at the lower ends of catchments, such as estuaries, labile DOC is still present and these pools of DOC are responsible for bacterial growth ([Raymond and Bauer 2000](#)). The DOC that leaves estuaries ultimately ends up in the coastal zone. [Miller *et al.* \(2016\)](#) examined transport of DOC from the river to the ocean through the Neuse Estuary following the major rainfall event associated with Hurricane Irene in 2011. Coloured dissolved organic matter (CDOM) and DOC nearly tripled in the three days following the storm. A strong linear relationship was observed between DOC and CDOM and a shift from higher to lower molecular weight dissolved organic matter (DOM) was observed as it transited through the estuary probably due to photodegradation.

[Aitkenhead-Peterson and Steele \(2016\)](#) showed concentrations and export of dissolved organic carbon (DOC) and organic nitrogen (DON) from terrestrial landscapes to near coastal zones varied with land use. They examined DOC and DON in four gauged sub-watersheds in the humid sub-tropical, upper Trinity River basin, upstream and downstream of the Dallas–Fort Worth metropolis in Texas, USA. DOC export was significantly correlated with medium density urban land use suggesting that land management practices and permitted point source discharges have a significant effect on aquatic DOC concentrations and exports derived from urban watersheds.

DOC transport mechanisms may also be affected in rivers modified by human activities. [Rohlf *et al.* \(2016\)](#) found that flow regulation and diversion changed DOC transport in an upland snowmelt/rainfall system. The upland snow melt stream systems that were not affected by water diversion had DOC concentrations positively correlated with discharge. However, below a large dam this pattern was not evident and below a smaller diversion on a tributary, the pattern was dampened. This study illustrated how impoundment of streams influenced the transport of DOC to downstream reaches.

Allochthonous DOC and ecological processes

There is a growing body of evidence to suggest that allochthonous DOC supply plays a key role in driving ecological process rates and structuring aquatic food webs. One such processes is ecosystem metabolism, which represents the net balance of respiration and photosynthesis occurring within a given system.

Substantial subsidies of allochthonous organic matter from the surrounding catchment can lead to the predominance of net heterotrophy, where respiration exceeds photosynthesis ([Cole *et al.* 2000](#)). The role of allochthonous DOC in driving ecosystem metabolism is increasingly understood for some river systems, though it is less well documented for some areas such as the southern hemisphere.

[Wallace and Furst \(2016\)](#) working in Australia showed that floodplain inundation increased gross primary productivity and ecosystem respiration during the period of return flows. During the floodplain scale watering, differences were observed between sites. Within the managed inundation zone, values for net ecosystem productivity switched from near zero during the baseline to strongly negative during the impact period whereas values at the river sites were either near zero or positive. The results contribute to our understanding of the relative role of allochthonous material in lowland rivers, and demonstrate potential for watering actions to have a positive influence on riverine productivity during periods of low water availability.

Metabolism is influenced in part by the competition between autotrophs and heterotrophs and this can be influenced by resource availability. The influx of allochthonous DOC to an aquatic system can advantage bacterioplankton over phytoplankton because of their smaller surface area to volume ratio allowing them to compete effectively for inorganic nutrients. This process is often complicated in natural environments where turbidity increases with allochthonous carbon inputs, hence reduced light availability also affects phytoplankton and benthic algae. To remove the confounding effect of turbidity, [Carney *et al.* \(2016\)](#) conducted a mesocosm experiment comparing microbial responses to N + P alone and DOC leachate with N + P combined. They found bacterial abundance increased in the leachate addition, whereas chlorophyll-*a* was reduced and the bacterial community shifted to one dominated by heterotrophic genera. Autotrophic microbes including *Synechococcus* and *Cyclotella* increased significantly in the N + P alone treatment. The observations supported the notion that DOC and nutrient inputs can lead to shifts in the competitive dynamics between bacteria and phytoplankton, reducing phytoplankton biomass and shifting the major pathway of carbon to higher trophic organisms from the phytoplankton grazer chain to the microbial food web.

The changes in microbial food structure as a result of allochthonous carbon inputs are suggested to influence higher trophic levels with studies showing substantial subsidies from terrestrial sources in lakes ([Tanentzap *et al.* 2014](#); [Karlsson *et al.* 2015](#)) whereas others argue that autochthonous sources of carbon are the dominant form ([Brett *et al.* 2009](#)). [Roach \(2013\)](#) in a review and meta-analysis of food sources for large rivers using stable isotope data found that algal sources dominated but also found that many consumers did assimilate material from C₃ plants in large rivers with high sediment load and low transparency during high-flow pulses. They also found that terrestrial DOC subsidised consumers in rivers with high DOM concentrations via the microbial loop. [Hitchcock *et al.* \(2016\)](#) demonstrated the complexity of untangling the influence of allochthonous DOC on ecosystems delivered during flows from other concomitant forces. In an estuary in south-east Australia the density of select genera of rotifers, cladocera,

and in the upper estuary copepods, increased following inflows, concurrent with increases in dissolved organic carbon concentration and bacterial biomass and changes in salinity. Redundancy analysis (RDA) indicated that increased DOC with flow events was a strong driver of many zooplankton, whereas others appeared more influenced by changing salinity. Stable isotopes were used to trace the sources of carbon supporting zooplankton biomass showing all tested species were predominantly supported by allochthonous carbon from terrestrial sources. The study highlights the importance of using tracers or biomarkers alongside field observations to understand the importance of allochthonous DOC to ecosystem production.

Management of allochthonous DOC

Given the role of allochthonous DOC in supporting and structuring aquatic ecosystems, there are a wealth of opportunities to incorporate DOC to support process-based river rehabilitation and management (Stanley *et al.* 2012). To build on this interest in allochthonous DOC in management, Baldwin *et al.* (2016) present a review paper on the use of environmental flows to restore allochthonous DOC to lowland river systems. They argue that the apparent lack of importance of terrestrial subsidies to many lowland river food webs may reflect an artefact resulting from historical anthropogenic changes to lowland river–floodplain ecosystems, including the loss of lateral connectivity between rivers and their floodplains, changes in floodplain land use and carbon stores, and loss of sites of transformation within the main channel. They suggest that key biotic targets for environmental flow releases may not be achievable unless river–floodplain subsidies are sufficiently restored. Allochthonous floodplain DOC subsidies to river channels need to be explicitly included in the design and management of environmental flows.

There are also numerous opportunities to achieve a more natural supply of allochthonous DOC in situations where floodplain inundation is not feasible or appropriate. For example, to address the barrier that large dams place on allochthonous DOC transport, protection of water in tributaries below dams has been utilised to deliver increases in DOC (Rohlf *et al.* 2016). This study illustrates how an ecologically valuable tributary function can be addressed and quantified to guide the management and rehabilitation of a regulated river system. Also in lowland river systems, Nielsen *et al.* (2016) suggested only larger floods that result in large volumes of floodplain water returning to the river will provide substantial subsidies of terrestrially derived resources, which gives an indication of the types of flow events that need to be protected. Similarly Robertson *et al.* (2016) suggested piggybacking dam releases on tributary flows to deliver better in-channel flows for more significant benefit for riverine organic matter cycles.

Collectively the papers in this special issue provide a range of interesting perspectives on the role of allochthonous DOC in aquatic systems. They contribute to a growing understanding of the importance of allochthonous DOC in the functioning of aquatic systems as well as the management of allochthonous DOC through mechanisms such as environmental flows. This is especially relevant in the context of climate change, which will cause increased precipitation in many regions of the world (Jones and Lennon 2015) and may lead to higher allochthonous DOC

runoff into aquatic systems. This may have a major effect on biomass, productivity and community composition of microorganisms (Roiha *et al.* 2012).

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References

- Aitkenhead-Peterson, J. A., and Steele, M. K. (2016). Dissolved organic carbon and dissolved organic nitrogen concentrations and exports upstream and downstream of the Dallas–Fort Worth metropolis, Texas, USA. *Marine and Freshwater Research* **67**, 1326–1337. doi:10.1071/MF15280
- Baldwin, D. S., Colloff, M. J., Mitrovic, S. M., Bond, N. R., and Wolfenden, B. (2016). Restoring dissolved organic carbon subsidies from floodplains to lowland river food webs: a role for environmental flows? *Marine and Freshwater Research* **67**, 1387–1399. doi:10.1071/MF15382
- Brett, M. T., Kainz, M. J., Taipale, S. J., and Seshan, H. (2009). Phytoplankton, not allochthonous carbon, sustains herbivorous zooplankton production. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 21197–21201. doi:10.1073/PNAS.0904129106
- Carney, R. L., Seymour, J. R., Westhorpe, D., and Mitrovic, S. M. (2016). Lotic bacterioplankton and phytoplankton community changes under dissolved organic-carbon amendment: evidence for competition for nutrients. *Marine and Freshwater Research* **67**, 1362–1373. doi:10.1071/MF15372
- Cole, J. J., Pace, M. L., Carpenter, S. R., and Kitchell, J. F. (2000). Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. *Limnology and Oceanography* **45**, 1718–1730. doi:10.4319/LO.2000.45.8.1718
- Cole, J. J., Carpenter, S. R., Kitchell, J. F., and Pace, M. L. (2002). Pathways of organic carbon utilization in small lakes: results from a whole-lake ¹³C addition and coupled model. *Limnology and Oceanography* **47**, 1664–1675. doi:10.4319/LO.2002.47.6.1664
- Cole, J. J., Carpenter, S. R., Pace, M. L., Van de Bogert, M. C., Kitchell, J. L., and Hodgson, J. R. (2006). Differential support of lake food webs by three types of terrestrial organic carbon. *Ecology Letters* **9**, 558–568. doi:10.1111/J.1461-0248.2006.00898.X
- Cole, J. J., Carpenter, S. R., Kitchell, J., Pace, M. L., Solomon, C. T., and Weidel, B. (2011). Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 1975–1980. doi:10.1073/PNAS.1012807108
- Hinton, M. J., Schiff, S. L., and English, M. C. (1997). The significance of storms for the concentration and export of dissolved organic carbon from two Precambrian Shield catchments. *Biogeochemistry* **36**, 67–88. doi:10.1023/A:1005779711821
- Hinton, M. J., Schiff, S. L., and English, M. C. (1998). Sources and flowpaths of dissolved organic carbon during storms in two forested watersheds of the Precambrian Shield. *Biogeochemistry* **41**, 175–197. doi:10.1023/A:1005903428956
- Hitchcock, J. N., Mitrovic, S. M., Hadwen, W. L., Grows, I. O., and Rohlf *s*, A. -M. (2016). Zooplankton responses to freshwater inflows and organic-matter pulses in a wave-dominated estuary. *Marine and Freshwater Research* **67**, 1374–1386. doi:10.1071/MF15297
- Jones, S. E., and Lennon, J. T. (2015). A test of the subsidy–stability hypothesis: the effects of terrestrial carbon in aquatic ecosystems. *Ecology* **96**(6), 1550–1560. doi:10.1890/14-1783.1
- Junk, W. J., Bayley, P. B., and Sparks, R. E. (1989). The flood pulse concept in river–floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences* **106**, 110–127.

- Karlsson, J., Bergstrom, A., Bystrom, P., Gudas, C., Rodriguez, P., and Hein, C. (2015). Terrestrial organic matter input suppresses biomass production in lake ecosystems. *Ecology* **96**, 2870–2876. doi:10.1890/15-0515.1
- Miller, R. L., Brown, M. M., and Mulligan, R. P. (2016). Transport and transformation of dissolved organic matter in the Neuse River estuarine system, NC, USA, following Hurricane Irene (2011). *Marine and Freshwater Research* **67**, 1313–1325. doi:10.1071/MF15352
- Nielsen, D. L., Cook, R. A., Ning, N., Gawne, B., and Petrie, R. (2016). Carbon and nutrient subsidies to a lowland river following floodplain inundation. *Marine and Freshwater Research* **67**, 1302–1312. doi:10.1071/MF14390
- Raymond, P. A., and Bauer, J. E. (2000). Bacterial consumption of DOC during transport through a temperate estuary. *Aquatic Microbial Ecology* **22**, 1–12. doi:10.3354/AME022001
- Roach, K. A. (2013). Environmental factors affecting incorporation of terrestrial material into large river food webs. *Freshwater Science* **32**, 283–298. doi:10.1899/12-063.1
- Robertson, A., Burns, A., and Hillman, T. (2016). Scale dependent lateral exchanges of organic carbon in a dryland river during a high flow experiment. *Marine and Freshwater Research* **67**, 1293–1301. doi:10.1071/MF15371
- Rohlf, A. -M., Mitrovic, S. M., Williams, S., and Coleman, D. (2016). Can tributary in-flows improve the recovery of the dissolved organic carbon regime in a snowmelt river regulated by a large reservoir? *Marine and Freshwater Research* **67**, 1338–1345. doi:10.1071/MF14230
- Roiha, T., Tirola, M., Cazzanelli, M., and Rautio, M. (2012). Carbon quantity defines productivity while its quality defines community composition of bacterioplankton in subarctic ponds. *Aquatic Sciences* **74**, 513–525. doi:10.1007/S00027-011-0244-1
- Stanley, E. H., Powers, S. M., Lottig, N. R., Buffam, I., and Crawford, J. T. (2012). Contemporary changes in dissolved organic carbon (DOC) in human-dominated rivers: is there a role for DOC management? *Freshwater Biology* **57**, 26–42. doi:10.1111/J.1365-2427.2011.02613.X
- Tanentzap, A. J., Szkokan-Emilson, E. J., Kielstra, B. W., Arts, M. T., Yan, N. D., and Gunn, J. M. (2014). Forests fuel fish growth in freshwater deltas. *Nature Communications* **5**, 4077. doi:10.1038/NCOMMS5077
- Thorp, J. H., and DeLong, M. D. (1994). The riverine productivity model: a heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos* **70**, 305–308. doi:10.2307/3545642
- Vannote, R., Minshall, G., Cummins, K., Sedell, J., and Cushing, C. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130–137. doi:10.1139/F80-017
- Wallace, T. A., and Furst, D. (2016). Open water metabolism and dissolved organic carbon in response to environmental watering in a lowland river–floodplain complex. *Marine and Freshwater Research* **67**, 1346–1361. doi:10.1071/MF15318
- Westhorpe, D. P., and Mitrovic, S. M. (2012). Dissolved organic carbon mobilisation in relation to variable discharges and environmental flows in a highly regulated lowland river. *Marine and Freshwater Research* **63**, 1218–1230. doi:10.1071/MF12122
- Wiegner, T. N., Kaplan, L. A., Ziegler, S. E., and Findlay, R. H. (2015). Consumption of terrestrial dissolved organic carbon by stream microorganisms. *Aquatic Microbial Ecology* **75**, 225–237. doi:10.3354/AME01761
- Wilson, H. F., Raymond, P. A., Saiers, J. E., Sobczak, W. V., and Xu, N. (2016). Increases in humic and bioavailable dissolved organic matter in a forested New England headwater stream with increasing discharge. *Marine and Freshwater Research* **67**, 1279–1292. doi:10.1071/MF15286