

Review Article

Expanding the concept of trophic state in aquatic ecosystems: It's not just the autotrophs

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Abstract. “Trophic state” is often used to classify aquatic ecosystems according to biotic productivity. Primary productivity (or a surrogate for it) has always been used as the metric of trophic state. We make the case here that both primary production and key heterotrophic processes are needed to evaluate trophic state. Defined as the relative flux rate of carbon (C) into the food web, trophic state is a fundamental property that is intimately related to both ecosystem structure and how humans influence water quality. Rates of heterotrophic activity can exceed primary production in many aquatic ecosystems including oceans, lakes, and streams. A comprehensive definition of trophic state with respect to aquatic food webs requires accounting for both the oxidation of organic C (respiration) and photosynthetic fixation of inorganic C (primary production). This inclusive defini-

tion is required because food webs can be fueled in part by allochthonous C. We propose autotrophic and heterotrophic states be defined by rates of photosynthetic and respiratory C fluxes respectively, and both be used to characterize ecosystems. Cumulative frequency distributions of both can be developed for minimally impacted aquatic systems as a baseline against which to compare human-influenced sites as well as for describing the range of conditions that aquatic organisms have experienced in their recent evolutionary history. Subsidies of organic C and inorganic nutrients to aquatic ecosystems influence heterotrophic state, so characterizing the base of the food web necessitates a stoichiometric view of supply rates, use efficiencies, and recycling of inorganic and organic materials.

Key words. Trophic state; heterotrophic; autotrophic; ecosystem.

Introduction

The word “trophic” signifies nourishment. Nourishment in ecological terms can be considered the primary source of food at the base of the food web (Lindeman, 1942). When Naumann (as cited in Hutchinson, 1967) in the early 20th century first

applied the concept of “trophic state” to aquatic ecosystems and used the terms “oligotrophic” and “eutrophic”, he envisaged this nourishment as the supply of organic matter from autochthonous primary production (e.g. primary production occurring within the aquatic system) stimulated by input of nitrogen and phosphorus. In fact, this nourishment can include the organic carbon (C) supply to ecosystems from outside the system’s boundaries (allochthonous supply). Thus, trophic state is a fundamental property of ecosystems because it describes the potential food

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base (Odum, 1956). Characterization of trophic state in aquatic ecosystems is necessary for understanding food web linkages as well as biogeochemical features and subsequently water quality (Smith, 2003).

Describing the reference or native (minimally impacted by human) conditions of aquatic ecosystems with regard to C fluxes indicates the range of habitats in which aquatic organisms evolved. A reference distribution of trophic state also provides a baseline against which to measure biotic integrity and a point of comparison for efforts to document and manage human influences, as well as providing a goal for restoration efforts. Thus, a comprehensive definition of trophic state and description of the natural distribution of trophic states has basic and applied implications for ecological and environmental sciences.

The greatest efforts of ecologists to define trophic state have been associated with research on the control of cultural eutrophication (increase in the autotrophic state caused by humans) of lakes (e.g., Vollenweider, 1968; Nürnberg, 1996; Schindler, 2006). These efforts have focused mostly on primary production, indirectly indicated by the amounts of planktonic chlorophyll, degree of water transparency, and total mass of nutrients in lake water columns (Carlson, 1977; OECD, 1982). These variables are useful determinants of one aspect of trophic state of lakes because they are directly or indirectly related to one potentially key C source: autochthonous inputs. That is, nutrients are positively correlated with chlorophyll concentration, which is in turn positively correlated with photosynthetic rate. Further, these indices help determine the probability of noxious algal blooms that harm water quality. The classification system of autotrophic state in lakes has formed the basis of tremendously successful management programs in lakes and reservoirs; we hope to expand this useful classification system to more general applications.

With progressively increasing nutrient input (Howarth et al., 1996) and greater eutrophication in estuaries (e.g. Pinckney et al., 2001; Howarth and Marino; 2006 Smith, 2006) and other coastal waters (e.g. Rabalais et al., 2002; Berman et al., 2005), there has been expanded interest in examining the roles of nutrients that limit primary production in aquatic ecosystems. On the other hand, attention focused solely on photosynthetic C sources misses the important trophic fluxes dominated by heterotrophic pathways, an important aspect of ecosystem structure as well as function.

The external loading of organic C from allochthonous sources often exceeds autochthonous primary production in aquatic systems. The common conceptual model of stream ecosystems, the River Continu-

um Concept (Vannote et al., 1980), clearly delineates the importance of allochthonous and autochthonous C sources (Caraco and Cole, 2004). This dominance of allochthonous sources allows total respiration to exceed gross primary production, an effect that has not only been demonstrated in streams (Mulholland et al., 2001), but also lakes (Cole et al., 2000; Pace and Prairie, 2005), estuaries (Cole et al., 1992), rivers (Kempe, 1982; Cole and Caraco, 2001; Richey et al., 2002) and oligotrophic portions of the ocean (del Giorgio et al., 1997; Hoppe et al., 2002; Agustí and Duarte, 2005). While these reports may be somewhat limited in scope relative to the sheer numbers of streams, lakes, and other aquatic habitats, Caraco and Cole (2004) report net heterotrophy based on CO₂ supersaturation from samples of 85 rivers and 2000 lakes. Furthermore, the linkage of the microbial loop to upper levels of the food web in pelagic systems has been established, and phytoplankton biomass only explains about 20% of bacterial production rates in lakes (Kalf, 2002). Heterotrophy has implications for carbon flux to the entire food web, and food web and ecosystem stability may be enhanced by reliance on allochthonous carbon sources (Wetzel, 1995).

This under-appreciated importance of allochthonous inputs in lakes and oceans leads us to think that a traditional definition of trophic state based solely on autotrophic production (i.e., what most ecologists are referring to when they say a system is "oligotrophic" or "eutrophic") may not adequately characterize carbon sources in aquatic systems. The focus on the balance of allotrophy (*sensu*, Wetzel, 2001) or autotrophy in streams masks the total flux rates of the processes considered individually (trophic state). Traditional definitions of trophic state are stymied, for example, in turbid reservoirs where external carbon loading adsorbed to sediments can drive a productive food web in the absence of substantial photosynthetic activity (Arruda et al., 1983); similar conditions can occur in turbid and highly productive estuaries (Cole et al., 1992). Given this duality of carbon sources, Dodds (2006) suggested that trophic state should distinguish between heterotrophic and autotrophic condition in rivers and streams.

The purpose of this paper is to explore how the distinction of trophic state applies across aquatic ecosystems, as well as similarities and dissimilarities across systems with regard to factors that may influence the reference trophic states. We begin with a conceptual basis and definitions of trophic state, explore how to characterize distributions of trophic state, and describe some factors that may influence trophic state. Finally, we argue that a stoichiometric view of inorganic and organic nutrient supply is necessary to adequately characterize aquatic ecosystems.

Definitions and concepts

We define heterotrophic state as area-normalized gross carbon oxidation indicated by the total production of carbon dioxide from respiration. Total respiration (R) is the sum of the respiration of all autotrophs (R_a) and all heterotrophs (R_n) and can be directly compared to gross primary production, GPP (see Cole, 1999). For R we use the area-normalized rate of carbon dioxide production averaged across at least a 24-hour period.

The value of R determined by carbon dioxide flux rate includes oxic respiration, anoxic respiration (e.g., denitrification, dissimilatory sulfur reduction), and part of fermentation. Some of the energy producing reactions of fermentation do not yield carbon dioxide, but for our purposes, we assume that this is a relatively minor part of the heterotrophic activity of an ecosystem with the caveat that this generalization may not hold for some habitats. Defining respiration as carbon dioxide production rather than oxygen consumption at least accounts for a substantial portion of anaerobic metabolism, but in practical terms dissolved oxygen dynamics are often used to estimate ecosystem metabolism. Other methods of determining heterotrophic activity (e.g., bacterial counts, thymidine or leucine uptake, enzyme assays, ergosterol contents) are difficult to scale to whole-ecosystem rates and often cannot be compared consistently across ecosystems. Further, these microbial methods miss entirely the respiratory contribution of metazoans which can be significant in some ecosystems (Cole et al., 1988). For these reasons, we focus here on whole-system accounting of metabolism using dissolved oxygen or carbon dioxide, accepting that the metric is imperfect.

Autotrophic state is the area-normalized gross carbon fixation rate (gross primary production, or GPP) over at least a 24-hour period. While a minimum of 24 hours is required to control for light and dark periods, annual means will control for seasonal effects and are probably the best characteristic to define aquatic ecosystems (Wetzel, 2001). Detailed annual measures of respiration and photosynthetic rate are difficult to perform and rarely reported. Trophic state usually is based on several measurements across a season of interest. For example, trophic state of lakes is often measured for the epilimnion during the time of summer stratification.

Rates of GPP can be inferred from the production of dissolved oxygen under many conditions. Oxygen-derived rates of GPP will be in error in a few systems such as deep-sea hydrothermal vents in which the fixation of inorganic C depends on the chemoautotrophic oxidation of reduced inorganic compounds. For R , dissolved oxygen can be used to infer rates

when anaerobic metabolism is negligible, which will be true for many surface waters.

Our separation of autotrophic state and heterotrophic state is not new. Odum (1956) plotted GPP against R and suggested that aquatic ecosystems could be classified as hetero-oligotrophic, auto-eutrophic, etc. What is new since Odum's treatment is that systems that were previously thought to be predominantly net autotrophic (oceans, unpolluted open streams, many lakes) can be, and often are, net heterotrophic. Odum's suggestions for classification have been mostly ignored in the half century since they were published. Stream biologists have focused on a dichotomy (a stream is either autotrophic or heterotrophic), but many have not considered autotrophic and heterotrophic states independently. The main emphasis in lakes has been on autotrophic state and "trophic state" of a lake generally does not reference the allochthonous inputs. Functionally, most marine scientists have also focused on autotrophic production. A comprehensive system of trophic characterization would emphasize both autotrophic and heterotrophic state across all ecosystem types.

Autotrophic and heterotrophic states are obviously linked to allotrophic and autotrophic supply rates (Table 1). With these definitions, there are two ways to think about trophic state. First, we can use it to characterize the net rate of accumulation or consumption of carbon in an ecosystem by the biotic components. Second, we can establish the rate of supply of organic carbon to the food web. The reason that these two are distinct is that with external carbon subsidies the heterotrophic component can fuel the food web, but this source to the food web is indirectly accounted for using net carbon production or consumption.

Table 1. Potential autotrophic and eutrophic states, and the separation of autotrophic and heterotrophic states based on autochthonous and allochthonous inputs. Note that greater rates of allochthonous inputs often preclude autotrophic production because of light limitation. A system with high rates of autotrophic production must have correspondingly greater heterotrophic activity unless autochthonous production is removed from the system and not available to heterotrophs.

	Low Allochthonous	High Allochthonous
Low Autotrophy	Oligo-autotrophic Oligo-heterotrophic	Oligo-autotrophic Eu-heterotrophic (dystrophic)
High Autotrophy	Eu- autotrophic Eu-heterotrophic	Eu- autotrophic Eu-heterotrophic

To characterize the net accumulation or consumption of organic carbon by the biotic components in an ecosystem, the energy budget for the autotrophic

activities in an ecosystem is characterized by the commonly used (e.g. Cole et al., 2000; Lovett et al., 2006) expression:

$$\text{NEP} = \text{GPP} - \text{R} \quad (1)$$

where NEP is net ecosystem production due to autotrophs in the ecosystem less losses mediated by organisms (respiration). Organic carbon can be imported to the system from outside (I) as allochthonous carbon input. Organic carbon that originated from primary production (GPP) within the system is termed autochthonous carbon production.

Since inputs must balance outputs, it follows that to account for all organic C in a system,

$$\text{NEP} + \text{I} = \text{E} + \text{S} \quad (2)$$

because NEP has only two possible fates: export (E) from the system or storage (S) as detritus or biomass within the system. Storage also includes terms such as the burial of organic carbon. Storage includes organic carbon that enters the food web produced by photosynthesis within the system or imported and subsequently converted into heterotrophic biomass. The acquisition of non-living organic carbon by organisms can also be viewed as a form of production, so:

$$\text{S} = \text{S}_h + \text{S}_a + \text{S}_{\text{other}} \quad (3)$$

where S_h is the net secondary production of organisms in the system, including that of primary and higher level consumers and that of detritivores, and S_a is the accumulated biomass of autotrophs. S_{other} is the burial or other forms of storage of organic material. The two forms, S_h and S_a , generally have much more rapid rates of turnover than S_{other} , but to fully account for C, all three must be considered. A major point of this paper revolves around the idea that the portion of S_h accounted for by detritivory indicates a potential pathway of C into the ecosystem's food web in addition to that in NEP.

Thus, both heterotrophic and autotrophic states are necessary to define ecosystem carbon flux. NEP or GPP/R alone indicates whether the ecosystem is a net synthesizer or net oxidizer of organic carbon (C), but these metrics do not completely portray trophic state. For example, NEP could be close to 0 in both an ultra-oligotrophic system where GPP and R are very low and it could also be close to zero in a very eutrophic lake where C is recycled very efficiently. A specific example of why trophic state measurements need to account for both GPP and R comes from studies of large river metabolism. While the large rivers and estuaries have an NEP that is less than 1, much of the

secondary productivity of the food web can be based upon GPP, not consumption of C by heterotrophic organisms (Hamilton et al., 1992; Thorp and DeLong, 2004; Martineau et al., 2004).

Net Primary Production (NPP) is a term widely used in the literature that is sometimes confused with NEP. In fact,

$$\text{NPP} = \text{GPP} - \text{R}_a \quad (4)$$

where R_a is autotrophic respiration. NPP is the amount of material photosynthesized by a plant which is potentially available to consumers. NPP may be the most useful concept in systems dominated by vascular plants where the plants can be harvested and measured as an estimate of NPP. The concept is less useful for algae that turn over more rapidly. While we will not refer further to NPP, it can be related to NEP in a closed system as:

$$\text{NEP} = \text{NPP} - \text{R}_h \quad (5)$$

Metabolic rate measurements to estimate heterotrophic and autotrophic states are, for the purposes of this paper, made only in the water. Considering rates in the water alone excludes emergent and floating vegetation in wetlands, rivers, estuaries and shallow lakes. Such systems may have a very strong autotrophic state if emergent vegetation is included, but not if it is excluded. It is difficult to draw a clear line between allochthonous (outside the system) and autochthonous (from within the system) production in aquatic systems if emergent vegetation is included with autochthonous production. Furthermore, biogeochemical effects within the water are directly influenced by changes in dissolved oxygen concentrations. Dissolved oxygen concentrations are poorly correlated with photosynthetic oxygen production by plants with leaves in the atmosphere above the aquatic habitat (see Caraco and Cole, 2002). Carbon input from emergent vegetation then becomes part of term I in equation 2.

Defining the boundaries of aquatic systems with regard to what should be included in the water relative to areal estimates of metabolic rate can be difficult. For example, if the hyporheic zone (the zone where groundwater interacts with surface water) is included in metabolism measurements for streams, rates of whole-system respiration can be higher (e.g., Mulholland et al., 1997; Fellows et al., 2001). In the open ocean, a true accounting of areal metabolic rate could include the entire water column to thousands of meters of depth. However, the deep water could only mix with the photic zone of the upper water column over time scales of thousands of years.

We suggest that the characterization of trophic state explicitly consider spatial and temporal scales, such that a specific ecosystem area is delineated by portions of the aquatic environment that have a chemical influence on the waters of interest over ecologically relevant timescales. Thus, the hyporheic zone in a stream or the shallow groundwater below a wetland or in lake sediments would be included because respiration in all these areas can influence dissolved oxygen and organic C concentrations in the water column above. The hypolimnion of a mictic lake would be included on an annual basis because it mixes with the surface waters at least once a year. The epilimnion or hypolimnion may be considered separately during periods of stratification if the organisms of interest have multiple generations during the period of stratification. Thus, the definition of trophic state in lakes would depend upon the timescale of interest; hypolimnetic respiration is substantial on an annual basis but less relevant during the period of summer stratification. Lake scientists already commonly use this approach to define autotrophic state; they base the state upon nutrient and chlorophyll concentration means over the period of summer stratification. The profundal zone of the open ocean and the hypolimnion of amictic lakes would not be included as part of the photic (lighted) zone because they are functionally separate from the water column above except over very long time periods (they are influenced by the water column above but have little influence on it on an annual basis or less).

Given the delineations of heterotrophic and autotrophic state, further accounting is required to establish controlling factors and the rate that C enters the food web. In systems where light reaches the bottom, benthic as well as planktonic production can be important.

$$GPP = GPP_{\text{plankton}} + GPP_{\text{benthic}} \quad (6)$$

Where GPP_{plankton} = planktonic primary production, and GPP_{benthic} = production of the periphyton (microphytobenthos) and macrophytes. This would include production by zooxanthellae in coral reefs and kelps in other shallow marine habitats. The importance of GPP_{benthic} probably has been vastly underestimated in lakes and shallow marine systems (Wetzel, 2001; Santos et al., 2004; Vadeboncoeur et al., 2006), and may even tip the NEP to values greater than 0 in some lakes (Andersson and Brunberg, 2006).

Heterotrophic state is determined by the source of C and the rates of assimilation (A) and growth (G). Any C that is assimilated, but does not go to growth, is respired.

$$R_h = A - G \quad (7)$$

In general, allochthonous inputs are thought to be more recalcitrant than autochthonous inputs because they already have been processed by heterotrophs and terrestrial plants tend to synthesize compounds that are more difficult to metabolize than those produced by aquatic primary producers (Wetzel, 2001). While R_h decreases NEP, it also reflects (depending upon A/G) the rate of C supply into the food web via heterotrophic processing of allochthonous inputs. We recognize that using R to indicate relative heterotrophic state assumes that A/G is fairly constant across systems. However, there are numerous technical problems with determining how much C enters many food webs, particularly when considering systems with high rates of allochthonous input (e.g., leaves in streams). Though imperfect, R is probably the best relative indicator of heterotrophic state across a wide range of systems and states.

The definitions presented in this section allow explicit description of the rate of C flux in ecosystems. Careful consideration of spatial (e.g., hypolimnion versus epilimnion) linkages within aquatic environments as well as temporal characteristics (e.g., seasonal trophic state may differ from annual accounting) is necessary when characterizing autotrophic and heterotrophic state. In other words, if a publication only states that a lake is oligotrophic, it can mean several things. It probably means that during summer in the epilimnion, chlorophyll and nutrient concentrations are less than most other lakes and transparency is greater. It is not possible to infer that this system is also oligo-heterotrophic. Thus, we are arguing for more complete characterization of C fluxes in aquatic ecosystems.

Given the distinction between heterotrophic and autotrophic state, eutrophication can be defined as an increase in the nutritive factor or factors that leads to greater rates of whole-system heterotrophic or autotrophic metabolism (Dodds, 2006). The process of eutrophication can be natural or cultural. This broader definition of eutrophication accounts for increases in C loading to systems and nutrients that may alter GPP as well as R of an ecosystem. For example, a system that received organic C loading from sewage, but due to water color or turbidity had very little sunlight, would be characterized by a eu-heterotrophic state and an oligo-autotrophic state. This system of definition in essence provides a more complete stoichiometric accounting of ecosystem structure than simply considering trophic state based on GPP. So how should scientists characterize the possible range of autotrophic and heterotrophic states?

Characterizing trophic state

Many ecologists use three basic categories of trophic state (oligotrophic, mesotrophic, and eutrophic) to describe the distribution of trophic states. These categories can be expanded to indicate the tails of the distribution (ultraoligotrophic, hypertrophic) and subdivided (e.g., oligo-mesotrophic, meso-eutrophic). So how do aquatic systems and autotrophic and heterotrophic states fit into this terminology?

Autotrophic state has been well characterized in lakes. Carlson (1977) viewed lakes as a continuum of trophic states and proposed a trophic index for lakes that would characterize autotrophic state on a logarithmic scale with regard to chlorophyll, Secchi depth, total N and total P. This approach has the strength of capturing the wide variety of autotrophic states on a numerical scale. The disadvantage is that it does not describe the natural distribution of trophic states (though they may be distributed logarithmically). The three basic trophic states have been defined with regard to distributions (OECD, 1982) of nutrients, chlorophyll and transparency in lakes in each type of category, and with boundaries that delineate the categories (Nürnberg, 1996). In general, these schemes allow categorization of lakes, but they are mostly based on subjective initial criteria (e.g., the OECD oligotrophic characteristics are based on data from lakes that were qualitatively assigned to the category of oligotrophic lakes). The original OECD (1982) report recognized the utility of trophic categories as well as their qualitative nature.

A more quantitative method for characterizing the trophic state of aquatic systems has been proposed for streams based on observed data distributions (Dodds et al., 1998). In this method, cumulative frequency distribution is plotted and oligotrophic systems are those in the bottom third of the distribution, mesotrophic in the middle third and eutrophic in the top third. This method has the benefit of describing the distribution of trophic states based upon their relative occurrence. The method is also non-parametric (i.e., does not depend on the shape of the distribution). More categories could be used (e.g., quartiles), but three categories are consistent with ecological convention and terminology. One disadvantage with this approach is that the bottom third of the frequency distribution may contain systems that are not pristine. A second disadvantage is that natural boundaries between trophic states (e.g., the presence or absence of cyanobacterial blooms) are not included in the system. There may be multi-modal distributions of trophic state (Peckham et al., 2006) that the cumulative frequency distribution may miss. Good judgment of the researchers is still required.

We suggest adopting the cumulative frequency approach to delineating reference trophic states for several reasons. First, it is non-parametric, so scaling is based on the proportion of the aquatic habitat of interest at a certain level, not an *a priori* assumption of how trophic conditions should be apportioned. Stated alternatively, there is no *a priori* assumption of the functional relationship between abundances of different trophic states. Not making this assumption is important because, for example, in some cases frequency distributions of trophic state may be multi-modal and reveal alternate stable states of the aquatic ecosystems (Peckham et al., 2006). Second, cumulative frequency distributions can be broken into any proportion of the distribution desired (i.e., thirds or tenths). Third, the method can be applied to accommodate the fact that there may be different natural distributions of trophic state in different regions or with different subpopulations of systems. Finally, the cumulative frequency method can be used to assign a probability that a specific trophic state will occur.

The first step in characterizing the distribution of trophic states of an ecosystem type should be identification of reference or relatively pristine conditions. Determination of reference is necessary because the degree of human influences can vary widely, and considering human-influenced systems provides a moving target for defining trophic state distributions. A reference approach has been proposed for rivers and streams (Dodds, 2006), and it should not be difficult to extend to other aquatic systems. A potential problem arises when there are few or no reference systems left to construct a reference trophic distribution. For example, temperate estuaries are almost all heavily influenced by human activities, so how can we define a reference distribution of trophic state? It is possible to use historic (paleolimnological) records (occasionally created for lakes or coastal marine systems) or statistical methods to remove the effects of humans, as has been done for lotic systems (Dodds and Oakes, 2004). Paleolimnological approaches are limited to systems where good records of past conditions are preserved and the statistical method is an extrapolation and may be plagued by high variance.

There is far less information available to assess reference trophic state in estuaries compared to lakes, streams and the open ocean. One potential method for determining reference state of estuaries would be extrapolation to remove the effect of human uses. There are significant positive relationships between population density in a watershed and the rate of loading ($\text{kg}/\text{m}^2/\text{y}$) of nitrate and dissolved N (Caraco and Cole, 1999), and a good relationship between N and phytoplankton biomass (Rizzo et al., 1996; Paerl,

1997; Cloern, 2001; Smith, 2006). The predicted fluxes for low human population density, and watershed-scaled fluxes could be coupled with physical models of estuaries to construct an expected heterotrophic and autotrophic state in the absence of human impacts.

A cumulative frequency diagram of trophic state at a global scale, where each aquatic habitat is sampled relative to its surface area, could be created. In this case, the open ocean would vastly dominate the distribution, and autotrophic and heterotrophic states would be dominated by distribution of rates of C cycling not applicable to habitats such as estuaries, dystrophic lakes, or small streams under dense canopy cover. If respiration is summed over the entire water column of a deep area of open ocean, rates of R could be higher than many other habitats.

A global distribution of trophic states is unlikely to be useful for most applications. Thus, aquatic habitat types can be broken down into their more traditionally studied units (e.g., algal beds and reefs, coastal upwelling zones, estuaries, lakes, rivers and streams, freshwater wetlands), and even more regional units (e.g., prairie streams, temperate estuaries). Cumulative frequency distributions for reference states of rivers and streams in the United States have been produced (Dodds, 2006). Such distributions do not exist yet for lakes and marine environments. The more local the distribution data set, the more useful it will be to managers and scientists concerned with specific ecosystems within a region.

We make a preliminary comparison of autotrophic and heterotrophic state of streams and the open ocean to provide an idea of the range of trophic state distributions that may be expected. Given the limited number of data points and the geographic limitations of available data, the shapes of these distributions should not be over-interpreted. Streams are the most influenced by terrestrial processes (both canopy of riparian vegetation and dissolved organic C in runoff from land); open oceans, the least. Streams are also systems with very rapid rates of hydrologic exchange (minutes to hours), whereas large areas of the photic zone in the open ocean are stable for days or much longer. Mulholland et al. (2001) and Webster and Meyer (1997) described metabolic rates determined with daily measurements of dissolved oxygen dynamics measured over 24 hour periods from 19 reference streams across a variety of biomes, including forested (coniferous, temperate deciduous, and tropical), prairie, and desert streams. These studies directly measured aeration rates, a very important variable affecting primary production measurements made with gas methods. Such estimates are often estimated indirectly. While none of these streams were free of human impacts, the impacts on them were less than experi-

enced by most streams. Hanson et al. (2003) published metabolic data from 25 lakes in the north-central United States across a range of trophic states determined using both dissolved oxygen and carbon dioxide methods and demonstrated that both methods were comparable. These lakes were not reference lakes, so the trophic distributions should not be considered baseline natural distributions. Serret et al. (2002) provided their own results and those from 17 other cruises where metabolic rates from transects from a largely unimpacted part of the open ocean (eastern North Atlantic) were measured (derived from 24-hour dissolved oxygen incubations). These ocean transects ranged from open ocean gyres to relatively near coastal areas, from the tropics to the arctic, across regions with chlorophyll concentrations from 1 $\mu\text{g/L}$ to those with less than 0.05 $\mu\text{g/L}$. Given the ocean incubations were for 24 hours each, these measurements should not be assumed to be annual production rates reflective of pristine ocean.

Not surprisingly, many of the streams are net heterotrophic ($\text{GPP/R} < 1$ in more than two-thirds of the sites). If we assume that $R_a = 0.5 \text{ GPP}$ (Webster et al. (2003) used a value of 0.3, but we used a more conservative value of 0.5), many sites across all three habitats had measured heterotrophic respiratory rates greater than autotrophic respiration $R_h \gg R_a$ (Table 2, Fig. 1). When all these sites are considered, most lake, stream and ocean sites were net respiratory as well (median $\text{GPP/R} < 1$; Fig. 2). While median GPP/R in the open ocean was slightly greater than 1, almost half the sites had a $\text{GPP/R} < 1$ (Table 2).

Median GPP was less in streams than in the open ocean, although the maximum in streams exceeded that for the ocean sites. Relative ranges of R were greater in the open ocean, but the median values of R were higher in streams. Some of these patterns may be considered surprising, given the heavy terrestrial influence on streams and the widely variable rates of C cycling of terrestrial vegetation across biomes. Respiratory rate of streams could be relatively more variable than in the ocean. Much more data are necessary to solidify these comparisons, but they are provocative. When compared to the original data plotted by Odum (1956), heterotrophy is much more common than he reported for fewer sites (Fig. 2)

Aquatic systems are expected to vary widely across the range of trophic states. Groundwaters have a low autotrophic state, with chemoautotrophy the only possible autochthonous source. Oligo-heterotrophic groundwaters have among the lowest respiration rates ever documented for aquatic ecosystems (Dodds, 2002). On the other side of the spectrum, highly nutrient-rich lakes, such as many hypersaline lakes, naturally have relatively rapid primary production

Table 2. Distributions of gross autotrophic state (GPP) and respiratory state (R) for the open ocean, lakes, and streams. Mean values taken from literature were used as reported in Serret et al. (2002) in 18 studies for oceans, Mulholland et al. (2001), Mulholland (personal communication) and Webster and Meyer (1997) for 19 studies in pristine streams across North America, and Hanson et al. (2003) for 25 lakes in Michigan and Wisconsin of a variety of trophic states. Rates are in $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$. The sample sizes are small and the lake and ocean data are not corrected for human influences so these data should not be taken to represent reference trophic states.

Habitat	Parameter	Median	Minimum	Maximum	Lower 1/3 boundary	Upper 1/3 boundary
Pristine streams	GPP	25	1.6	469	6.25	37.5
Pristine streams	R	205	47	906	119	243
Pristine streams	GPP/R	0.22	0.002	2.66	0.19	0.63
Lakes	GPP	30	3	144	13	34
Lakes	R	42	6	146	35	46
Lakes	GPP/R	0.76	0.09	1.39	0.68	0.90
Open ocean	GPP	74	15	329	42	94
Open ocean	R	112	30	202	72	120
Open ocean	GPP/R	1.02	0.20	2.33	0.67	1.38

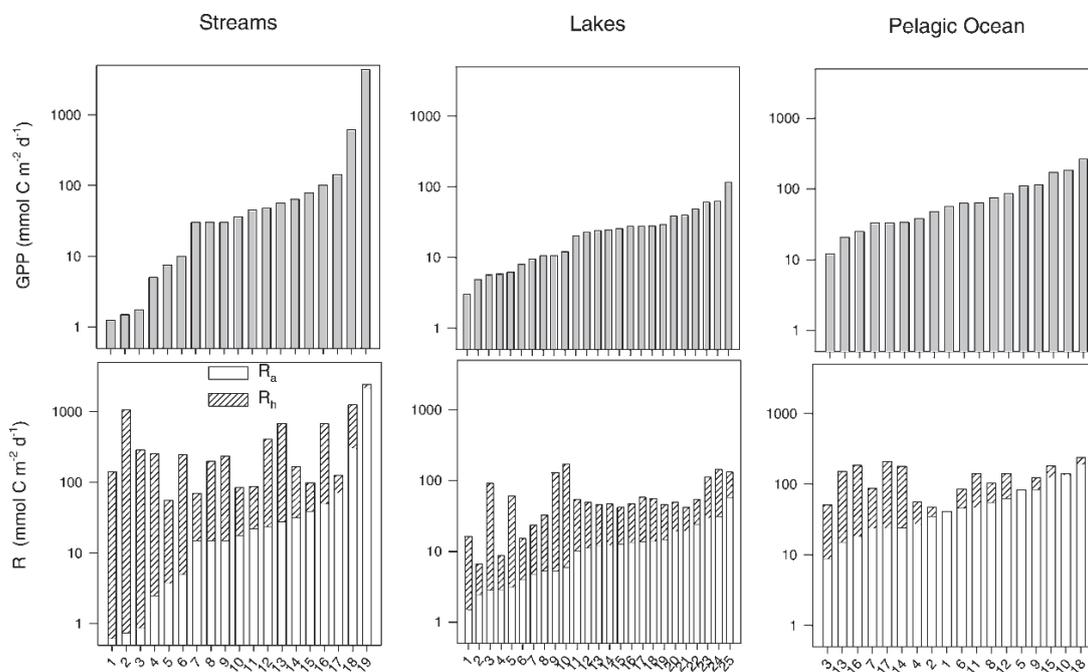


Figure 1. Relationships between gross primary production (GPP), autotrophic respiration (R_a), and heterotrophic respiration (R_h). Data from the same sources as listed in Table 1. R_a is calculated as half of GPP. Note the log scale in the respiration plots can make it seem that R_a exceeds R_h when this is not always the case. Stream labels are 1) Ball Creek 1, 2) Ball Creek 2, 3) Q. Bisley, 4) Bear Brook, 5) Walker Branch, 6) Gallina Creek, 7) W branch 2, 8) W branch 3, 9) Eagle Creek, 10) Dev. Club Creek, 11) Kings Creek, 12) Mack Creek 2, 13) Creeping Swamp, 14) Mackenzie River, 15) Mack Creek, 16) WS10 stream, 17) Lookout Creek, 18) Fort River, 19) Deep Creek. Lake labels are 1) Crampton, 2) Crystal, 3) Northgate Bog, 4) Trout Lake, 5) Helmet, 6) Diamond, 7) Big Muskellunge, 8) Hiawatha, 9) Reddington, 10) Hummingbird, 11) East Long, 12) Plum, 13) West Long, 14) Tenderfoot, 15) Ward, 16) Allequash, 17) Cranberry Bog, 18) Mary, 19) Brown, 20) Muskellunge, 21) Trout Bog, 22) Peter, 23) Bog Pot, 24) Kickapoo, 25) Little Arbor Vitae. Marine data are listed by transect number from the original publication.

and correspondingly are eu-heterotrophic and eu-autotrophic. The positive correlation between numbers of active bacteria and chlorophyll concentration in lakes and marine habitats (del Giorgio and Scarborough, 1995; Kalff, 2002) illustrates how autotrophic state and heterotrophic state can be linked and organic C can move up the food web through the microbial loop. A wetland with very colored water may be in an oligo-autotrophic state, but eu-heterotrophic due to influx of organic materials from emergent vegetation.

One important observation is that while any volume of water in the open ocean generally has slow rates of metabolism, summing across the photic zone leads to areal numbers for gross primary production that are roughly similar to those found in small streams where benthic production dominates and in lakes that are moderately eutrophic (Fig. 1). This similarity is because the photic zone in the open ocean is much deeper in lakes and each unit area of ocean has a large volume of photosynthetically active water below it. The equalization of metabolic rates

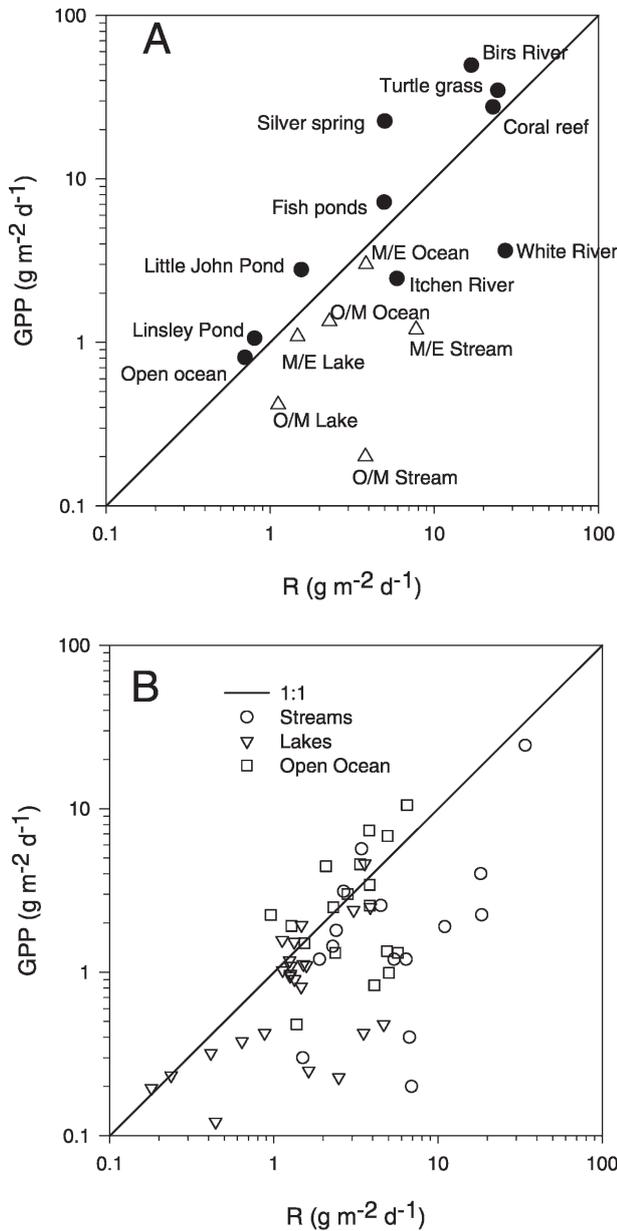


Figure 2. (A) Data from Table 2 (open symbols) plotted against the original data published by Odum (1956) comparing respiration (R) and gross primary production (GPP) across ecosystem types and (B) data from figure 1 plotted in similar format as in panel A.

when expressed per unit area is consistent with analysis of respiration rates in lakes and oceans (del Giorgio and Williams, 2005).

When the data are plotted by increasing GPP within each habitat (Fig. 1), the values of R do not necessarily follow the same distribution. This is especially true if R_a is removed from R. In general, systems with a small GPP have a relatively larger R_h , consistent with the observations of Duarte and Agusti (1998). This analysis highlights two areas where significant research is still needed. First, we assumed

that R_a is 0.5 GPP, and this could be highly variable depending upon organisms and environment. Few data have been published on autotrophic respiration in the natural environment. Second, the degree to which R_h reflects the amount of C entering the foodweb from allochthonous sources depends upon the bioavailability of C and the assimilation and growth efficiencies of heterotrophic organisms. This is also an area where few data have been published from natural ecosystems and additional research is needed. Still, the decoupling of R and GPP strengthens the argument that heterotrophic state and autotrophic state should be considered separately and opens the question of what factors determine both states.

Factors controlling trophic state

A variety of factors may influence autotrophic and heterotrophic state and these may vary across systems. In general, light, nutrients, and sometimes food web structure and disturbance influence autotrophic state. Regulation of heterotrophic state can be coupled to inputs of external C. Other factors are less well known, but all of the above factors may play a role. Light may even be important to heterotrophic state because photolysis can make organic C more bioavailable (Lindell et al., 1995).

Many factors may influence heterotrophic and autotrophic state, but a comprehensive review of these factors is beyond the scope of this paper. In practical terms, humans have the greatest influence on trophic state through alteration of nutrients and light entering aquatic ecosystems, so these are concentrated on in this review, but focusing on other factors could be important. For example, abiotic disturbances can play a role in autotrophic and heterotrophic state (Young and Huryn, 1996; Uehlinger 2000), particularly in streams where flooding can alter autotrophic state and this could influence models used to link autotrophic state (chlorophyll) to nutrients (e.g., Biggs, 2000). Top-down control (cascading food web effects) can also influence the relative balance of heterotrophic and autotrophic state (Schindler et al., 1997; Cole et al., 2000). We concentrate here on light and nutrients because of their current relevance to management and pollution in aquatic ecosystems.

Nutrient bioassays are commonly employed to estimate the response of primary producers to nutrient additions. While there has not been any systematic sampling of aquatic habitats over broad scales that we are aware of (i.e., no spatially-weighted randomly stratified sampling designs), and not all nutrients are tested in all habitats, the results of these bioassays indicate the importance of nutrients in primary production (Fig. 3). First, N stimulates autotrophic production across all habitats in at least some cases.

Second, iron, silicon, and potassium are important in some cases, but not across all habitats (but were not tested in all habitats either). For example, iron limitation is only commonly reported in the open ocean (e.g., the southern ocean, high-N low chlorophyll areas; de Baar et al., 2005), but this could be the only habitat it is routinely tested in. Third, P is second in importance across habitats to N. Fourth, colimitation of autotrophic production is a feature that can occur in any habitat. Finally, if other elements were strongly limiting, there would be no N and P response, so the common N and P response indicates other nutrients could be less frequently limiting.

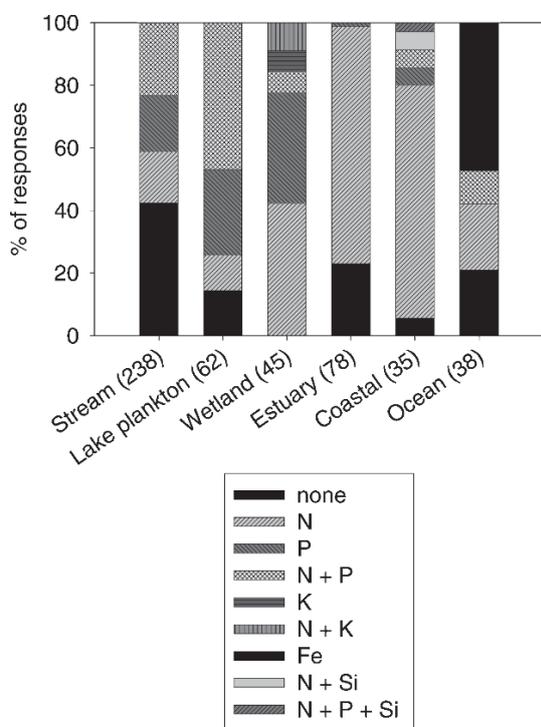


Figure 3. Results from nutrient enrichment bioassays of primary producer growth across aquatic habitats. Data for streams, lakes and wetlands compiled by Dodds (2002) and from marine systems by Downing et al. (1999). Total number of bioassays performed is given in parentheses following the habitat type in the x-axis label. Not all combinations of nutrients were tested in all experiments, but most at least had fully factorial designs for N and P (control, N, P and N+P treatments). Note sequence of fills in graph starts at none and finishes with N + P + Si from bottom to top of each bar.

Nutrient effects on heterotrophic state are less well documented. A substantial amount of research on the effects of nutrient enrichment on heterotrophic activity has been directed toward microbial degradation of leaf material in streams (e.g., Bärlocher and Corkum, 2003). The few bioassay experiments from streams indicate that N and P may limit accumulation of heterotrophic microbial biomass in streams, and colimitation occurs in some cases (Tank and Dodds,

2003). In a Portuguese stream, N and P together stimulated fungal sporulation, but not P alone (Abhe-lo and Graça, 2006). Nutrient enrichment with both N and P stimulated litter decomposition and secondary production in an Appalachian stream (Cross et al., 2006). Given that many lakes and broad areas of the open ocean may be net heterotrophic, the effect of nutrient enrichment on utilization of dissolved organic C is certainly an area that is deserving of substantially more research.

Some studies indicate the potential importance of inorganic nutrient stimulation on heterotrophic marine activity. For example, phosphate addition stimulated bacterial activity but not phytoplankton production in the Mediterranean (Thingstad et al., 2005), P appears to limit bacterial growth in the Sargasso Sea (Cotner et al., 1997), and dilution experiments in eight lakes and two stations in the Pacific Ocean indicate inorganic nutrients limit bacterial productivity (Elser et al., 1995).

In lakes, bacterial abundance can be explained in part by algal biomass, but a significant proportion of the residual variance can be attributed to total P. There is substantial variance in the ratio of bacterial biomass to phytoplankton biomass in both marine and lake ecosystems, particularly at low phytoplankton biomass where the ratio can vary more than fivefold (Kalf, 2002). Taken together these observations suggest that bacteria and phytoplankton compete for nutrients, and if bacteria are P limited they may be less effective in using available C.

Nitrogen regularly stimulates heterotrophic and autotrophic activities in spite of biogeochemical arguments that P is the most limiting element in aquatic ecosystems and the assumption by some that P is the limiting element in freshwaters. Hutchinson (1957) noted that the ratio of P to other elements in organisms was much greater than the ratio in the primary sources of those elements. Short-term bioassays indicate autotrophs and heterotrophs often are under N stress in aquatic ecosystems.

Given that nutrients can be co-limiting in all these systems, stoichiometric effects on primary production as well as heterotrophic state could be broadly important in aquatic ecosystems. For example, changes in coastal marine stoichiometry can alter algal species composition (Justic et al., 1995). Alteration in species composition may change energy transfer up the food web and may alter autotrophic state.

Light directly influences autotrophic and heterotrophic state. Direct effects on autotrophic state are obvious; light can limit photosynthetic rates. Solar radiation can also influence heterotrophic state by degrading recalcitrant dissolved organic materials in

surface waters and making them more available to microbial consumption (e.g., De Lange et al., 2003). Thus, light increases the growth term, G , in equation 7 by increasing the efficiency of C acquisition. Several factors may influence light, including depth, canopy cover, mixing depth, latitude, and abiotic absorption. Obviously, shallow aquatic habitats with emergent vegetation or substantial canopy cover will be oligo-autotrophic, but heterotrophic state may be fueled by input of terrestrial litter.

Carbon loading influences heterotrophic state. This is particularly true in streams where sewage stimulates heterotrophic activities to the point where the waters became anoxic (Huntsman, 1948). Alternatively, removal of C sources can cause heterotrophic state to become more oligotrophic and lower heterotrophic demand for nutrients, subsequently decreasing nutrient retention in streams (Webster et al., 2000). Broad scale alteration of riparian vegetation may have unintended effects on heterotrophic state of small lakes and flowing waters.

Conclusions

Both autotrophic and heterotrophic state should be considered to adequately characterize the so-called “trophic state” of aquatic ecosystems. Few distributions of trophic state have been published that can be used to represent the natural range of ecosystems, although some methods are available to create such distributions. While there has been substantial research on factors that control autotrophic state, less is known about factors that control heterotrophic state. Inorganic nutrients and light can influence heterotrophic state as well as autotrophic state. The net ecosystem trophic state is often tilted toward heterotrophy, even in ecosystems such as lakes and oceans that have traditionally been considered net autotrophic. Thus, a stoichiometric view of inorganic nutrient and C supply rates is necessary to describe the bottom up forces that constrain ecosystem structure. The whole-stream nutrient enrichment study of Cross et al. (2006) demonstrates how secondary production in a heterotrophic stream can be increased by inorganic nutrient fertilization.

We can consider multiple human influences that occur in large river ecosystems to illustrate why the stoichiometric view is important. Human activities (fertilized cropland, watershed disturbance, sewage releases) increase inorganic nutrient loading to rivers and streams. Concurrently, channelization and removal of riparian vegetation decreases allochthonous C inputs while increasing the potential for autochthonous production by increasing light input. Addition-

ally, numerous impoundments lead to settling of recalcitrant organic particles while increasing the concentration of more bioavailable sources of organic C (planktonic organisms) downstream. Finally, increases in atmospheric CO₂ may decrease quality of allochthonous carbon and alter the rate at which it enters food webs (Wetzel, 2006). The combined consequences of these human activities could be substantial for water quality and biotic integrity. Water quality regulations that solely focus on toxins, nutrients or sediment inputs (as is currently the case in North America and Europe) will not necessarily protect biotic integrity because they do not take stoichiometry, heterotrophic, and autotrophic state into account.

Our ability to understand and manage aquatic ecosystems requires characterizing how C enters the food web and is cycled. Characterizing autotrophic and heterotrophic state is a first step in describing ecosystem structure and function. Explicit definitions of trophic state and approaches to describe distributions of autotrophic and heterotrophic state will assist communication within and across disciplines concerned with aquatic ecosystems.

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