The renewed interest in trait-based approaches has offered a stimulating, conceptual framework for predicting species distributions, assessing community composition and determining biodiversity–ecosystem linkages. However, despite previous attempts to clarify trait terminology and its application, selecting ecologically meaningful traits that mechanistically link levels of biological organization remains a challenge in aquatic ecology. Response traits can be used to capture community assembly processes along environmental gradients, while effect traits hold the potential to predict ecosystem functions. Although effect traits related to organismal physiology and body composition best allow for extrapolation from individuals to ecosystem processes, such traits are still rarely incorporated within plankton functional approaches or classifications for numerous reasons. Synthesizing current knowledge on effect traits in zooplankton, we call for a better implementation of such metrics as descriptors of community structure. We then capitalize on concepts of bioenergetics and ecosystem ecology to propose a hierarchical framework for zooplankton trait classification, identifying key traits fulfilling organismal functions and linking these to ecosystem processes likely to be influenced. Our framework provides insight regarding trait trade-offs, with implications for feedbacks to ecosystems, aiming to bridge the gap between plankton community ecology and aquatic biogeochemistry.

KEYWORDS: body size; ecophysiology; ecosystem function; energy budget; functional traits; trade-offs
INTRODUCTION

Traits are fundamental descriptors of organismal phenotype, functionality and performance (Arnold, 1983). Their use in ecology provides a framework that enables the linking of different levels of biological organization, from individual morphology and activity to the dynamics of food webs and ecosystems (Chapin et al., 1996; Violle et al., 2007). In population and community ecology, traits have served to generalize across species to better address mechanisms of assembly, coexistence and reactivity (Sæther and Bakke, 2000; McGill et al., 2006). Compelling evidence has since accumulated for the relevance of a trait-based approach in organism–ecosystem linkages in terrestrial ecosystems (Eviner and Chapin, 2003; Hooper et al., 2005; de Bello et al., 2010), prompting analogous investigations in aquatic environments (Giller et al., 2004; Yvon-Durocher and Allen, 2012), with some studies highlighting the promising use of plankton traits (Litchman et al., 2007; Merico et al., 2009; Zwart et al., 2015). However, from an ecosystem perspective, the wide variety of plankton traits identified are not equally useful for larger-scale implications. A critical point in deriving trait-based indicators of ecosystem functioning lies in meaningfully choosing traits or trait types (Petchey and Gaston, 2006), which may sometimes be erroneously perceived as a trivial step.

Currently, trait choice remains constrained by the amount of information available and the cost of new observations (Gayraud et al., 2003), and while traits can characterize species performance, responses and interactions, fewer have been directly linked to specific ecosystem processes. It is important to recognize that traits may differentially affect multiple ecosystem functions, with some being more or less directly linked to a specific process, and others only exerting indirect effects (Lavorel and Garnier, 2002). Further, including traits that are not explicitly, nor directly related to an ecosystem function of interest may potentially introduce bias and spurious relationships in analyses, thereby hindering the detection of true ecological linkages. As a result, the traits chosen for inclusion in biodiversity studies (functional diversity; biodiversity–ecosystem function relations) or ecosystem models can affect conclusions. Therefore, it has been recommended that the nature, type and even number of traits used in such approaches be carefully selected based on the particular aims of a study (Petchey and Gaston, 2002, 2006).

Over the last decade, numerous plankton traits have been described for many taxa and their use has been increasingly encouraged to characterize the community structure of both phytoplankton (Reynolds et al., 2002; Litchman and Klausmeier, 2008; Litchman et al., 2010) and zooplankton (Barnett et al., 2007; Kiørboe, 2011; Litchman et al., 2013). Many such studies focus on categorical or qualitative traits related to individual performance and behaviour, with implications mostly at individual, population or community levels, whereas quantitative traits directly affecting ecosystem processes are either absent or poorly represented. Indeed, the link between individual traits characterizing community structure and how these contribute concretely to aggregate processes has been weakly established to date, especially for zooplankton, in part owing to the non-quantitative nature of most plankton traits that have wide species coverage (Barnett et al., 2007; Litchman et al., 2013). Quantitative traits such as zooplankton size, body composition/requirements or physiological measurements of elemental fluxes (e.g. observations related to functions of excretion, egestion, respiration, growth, etc.) are best suited for extrapolation from organisms to ecosystem stocks and fluxes of material, and should thus be the focus of studies linking plankton individuals and communities to ecosystems.

Our objective here is to bring the discussion of plankton functional traits, formal descriptors of species’ ecological roles (Diaz and Cabido, 2001), back into the framework of response and effect traits (Lavorel and Garnier, 2002; Nock et al., 2016). We argue that this framework must be adopted to: (i) preserve consistency and improve dialogue with other subfields of trait-based ecology, thereby facilitating future comparison, generalization and synthesis; (ii) better clarify the rationale for trait selection with respect to a study’s objectives; and (iii) derive more mechanistic relationships between plankton community structure and ecosystem functioning. While the response and effect trait framework has been implemented and applied widely in terrestrial studies, it is our contention that it is still not commonly used in aquatic ecology, especially for plankton. In particular, despite the recognized relevance of many zooplankton traits for biogeochemical processes, including a considerable amount of trait data available in the literature, most of these effect traits have yet to be incorporated within a functional trait context. By synthesizing effect traits in zooplankton, we revisit the relevance of zooplankton stoichiometry and physiology in an effect trait-based framework, and emphasize the use of body size as a proxy for traits that are more difficult to measure. Finally, we propose a functional classification scheme based on both organismal and ecosystem functions, identifying key traits for linking these two levels of organization.
FUNCTIONAL TRAITS AND THEIR RELEVANCE ACROSS LEVELS OF BIOLOGICAL ORGANIZATION

Response versus effect traits

An appreciable number of definitions for traits, functional traits and trait types exist in the current ecological literature (for plankton examples, see: Le Quéré et al., 2005; Litchman et al., 2007, 2010, 2013). Defined most simply, traits are measurements of behavioural, molecular, morphological, phenological or physiological features of organisms, all of which are, and must be, measured at the organismal level (Violle et al., 2007). Traits have long been used to anatomically describe and classify species (e.g. taxonomy) and to link individual variation with fitness (e.g. in evolutionary ecology). However, it is only relatively recently that the concept of “functional traits” has emerged, which aims to describe species in terms of their ecological roles based on how they interact with each other and with their environment (Chapin et al., 1996; Diaz and Cabido, 2001). Functional traits are now part of a multi-scale framework using species’ responses and effects within a tropho-dynamic and evolutionary context, with respect to scenarios of climate and other anthropogenically-induced changes (Diaz et al., 2007; Thomas et al., 2016). While functional traits are properties of organisms, reflecting individual performance and fitness (e.g. life-history traits), they can also encapsulate information on population dynamics (i.e. demographic traits), community response mechanisms to changing conditions (through relative abundance fluctuations) and realized food web interactions (i.e. response traits), and ultimately indicate emerging properties of ecosystems (i.e. effect traits; Fig. 1; for additional examples, see Violle et al., 2007). Thus, response and effect trait types can respectively be used to model species’ fitness and niches as a function of biotic or abiotic conditions (Kearney and Porter, 2009), and to document organisms’ contributions to ecosystem function (Lavorel and Garnier, 2002). That said, some traits are more versatile than others, affecting processes at multiple ecological scales, and thus falling into more than one category of trait type; for example, in a response and effect trait framework, traits such as size and growth rate could be considered as either a response or effect type (Fig. 1).

For plankton, ecologists have thus far focused primarily on response traits, which are useful to assess species interactions and community succession as a function of environmental conditions (Barnett and Beisner, 2007; Merico et al., 2009; Beisner and Longhi, 2013). This has been especially the case for phytoplankton, for which quantitative trait measurements are becoming increasingly available (e.g. Edwards et al., 2015). For example, phytoplankton response traits have been shown to predict dominance amongst species based on their resource competitive abilities (Edwards et al., 2013a, 2013b). Having been the focus, this trait type now forms the core of the emergent field of functional biogeography, which aims at characterizing organisms as a continuous distribution of traits along biological gradients (Barton et al., 2013; Violle et al., 2014). However, when the goal is to gain mechanistic insight as to how organismal

![Fig. 1. Integrative framework linking functional trait classification across levels of biological organization inspired from Violle et al., 2007. Particular trait types operate predominantly (but not exclusively) on processes at specific levels of biological organization, affecting individuals, populations, communities or ecosystems (i.e. level of application). Some traits affect several or all levels of organization and can thus be classified as multiple trait types (e.g. body size and growth).](https://academic.oup.com/plankt/article-abstract/39/1/3/2528007/Linking-zooplankton-communities-to-ecosystemfunctioning/5)
presence and activity influence major biogeochemical cycles, the focus should instead shift toward effect traits, so as to incorporate feedbacks in ecosystems (e.g. Suding et al., 2008). In stark contrast to response traits, effect traits have been poorly described and applied in plankton ecology. Only very recently have two studies referred to plankton effect traits: Zwart et al. (2015), where taxon-specific values of phytoplankton light use efficiency were used in a trait-based model to predict lake primary productivity, and Litchman et al. (2015), where phytoplankton traits affecting biogeochemistry were reviewed. In their consideration of phytoplankton, this recent work provides strong cases revealing the relevance of effect traits in aquatic ecosystem ecology. However, the fact remains that effect traits are still rarely used, and the focus thus far, when it is on effect traits, has been for phytoplankton. We hereby call for an increased implementation of effect traits in plankton ecology, in particular for zooplankton, to remedy this situation.

Using effect traits to link zooplankton to ecosystem function

Adequately selecting effect traits implies a clear definition of the ecosystem function that is of interest. Although the term “ecosystem function” is used pervasively in the literature, it is not always clearly defined; ecosystem function refers to the properties or processes of ecosystems. It is possible to decompose ecosystem functioning into: (i) the size of stocks of energy and material (e.g. biomass, batch nutrients), (ii) the flow of energy and transformation of material (e.g. primary or secondary productivity, decomposition of organic matter, nutrient recycling), and (iii) variation in the stocks and flows over time (Pacala and Kinzig, 2002). The potential influence of zooplankton on these ecosystem-level parameters has already been recognized, although largely outside of the functional ecology literature (Sirotnak and Huntly, 2000; Sterner, 2009). Zooplankton can impact the bioavailability of nutrients and energy flow in food webs through several direct and indirect pathways (Fig. 2). Direct effects represent changes occurring via the passage of elements through organisms, as a result of their bodily requirements: ingested elements are partially absorbed by the body for tissue growth and storage, with excesses released as metabolic waste via excretion or egestion (Vanni, 2002). Given their central trophic position in aquatic food webs, zooplankton also directly affect biomass stocks and community structure of their prey (via consumption) and predators (by being consumed), and thereby indirectly influence how other trophic levels affect ecosystem function (Fig. 2; Vanni, 2002). There are many examples of zooplankton modulation of elemental stocks and fluxes of carbon (C), nitrogen (N), and phosphorus (P) in the literature (e.g. Frangoulis et al., 2005; Steinberg and Saba, 2008; Alcaraz et al., 2010, 2014). While the existence of such data should allow for effect trait characterization across taxa, it should be noted that this information has mostly been made available for marine species (Hébert et al., 2016a); a bias that has likely constrained their use in freshwater studies.

Zooplankton effect traits should thus most likely include measurements related to organismal biomass and body composition (e.g. size and elemental requirements), and physiology (e.g. material fluxes over time such as growth, feeding, respiration, ingestion or excretion rates); traits that best capture the elemental exchanges between individuals and their environment (Calow, 1987; Allen and Polimene, 2011). For example, using stoichiometric metrics to describe zooplankton community structure can inform on nutrient transfer through food webs (e.g. based on relative body content of species groups; Andersen and Hessen, 1991; Sterner et al., 1992), while physiological characters of zooplankton can be used to predict ecosystem processes such as nutrient recycling, primary productivity or carbon export (Jawed, 1973; Urabe et al., 1995; Tamelander...
Table I: Examples of hard effect traits and soft (proxy) traits in zooplankton and their potential impact on ecosystem processes (fluxes of energy and material)

<table>
<thead>
<tr>
<th>Hard effect trait</th>
<th>Soft trait (proxy)</th>
<th>Ecosystem process</th>
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<tbody>
<tr>
<td>Growth rate</td>
<td>Body length</td>
<td>Secondary productivity</td>
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<td></td>
<td>Body mass</td>
<td>Carbon cycling</td>
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<tr>
<td>Feeding (clearance or grazing) rate</td>
<td>Body mass</td>
<td>Nutrient and energy transfer (from prey to predator)</td>
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<td></td>
<td>Feeding mode or apparatus</td>
<td>Primary productivity</td>
</tr>
<tr>
<td>Sloppy feeding</td>
<td>Feeding mode</td>
<td>Nutrient recycling</td>
</tr>
<tr>
<td>Excretion rate</td>
<td>Body mass</td>
<td>Nutrient recycling</td>
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<td></td>
<td></td>
<td>Heterotrophic bacterial productivity</td>
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<tr>
<td>Faecal pellet production and sedimentation rates</td>
<td>Body length</td>
<td>Nutrient vertical export (translocation)</td>
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<tr>
<td></td>
<td>Body mass</td>
<td>Carbon sedimentation/ cycling</td>
</tr>
<tr>
<td>Respiration rate</td>
<td>Body mass</td>
<td>Ecosystem respiration</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Carbon cycling</td>
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Body size as a proxy for effect traits

Body size transcends multiple organismal functions, determining fitness and much of the ecology of zooplankton (Litchman et al., 2013). Several corporeal properties and physiological rates scale with size, such as the total body content in energy and elements, feeding, excretion, and basal metabolism, all of which directly affect ecosystem stocks and/or fluxes (Fig. 2). To some extent, most biological rates increase as a function of body mass following a power law (Kleiber, 1961; Peters, 1983), after accounting for ambient temperature (Brown et al., 2004). Thus, individual size is a major determinant of other traits, including several effect traits that also influence ecosystem function (Table I). Body size can be expressed in many possible units or energy currencies and be used as an indicator of informative hard traits. For example, length:mass ratios indicate body shape and mass:volume ratios indicate body density; features that can be related to zooplankton feeding and vertical transport (Litchman et al., 2013). Further, body mass expressed in carbon, joules or calories can be used as a common energetic currency for bioenergetic modelling, e.g. to assess consumer–resource interactions or biomass ratios under changing conditions (Gilbert et al., 2014). Importantly, size is also the typical denominator for most physiological rates (e.g. excretion, respiration) and, combined with mass-scaled exponents or empirical relationships for such rates (e.g. Ikeda et al., 2001; Kiørboe and Hirst, 2014), body size can provide quantitative estimates of organismal contribution to elemental flow (e.g. N, P, and C; Frangouli et al., 2005; Alcaraz et al., 2010). As a result, individual body size is both an important descriptor for zooplankton communities, providing information on overall biomass and size structure related to abiotic and biotic gradients, but equally, holding the potential for broader application for predicting ecosystem properties and processes (Yvon-Durocher and Allen, 2012).

Allometric mass–length equations and mass-scaled exponents of physiological rates can be jointly used in trait-based approaches to model the effects of particular communities on specific processes. For example, abundance and body length data can be converted to biomass using allometric equations and, combined with mass-specific metabolism data, it is possible to quantify overall community respiratory fluxes and thereby evaluate biotic contributions to ecosystem C-cycling (as shown in reef-fish communities by Barneche et al., 2014, for example). Similar relationships could be established with plankton community matrices and trait databases (for trait compilations, see: Barnett et al., 2007; Edwards et al., 2015; Hébert et al., 2016b), linking...
plankton species to large-scale nutrient fluxes through community structure. However, care should be taken to not extrapolate trait relationships based on size beyond the size spectrum covered by particular established equations. Likewise, using mass-scaled exponents derived from extremely large size spectra, for example the general $\frac{3}{4}$ power law, to estimate any physiological rates can result in inaccurate predictions (Finkel et al., 2004; Tilman et al., 2004; Glazier, 2006; Alcaraz, 2016). To some extent, certain allometric exponents and size–trait relationships may be taxon- or habitat-specific (Rall et al., 2011; Hébert et al., 2016a). Other traits of equal relevance can be included to increase predictive power and accuracy (e.g. De Bie et al., 2012). Despite these caveats, when no direct measurements of physiological traits are possible, body size information combined with adequate size–trait relationships can provide at least a rough estimate for important effect traits.

A BIOENERGETIC PERSPECTIVE ON ZOOPLANKTON EFFECT TRAITS

Energy allocation as a trait classification framework

Linking particular aspects of zooplankton to ecological processes likely requires a description of community composition in terms of functional traits. The scale of interest however determines the type of traits that are to be included in a classification. Litchman et al. (2013) proposed a categorization based on fundamental fitness components of organisms: feeding, growth, reproduction and survival. We propose expanding this classification by first decomposing these fundamental needs into energy allocation compartments, thereby more fully integrating physiological traits, and second, extending the scope of the functional trait framework to facilitate the identification of

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![Fig. 3. A non-exhaustive classification of zooplankton functional traits (upper part) based on the energy budget of an individual (organismal functions), aligned with their respective impact at the ecosystem scale (ecosystem functions; lower part). Functional traits that transcend more than one organismal function are framed with solid lines; likewise, zooplankton trait-influenced ecosystem functions transcending organismal functions are also framed with solid lines. Frames with dotted lines indicate the bidirectional control (top-down and bottom-up) on the algal communities. This scheme expands on Litchman et al. (2013).](https://academic.oup.com/plankt/article-abstract/39/1/3/2528007/Linking-zooplankton-communities-to-ecosystem by guest on 16 September 2017)
effect traits likely to affect ecosystem functioning. Our expanded framework (Fig. 3) categorizes traits based on the organismal functions they fulfill and represents the balance maintained between energy consumption and allocation to (active and basal) metabolism, growth and reproduction, with energy losses to excretion, egestion (Kiørboe et al., 1985; Bämstedt, 1988) and investment in anti-predator strategies (Visser, 2007; Kiørboe and Jiang, 2013). Our trait classification is thus based on a typical zooplankter’s energy budget (with energy compartments hereafter referred to as organismal functions) in the top half of Fig. 3, and explicitly links traits to particular ecosystem functions likely to be affected, represented in the bottom half.

As highlighted by Litchman et al. (2013), some traits such as motility and body size transcend several organismal functions. Our framework demonstrates that effect traits related to body composition may also do so (Fig. 3). In this classification some functional traits, more commonly considered as response traits in plankton studies (i.e. traits governing how species abundances vary under environmental conditions), may equally be regarded as effect traits if they also have implications for ecosystem functioning (Fig. 3). Different effect traits can influence the same ecosystem process in different, and sometimes opposing ways (Figs 2 and 3). For example, through feeding, zooplankton exert top-down control on algal biomass, reducing phytoplankton standing stock and influencing their community composition; yet, zooplankton also sustain the growth and biomass of phytoplankton via nutrient excretion which enhances primary productivity (Figs 2 and 3; Lehman and Sandgren, 1985; Sterner, 2009). Other effect traits such as sloppy feeding and faecal pellet production may also simultaneously contribute to nutrient and C-cycling (Moller and Nielsen 2001; Wexels Riser et al., 2008). Alternatively, a single trait may also influence several ecosystem functions: zooplankton excretion regenerates nutrient stocks, providing dissolved inorganic compounds for primary producers, but also supports heterotrophic bacterial growth (Fig. 3; Jumars et al., 1989; Carlson, 2002). Changes in zooplankton community composition can also directly affect ecosystem stoichiometry through shifts among taxa of different elemental content (e.g. high P requirements in Daphnia as opposed to other taxa), which in turn affect relative release through excretion or egestion (Sterner and Elser, 2002). Ultimately, ecosystem storage and fluxes modulated by zooplankton biomass and activity all contribute to larger biogeochemical cycles, either directly or indirectly (Figs 2 and 3). The magnitude of this contribution is subject to variation however, obviously depending on overall plankton standing stocks and turnover, environmental conditions, ecosystem type and nutrient or carbon budget.

Assessing trait trade-offs through bioenergetics

Traits can acclimate and adapt in response to external forces, optimizing fitness by balancing energetic investment in different organismal functions (Calow and Townsend, 1981). Strong plankton trait trade-offs include energy investment in size versus growth (Sauter et al., 2015), in feeding versus hiding (Gilwicz, 2003), or in defense versus competition (Yoshida et al., 2003). Energy allocation among organismal functions can be affected by environmental conditions (Calow and Sibly, 1983; Kiørboe, 2011), which alters favoured strategies and leads to differential upstream repercussions. Identifying and quantifying trait trade-offs can establish links within suites of organismal effect traits (“trait syndromes”; Poll et al., 2006), with overall consequences for ecosystem function.

The energy-based trait classification we propose (Fig. 3) provides a reliable framework to further investigate energy compensation amongst multiple traits with potential implications for ecosystem processes; not only for zooplankton, but for multiple groups of heterotrophic organisms. For example, because higher temperatures increase metabolic rates related to zooplankton organismal functions across species (e.g. Ikeda et al., 2001), greater basal metabolism can induce higher energy consumption and/or lower investment in growth or reproduction to maintain an overall energy balance (e.g. Kiørboe et al., 1985). A potential outcome for ecosystems undergoing warming is a strengthening of consumer–resource interactions (O’Connor et al., 2009), with zooplankton exerting stronger top-down control on primary producers (West and Post, 2016). However, if zooplankton individuals compensate for higher metabolic costs by consuming more, they will also excrete and thus recycle more nutrients, which could then benefit less edible phytoplankton species or primary producers (Miller and Landry, 1984). Such energetic trade-offs allow for clear a priori hypotheses to be framed and tested to further investigate the repercussions of linked effect traits on food web regulating processes (i.e. top-down versus bottom-up control) and ecosystem balance (e.g. stoichiometric pool/nutrient availability, productivity to respiration ratio). Hierarchical frameworks that clearly organize organismal energy allocation and associated effect traits along with ecological processes prone to be affected, such as the one provided in Fig. 3, are likely to be broadly applicable in this context.

CONCLUDING REMARKS

There are still many gaps in the zooplankton effect trait values available in the literature. Thus the most obvious
recommendation for future work is for more measurements and for making such data widely available, especially for less-studied taxa or habitats. More specifically, trait information is especially limited for freshwater species (Hébert et al., 2016a) as well as in some less-studied areas such as the more diverse tropics (Castilho-Noll et al., 2010). A recent compilation of reviewed taxa-specific values of zooplankton traits likely to influence C, N, and P stocks and fluxes in both marine and freshwater environments has been released, which can provide a base to be expanded upon (Hébert et al., 2016b). Increasing data availability on effect traits will not only help incorporate more mechanistic metrics in plankton community–ecosystem functioning linkages, but may also improve our ability to quantify and parameterize intra- and inter-specific trait variation and trade-offs, under static versus changing environmental conditions in ecosystem modelling.

Ecosystem functioning is the emergent property of multiple environmental drivers and filters operating at a hierarchy of scales, with assemblages of individuals optimally acclimated to their habitat conditions (Lavorel and Garnier, 2002). Because functional traits may interact or synergistically influence different aspects of ecosystem functioning, identifying which traits are most relevant still remains a major challenge in functional ecology (Hooper et al., 2005). In light of this challenge, we appeal to plankton ecologists to more clearly define their goals when developing trait-based approaches so as to facilitate the choice of traits in future studies. When the aim is to assess ecosystem-level properties or processes, functional effect traits with explicit, direct links between organisms and ecosystem function should be used; if the goal is to broadly determine how community composition may vary under changing conditions using traits instead of taxonomy, then response traits of interest should be identified. As trait-based ecology matures, we encourage the use of both response and effect traits, given that their joint implementation is relevant to assessing organismal feedbacks on ecosystems undergoing environmental change. Finally, we believe that using a bioenergetic approach as an alternative for trait categorization holds the potential to better link organismal activity to ecosystem function, offering an integrative framework to assess trait variation and trade-offs and their ecological repercussions.

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REFERENCES


