A cascade of evolutionary change alters consumer-resource dynamics and ecosystem function

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It is becoming increasingly clear that intraspecific evolutionary divergence influences the properties of populations, communities and ecosystems. The different ecological impacts of phenotypes and genotypes may alter selection on many species and promote a cascade of ecological and evolutionary change throughout the food web. Theory predicts that evolutionary interactions across trophic levels may contribute to hypothesized feedbacks between ecology and evolution. However, the importance of ‘cascading evolutionary change’ in a natural setting is unknown. In lakes in Connecticut, USA, variation in migratory behaviour and feeding morphology of a fish predator, the alewife (Alosa pseudoharengus), drives life-history evolution in a species of zooplankton prey (Daphnia ambigua). Here we evaluated the reciprocal impacts of Daphnia evolution on ecological processes in laboratory mesocosms. We show that life-history evolution in Daphnia facilitates divergence in rates of population growth, which in turn significantly alters consumer-resource dynamics and ecosystem function. These experimental results parallel trends observed in lakes. Such results argue that a cascade of evolutionary change, which has occurred over contemporary timescales, alters community and ecosystem processes.

Keywords: life-history evolution; local adaptation; eco-evolutionary dynamics

1. INTRODUCTION

There has been considerable interest in the potential for evolutionary diversification to impact ecological properties and promote reciprocal interactions between ecological and evolutionary forces, or eco-evolutionary feedbacks [1–3]. A requirement of eco-evolutionary dynamics is that evolutionary change, occurring on contemporary timescales (i.e. years to decades), has differential impacts on the environment. A link between genetics and ecology is evident from research showing that genotypes or genetic diversity can influence ecological processes [4–12]. Recent work has also shown that intraspecific diversification can impact the properties of communities and ecosystems [13–17]. However, this body of research has focused on feedbacks between variation in one organism and the rest of the environment. This is important because natural systems are inherently complex, and evolutionary changes in one organism, and associated ecological impacts of these changes, may alter the selective landscape and promote a series of evolutionary changes that propagate throughout the food web. Theory mimicking relatively simple communities predicts that evolutionary interactions among organisms could be an important component of eco-evolutionary dynamics [18–20], but the significance of such a ‘cascade of evolutionary change’ is unknown.

The zooplanktivorous fish the alewife (Alosa pseudoharengus) and water fleas (Daphnia sp.) have strong ecological impacts in lakes. Alewives structure the zooplankton community [13,21], while Daphnia sp. regulate phytoplankton abundance and nutrient cycling [22–23]. In lakes in Connecticut, USA, the presence or the absence of passages to the coastal ocean lead to lakes with anadromous alewives that migrate seasonally between marine and freshwater environments or lakes with permanent populations of landlocked alewives, respectively. These populations of alewives differ genetically as landlocked alewives diverged from a common anadromous ancestor as recently as 300 years ago [24]. In addition to lakes with landlocked or anadromous alewives, there are lakes without any alewife. All three lake types are comparable ecologically (size, depth and productivity) and contain identical compositions of non-alewife zooplanktivorous fish [13].

Adult anadromous alewives migrate into lakes to spawn during March–May, and young-of-the-year (YOY) alewives spend approximately six months in freshwater before migrating back to the ocean each autumn. In these lakes, Daphnia are abundant each spring, but are eliminated by YOY alewife predation in early summer [13]. Conversely, landlocked alewives are present in lakes year-round, and therefore Daphnia abundance is consistently low. Small-bodied zooplankton dominate the zooplankton community in lakes with landlocked alewives [13,21], and this has promoted morphological divergence of landlocked alewives from anadromous alewife [25]; anadromous alewives have a larger gape and larger spacing between gill rakers, and target larger prey (e.g. Daphnia), than landlocked alewives [13,15].

We recently demonstrated that variation in alewives selects for evolutionary divergence in the life histories of Daphnia. Daphnia from lakes with anadromous alewife
grow faster, mature earlier (but at the same size) and produce larger clutches of offspring than Daphnia in lakes with landlocked or no alewives [26]. Because Daphnia in lakes with anadromous alewives are present only during the spring, and also because lakes in Connecticut are colder during the spring than summer, these evolutionary changes are best explained as an adaptation to a very short growing season and colder environment (i.e. countergradient variation) [27] that are an indirect effect of predation by anadromous alewives. There were no significant life-history differences in Daphnia between lakes with landlocked and no alewives, despite differences in predation pressure [13]. Hypothesized explanations include selection by landlocked alewife on other components of fitness (i.e. behaviour), trade-offs associated with shifts in growth and development, or enhanced gene flow between these lakes [26].

Here we ask whether contemporary evolution in Daphnia differentially affects consumer-resource dynamics and ecosystem processes. On the basis of the known connection between life-history traits and rates of population growth [28], as well as the established impacts of Daphnia grazing on phytoplankton dynamics [22–23], we expect evolution in Daphnia to have consequences for community and ecosystem ecology. We evaluated the ecological impacts of Daphnia by rearing Daphnia from three ‘anadromous’, three ‘landlocked’ and three ‘no alewife’ lakes in a common environment for multiple generations, and then quantifying their impact on phytoplankton dynamics and primary production in laboratory mesocosms. By rearing Daphnia in a common environment prior to the experiment and then performing the laboratory experiment under standardized conditions, our experiment allowed us to isolate the impacts of genetically based divergence on ecological processes. We specifically targeted the mechanistic link between evolutionary change and divergent ecological properties by quantifying the influence of population-level effects (rates of Daphnia population growth) as well as individual-level effects (Daphnia grazing rates) on phytoplankton abundances. We predict that the earlier maturation and larger clutches exhibited by Daphnia from lakes with anadromous alewives will facilitate faster rates of population growth, and thereby faster declines in algal biomass and decreased rates of primary production in experimental mesocosms, compared with Daphnia from lakes with landlocked alewife or with no alewife. We evaluate the support for these predictions in the previously mentioned laboratory experiment, as well as in multiple years of data on plankton abundances at the whole-lake scale.

2. MATERIAL AND METHODS

We examined the ecological influence of Daphnia evolution using Daphnia ambigua from three anadromous (Bride, Dodge and Gorton), three landlocked (Amos, Long and Quinnipaug) and three no alewife (Black, Gardner and Wyassup) lakes. We have previously shown that these lake types do not differ significantly in size, depth, productivity or alewife biomass (between landlocked and anadromous lakes only) [13]. All lakes contain similar compositions of non-alewife zooplanktivorous species of fish [13]. These fish species include bluegill (Lepomis macrochirus), yellow perch (Perca flavescens), golden shiners (Notemigonus crysoleucas) and pumpkinseed (Lepomis gibbosus).

All clones used in these experiments were established from sexually produced resting eggs (ephippia) collected from lake sediment. Sediment was collected in August–September 2009 using an Ekman Grab. In January 2011, eight genotypes of Daphnia ambigua were established per lake. The first laboratory generation consisted of one female per clone reared in 120 ml glass jars containing COMBO media [29] and an abundant supply of algae, Scenedesmus obliquus (concentration: > 1.0 mg C l⁻¹ d⁻¹). The photoperiod for all phases of clone rearing and the mesocosm experiment was 12 L: 12 D cycle. For the second laboratory generation, three individuals were taken from the second clutch of each clone and reared under the same conditions as those of the first generation. Thereafter, each clonal population was allowed to grow to a maximum of 15 adults per container and was maintained at this density for approximately 14 days. This density is not uncommon for experimental rearing of Daphnia [30–32]. During this phase of rearing, all beakers were monitored every other day, and clones were transferred to fresh media and algae three times per week. Prior to the experiment, all clonal populations experienced approximately five generations of common garden rearing.

(a) Laboratory experiment

We initiated our experiment in March 2011 by filling 56 l rectangular containers with 201 of COMBO media [29] and added 400 ml of Scenedesmus obliquus to yield an initial algal concentration of 0.8 mg C l⁻¹ per mesocosm. Four days later, each mesocosm received 32 adult Daphnia from a single lake. Our definition of adult Daphnia was any individual that contained greater than 2 developing offspring. A clutch size of two is not uncommon for individuals that have released their first clutch into the brood chamber [26]. When initiating this experiment, we recorded the number of individuals that contained their first clutch versus slightly older individuals that contained the third to fifth clutch. Because there are differences in fecundity among our lake types [26], and also because fecundity increases with age (up to clutch no. approx. 5), we used a conservative approach when adding individuals to the mesocosms to minimize initial differences in fecundity. We ‘stocked’ mesocosms containing Daphnia from lakes with anadromous alewives with a higher proportion of individuals that contained their first clutch (electronic supplementary material, table S1). This approach minimized the influence of initial differences in fecundity on population growth in Daphnia (electronic supplementary material, table S1).

The initial populations of Daphnia in each mesocosm included eight equally represented clones per lake (four individuals per clone). Each lake was replicated three times (nine lakes × three replicates = 27 mesocosms). The experiment consisted of an additional three units that contained media and algae but no Daphnia. All mesocosms were randomly assigned locations in the laboratory and were stirred daily to resuspend algae. We quantified water temperature and light levels weekly.

We started monitoring algal and Daphnia abundances one week after the introduction of zooplankton. Prior to collecting samples, each mesocosm was stirred to homogenize its contents. Water samples (2–3 ml) were removed from the centre of each mesocosm with a pipette, and algal density was quantified via a laser particle counter (Spectrex PC-2200, Redwood City, CA). The average value of two replicate counts by the laser counter was used as the estimate of
algal cell density per mesocosm per date. *Daphnia* abundances were enumerated by filtering 11 of water through 80 μm mesh netting and preserving samples in 70 per cent ethanol. All individuals were subsequently counted. The densities of *Daphnia* and algae were quantified three times per week for a total of 15 sampling events over the course of the 41-day experiment.

Our dependent variables included rates of algal decline, rates of *Daphnia* population growth, day of peak algal and *Daphnia* abundances, and net primary production (NPP). The rate of decline of algae was measured for each mesocosm by fitting an exponential decay function \( y = ae^{-br} \) to the algae density data starting at day 8 through day 20 of the experiment. This period represents the time between the average (across lake types) maximum and minimum densities of algae. We used the rate of decay (parameter b) as the basis of comparison. The exponential decay model produced a strong fit to the data \( (r^2 \text{ mean} = 0.95; \text{range} = 0.82–0.99) \). We quantified rates of *Daphnia* population growth using two complementary approaches. First, we calculated rates of exponential growth over the first 10 days following the addition of algae using the formula \( N_t = N_0e^{rt} \), where \( N_t \) is the *Daphnia* density at day 10, \( N_0 \) is the initial density of *Daphnia*, \( r \) is the rate of increase and \( t \) is the time interval. Second, we fitted an exponential function \( y = ae^{br} \) to the *Daphnia* data for each mesocosm to obtain the parameter b, which describes the rate of increase for a given replicate. We evaluated differences in *Daphnia* growth over longer durations (i.e. the first 16 days of the experiment and from day 1 until peak *Daphnia* population size); the differences in *Daphnia* growth among lake types were similar irrespective of time period, although we did not evaluate differences in growth past day 20.

We evaluated primary production in the mesocosms as one measure of ecosystem function. To calculate primary production, we converted algal cell densities to rates of oxygen production and consumption from a previously established regression. Rates of NPP were then calculated as oxygen production and consumption from a previously established regression. Rates of NPP were then calculated as oxygen production and consumption from a previously established regression. Rates of NPP were then calculated as oxygen production and consumption from a previously established regression. Rates of NPP were then calculated as oxygen production and consumption from a previously established regression.

Our design used between-within subjects degrees of freedom. A likelihood ratio test was used for tests following significant \( (p < 0.05) \) lake type effects.

**Statistical analyses**

We analysed our data using linear mixed models (SAS v. 9.1, SAS Institute, Cary, NC) implemented with restricted maximum-likelihood estimation. For each variable, lake type was entered as a fixed effect, and replicate lake populations were nested within lake type as a random effect. Temperature and light level of each mesocosm were included as covariates.

**Daphnia and phytoplankton biomass in lakes**

To compare the results of our laboratory experiment with the patterns observed in lakes, we sampled *Daphnia* and phytoplankton abundances in lakes. We sampled for plankton in April because zooplankton and, to a lesser extent,
phytoplankton are abundant in our lakes in April [13], and YOY alewife are absent from anadromous lakes during this period. We sampled zooplankton on one date (between 1 and 15 April 2005) in three anadromous (Bride, Dodge and Gorton), four landlocked (Amos, Long, Quonnipaug and Rogers) and four no alewife (Black, Gardner, Hayward and Linsley) lakes. Zooplankton were collected from the deepest point in each lake with an 80 µm mesh plankton net [13]. Each sample was preserved in 70 per cent ethanol, and Daphnia were subsequently counted after samples were split with a plankton splitter. Zooplankton biomass (microgram per litre) was quantified for each lake via length–mass regressions [13]. The evaluation of Daphnia biomass among lake types, as opposed to the abundances of Daphnia, represents a proxy for total grazing pressure on phytoplankton. Differences in Daphnia biomass (log-transformed) were analysed using a one-way ANOVA, with lake type entered as a fixed effect.

Phytoplankton biomass was estimated from chlorophyll a concentrations. Chlorophyll a was quantified in three anadromous lakes (Bride, Dodge and Gorton), three landlocked lakes (Amos, Quonnipaug and Rogers) and three lakes without alewives (Linsley, Gardner and Hayward). All sampling occurred between 31 March and 15 April over at least two separate years. Sampling occurred in 2005–2006 and 2008–2009 in Bride, Dodge, Quonnipaug, Rogers and Linsley, and in 2005–2006 in Gorton, Amos, Gardner and Hayward. We sampled over multiple years to determine the consistency of any variation in phytoplankton abundance among lake types. Water samples were filtered onto Whatman GF/F filters (Whatman, Brentford, UK) and analysed for chlorophyll a concentrations on a Turner Designs TD-700 fluorometer (Turner Designs, Sunnyvale, CA) following Environmental Protection Agency method 445.0. We evaluated the mean epilimnetic chlorophyll concentration for the total plankton community. Differences in chlorophyll a concentration among lake types were analysed with a one-way analysis of variance. We used the mean chlorophyll concentration for each lake in the analysis.

3. RESULTS
(a) Mesocosm experiment
We observed significant differences in algal population dynamics and NPP among lake types (figure 1 and table 1; electronic supplementary material, table S2). Algal densities in mesocosms with Daphnia from anadromous lakes declined at rates that were 41 and 42 per cent faster (over days 8–20) than algae in mesocosms with Daphnia from landlocked or no alewife lakes, respectively (electronic supplementary material, tables S2 and S3; figure 1). NPP was 32 to 36 per cent lower during this same time period in mesocosms with Daphnia from anadromous versus landlocked and no alewife lakes (table 1 and figure 1). Post-hoc Tukey tests showed that anadromous lakes differed significantly from landlocked and no alewife lakes (figure 1). The results for primary production are similar if we evaluate the rate of decline of NPP over days 8–20; significant differences among lake types were observed as NPP declined at rates that were 51 and 56 per cent faster in mesocosms with Daphnia from anadromous lakes than NPP in mesocosms with Daphnia from landlocked or no alewife lakes, respectively (table 1; electronic supplementary material, tables S2 and S3). There were no significant differences in NPP among lake types over days 20–41 as all mesocosms converged on low algal densities (average NPP days 20–41 in mg O₂ 1⁻¹ d⁻¹: anadromous = 0.199 ± 0.011, landlocked = 0.243 ± 0.011, no alewife = 0.219 ± 0.010; F₂,₆ = 3.65, p = 0.092). There were also no significant differences in algae cell size at the peak abundances of Daphnia (average cell size in µm ± s.e.: anadromous = 5.25 ± 0.28, landlocked = 5.09 ± 0.1, no alewife = 4.92 ± 0.18; F₂,₆ = 0.79, p = 0.49).

We observed significant (p < 0.05) differences in rates of population growth of Daphnia among lake types (table 1; electronic supplementary material, tables S2 and S3); rates of exponential growth during the first 10 days were 23 to 28 per cent faster in mesocosms with Daphnia from anadromous versus landlocked or no alewife lakes (figure 1). Daphnia from anadromous lakes were approximately 2.5 times more abundant by day 10 of the experiment than Daphnia from the other lakes (figure 1), and peak abundances of Daphnia occurred significantly earlier (approx. 6 days; table 1, electronic supplementary material, tables S2 and S3; figure 1) in mesocosms with Daphnia from anadromous lakes. Post hoc Tukey tests revealed that Daphnia from anadromous lakes exhibited significantly faster rates of population growth and significantly earlier timing of peak abundances than Daphnia from landlocked and no alewife lakes (electronic supplementary material, table S2). There were no significant differences in the size-structure of the Daphnia populations (average proportion of juveniles ± 1 s.e.: anadromous = 0.57 ± 0.01, landlocked = 0.6 ± 0.014, no alewife = 0.58 ± 0.01; F₂,₆ = 0.56, p = 0.6).

(b) Grazing trials
We performed separate but complementary experiments using the same clones used in the mesocosm experiment to evaluate the ability of Daphnia to graze upon algae at an equal density. Our consumption experiments revealed no significant differences in Daphnia grazing rates among lake types (mean change in algal cells ml⁻¹ ± 1 s.e.: anadromous = 72.4 ± 17.1, landlocked = 93.1 ± 17.4, no alewife = 67.4 ± 13.0; F₂,₆ = 1.67, p = 0.27).

4. DISCUSSION
Our experimental results demonstrate that contemporary life-history evolution in Daphnia can significantly affect phytoplankton population dynamics and ecosystem
Figure 1. Algal and Daphnia population dynamics. Black circles denote anadromous lakes; white squares, landlocked lakes; grey triangles, no alewife lakes. Error bars = ± 1 s.e. (a) Algal density. We observed a significantly ($p < 0.05$) faster rate of decline of algae in mesocosms with Daphnia from anadromous lakes versus Daphnia from landlocked or no alewife lakes. Inset: rates of net primary production. A, anadromous; L, landlocked; N, no alewife. Significant ($p < 0.05$) differences among lake types were observed. (b) Daphnia density (all individuals). Daphnia from anadromous lakes exhibited significantly ($p < 0.05$) faster rates of population growth and earlier timing of peak abundances than Daphnia from landlocked or no alewife lakes.

Table 1. Analyses of algal and Daphnia dynamics. Parameters were analysed using linear mixed models, with lake type entered as a fixed effect, lake nested within lake type as a random effect, and individual mesocosm temperature and light level included as covariates. When a covariate was not significant ($p > 0.05$), it was removed from the model and the data were reanalysed. $b$, rate of exponential decay; $d$, days; $r$, intrinsic rate of increase.

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*p < 0.05; **p < 0.01; ***p < 0.001; †0.05 < p < 0.1; ††p > 0.1 (n.s.).
(iii) morphological traits are highly heritable [34–36], and (iv) intraspecific variation in alewives drives evolutionary divergence in Daphnia [26], our results argue that evolutionary interactions across trophic levels, or a cascade of evolutionary change, impact phytoplankton dynamics and ecosystem function (figure 3).

(a) Field versus laboratory

For there to be an ongoing feedback between ecological and evolutionary processes, evolutionary divergence must have significant and observable effects on ecological properties in a natural setting, and this link from evolution to ecology needs to be apparent at the scale at which selection operates. To gain insights into the importance of our laboratory experiment from the perspective of natural ecosystems, we evaluated Daphnia and phytoplankton abundances at the whole-lake scale over multiple years. This data allow us to ask whether our laboratory results are congruent with whole-lake data.

At the whole-lake scale, the differences in the biomass of plankton among lake types in April are similar to those observed in the laboratory experiment. Daphnia in lakes with anadromous alewives consistently reach abundances in April that are higher than Daphnia in lakes without alewives and at least two orders of magnitude greater than Daphnia populations in lakes with landlocked alewives [13] (figure 2a). These differences in the biomass of Daphnia in lakes are correlated with divergence in phytoplankton abundances. The biomass of phytoplankton in April is significantly lower in lakes with anadromous alewives than in lakes with landlocked alewives or lakes without alewives (figure 2b). These trends in plankton abundances are transient because the onset of intense predation by anadromous alewives in late spring alters plankton community structure in summer [13].

What explains the trends at the whole-lake level? In April, Daphnia are not subjected to predation by anadromous alewives, but landlocked alewives are present. Alewives are strong predators on Daphnia [21], and Daphnia are known as important consumers of phytoplankton [22–23]. As a result, differences in Daphnia and phytoplankton biomass between lakes with landlocked and anadromous alewives are likely to be influenced by variation in alewife predation pressure. Conversely, lakes with anadromous alewives and lakes without alewives do not differ in non-alewife zooplanktivorous fish community composition in April. Yet Daphnia abundances are higher and phytoplankton abundances are consistently lower in lakes with anadromous alewives than in those without alewives (figure 2). These results suggest that the observed differences in plankton biomass do not simply reflect variation in the strength of a fish-mediated trophic cascade. If this was the case, then Daphnia and phytoplankton abundances should be similar in lakes with anadromous alewives and no alewives in the spring. Many biotic and abiotic factors can influence plankton abundances in lakes, but we suggest that the whole-lake differences in plankton abundance we observe could signal the impact of evolution in Daphnia on the ecology of these lakes. This speculation is supported by similar magnitudes of divergence in the field and in laboratory; Daphnia are 147 per cent (field) and 141 per cent (laboratory) more abundant in lakes with anadromous

Figure 2. Phytoplankton and Daphnia biomass in lakes in April. (a) Daphnia biomass. Zooplankton sampling occurred in the three anadromous (Bride, Dodge and Gorton), four landlocked (Amos, Long, Quonnipaug and Rogers) and four no alewife (Black, Gardner, Hayward and Linsley) lakes in April 2005. Differences among lake types were marginally non-significant ($F_{2,8} = 3.26, p = 0.092$). (b) Phytoplankton biomass. Chlorophyll a was quantified in three anadromous (Bride, Dodge and Gorton), three landlocked (Amos, Quonnipaug and Rogers) and three no alewife (Gardner, Hayward and Linsley) lakes. The biomass of total chlorophyll differed significantly ($p < 0.05$) among lake types. Error bars = ± 1 s.e.
alewives, while phytoplankton biomass is 21 per cent (field) and 27 per cent (laboratory) lower in lakes with anadromous alewives.

(b) Link from evolution to ecology

The effect of evolution on ecology, and the potential for ecology and evolution to interact via reciprocal feedbacks, is a rapidly growing field of research [1–3]. There is evidence for a pathway from evolution to ecology from multiple perspectives. For instance, research has shown that specific genotypes or genetic diversity can differentially alter the properties of populations, communities and ecosystems [4–12]. Such work provides a clear link between genetics and ecology, and indicates the potential for contemporary evolution to influence ecology. Furthermore, laboratory experiments exploring interactions between rotifers (predator) and algae (prey) demonstrated that the evolution of prey can significantly alter the population dynamics of predator and prey [36,37]. Finally, recent studies of contemporary evolution in natural populations of guppies, sticklebacks and alewives illustrated the ecological importance of adaptive divergence [13–17]. For example, Bassar et al. [17] showed that populations of guppies (Poecilia reticulata) adapted to environments that differ in predation intensity alter variables such as algal standing stocks, primary production and nutrient fluxes. In all three species of fish, there is evidence for genetic differentiation [24,38,39], and in guppies and sticklebacks trait differences are maintained after multiple generations of laboratory rearing [40,41]. However, these experiments [13–17] all used wild-caught individuals to demonstrate the community and ecosystem impacts of intraspecific variation, which potentially confound environmental and genetic influences.

Our results build upon previous studies [4–17] by using laboratory-reared populations of locally adapted Daphnia to show that contemporary evolution can significantly influence prey population dynamics and one measure of ecosystem function (see also [10]). This common garden approach is important because it demonstrates the impact of genetically based variation on phytoplankton abundances and NPP, and identifies difference in life-history traits and population growth as an important mechanism. Collectively, it is becoming increasingly clear that recent evolutionary change could represent a significant agent of ecological change.

5 CONCLUSIONS

Explorations of feedbacks between ecology and evolution have primarily focused on the interplay between changes in one organism and the rest of the environment. Here we take a significant step in characterizing how diversification in multiple organisms in a community could alter the functioning of ecosystems. Prior work in this system showed that divergence in alewives has direct effects on phytoplankton abundances and NPP, and identifies variation in alewives as a key contributor to feedbacks between ecology and evolution.

Figure 3. A conceptual model illustrating key ecological and evolutionary pathways in the alewives–zooplankton system. Ecological interactions are depicted by solid arrows. Evolutionary interactions are depicted by dotted arrows. Pathways from evolution to ecology are depicted by dashed arrows.

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REFERENCES


