STREAMS IN MEDITERRANEAN CLIMATE REGIONS: Abiotic Influences and Biotic Responses to Predictable Seasonal Events

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■ **Abstract** Streams in mediterranean-climate regions (areas surrounding the Mediterranean Sea, parts of western North America, parts of west and south Australia, southwestern South Africa and parts of central Chile) are physically, chemically, and biologically shaped by sequential, predictable, seasonal events of flooding and drying over an annual cycle. Correspondingly, aquatic communities undergo a yearly cycle whereby abiotic (environmental) controls that dominate during floods are reduced when the discharge declines, which is also a time when biotic controls (e.g. predation, competition) can become important. As the dry season progresses, habitat conditions become harsher; environmental pressures may again become the more important regulators of stream populations and community structure. In contrast to the synchronous input of autumn litterfall in forested temperate streams, riparian input to mediterranean-type streams is more protracted, with fall and possibly spring peaks occurring in streams in the Northern Hemisphere and a summer peak existing in their Southern Hemisphere counterparts. We present 25 testable hypotheses that relate to the influence of the stream hydrograph on faunal richness, abundance, and diversity; species coexistence; seasonal changes in the relative importance of abiotic and biotic controls on the biotic structure; riparian inputs and the relative importance of heterotrophy compared to autotrophy; and the impact of human activities on these seasonally water-stressed streams. Population increases in mediterranean-climate regions (particularly in fertile regions) result in an intensification of the competition for water among different users; consequently, water abstraction, flow regulation, increased salinity, and pollution severely limit the ability of the streams to survive as sustainable, self-regulated systems.

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INTRODUCTION

Climatic and geomorphic setting strongly influence structural and functional features of rivers and streams (2, 45, 88). Consequently, lotic ecosystems within a large geographic area may exhibit greater similarity to those in other regions that have similar climates and geomorphology than to those occurring in the same region (58, 93, 134). Streams and rivers in mediterranean-climate areas throughout the world are excellent examples of such convergence. Although confined to relatively small regions (<1% or up to 4% of the continental area according to different definitions, e.g. 5 and 50, respectively) and widely separated on all continents, mediterranean ecosystems support similar types of sclerophyllous vegetation (50, 51, 156, 157). Thus, because of the strong influence of the climate and catchment vegetation on stream structure and function, streams of coastal California, for example, may better be compared with streams in other mediterranean-type climates in Australia, Europe, South America, or Africa than, for example, with coastal streams of the adjoining Pacific Northwest.

In a recent review of the history of research on mediterranean-type ecosystems, 89 comparative studies (in 13 subject categories) among regions with a mediterranean-type climate were listed (84); none of these studies involve aquatic ecosystems. The effect of human-influenced disturbance on the integrity of aquatic habitats in these regions and the need to understand the ecological basis for their rehabilitation prompted us to assess the extent of scientific understanding about the organization and functioning of such habitats and their responses to key environmental factors. Some topics that we examined in mediterranean-type streams are better understood (e.g. hydrology) than others (e.g. riparian inputs and in-stream dynamics, biotic structure and interactions). As a result, we often had to draw on principles and examples from studies on streams in more mesic and xeric regions.

What are the defining characteristics of streams in mediterranean climates? Our central thesis is that because these ecosystems have a distinct cool and wet season followed by a warm and dry season, they are influenced by a sequence of regular and often extreme flooding and drying periods. In this review we describe how (*a*) these streams are sometimes distinctly different from, and other times the same as, streams in either temperate mesic or xeric areas; (*b*) the annual, predictable floods determine the temporal and spatial dynamics of these systems; (*c*) the drying that follows the rainy season results in gradual increases in biotic (e.g. competition and predation) and abiotic (e.g. low oxygen, high temperatures, loss of habitat) controls in structuring biological communities; (*d*) annual variability in rainfall can lead to extreme conditions of flooding and drying, and populations and communities respond differently over a multiannual scale; (*e*) the timing and dynamics of riparian inputs in mediterranean-climate regions differ from those of temperate, forested streams; (*f*) human activities may impact these lotic systems more than their counterparts in more humid or arid regions because of the severe competition for water that occurs in mediterranean-climate regions. Following a description of

the environmental setting and the riparian vegetation of mediterranean regions, we organize our discussion of mediterranean-climate streams around a series of testable hypotheses about the response of the aquatic biota to the flooding and drying sequence. This first review of mediterranean-type streams is selective; aspects that deserve further treatment are mentioned in the conclusion.

CLIMATIC SETTING

On all continents, certain coastal regions (often westerly positioned) in the middle latitudes, most extending between 30° and 40° north and south of the equator, are governed by a symmetrical atmospheric circulation that produces a climate characterized by cool, wet winters and hot, dry summers (5). The moderating ocean influence keeps winter temperatures mild, with mean monthly minima ranging from about 8° to 12°C, and frosts infrequent except at high elevations or well inland; summer mean monthly maxima usually vary between 18° and 30°C (49).

Over one half of the area worldwide with this mediterranean-type climate is located in the Mediterranean Sea basin (latitude 30°–45° N) and embraces parts of three continents–Europe, Asia, Africa (see map in 102); hence, the commonly used name for the climate type. This climate and the associated biome occur in four other limited and widely scattered areas of the world (see Figure 1 in 93): the Pacific Coast of North America from southern Oregon to northern Baja California (latitude 31°–41° N); parts of West and of South Australia (latitude 32°–38° S); the south-western Cape Region of South Africa (latitude 32°–35° S); and the central Chilean coast (latitude 32°–41° S) (for further details see 51, 84). Except for Australia, where the topography is characterized by moderate relief, the mediterranean lands are often rugged with a marked change in elevation and, therefore, also in climatic conditions along relatively short horizontal distances (5). Consequently, headwaters of some streams may be in high elevation areas where the climate is too wet and cold to be mediterranean (e.g. Ter River, Spain; 145).

Seasonality and variability in rainfall is the principal attribute of the mediterranean-type climate. At least 65% and often 80% or more of the rain falls in the three months of winter, with most of the precipitation often falling during a few major storm events that may produce flooding (100, 102, 119). The strong seasonality in rainfall (during the cool wet season) and the associated seasonal flooding clearly distinguish the mediterranean climate from most mesic or xeric temperate climates; in the latter climate regions, storms can occur during the colder wet season but also at other times of the year. Although the seasonal precipitation pattern is highly predictable in mediterranean-climate areas, annual rainfall can vary markedly in some regions from year to year; a deviation of 30% or more from a multiannual average is not uncommon. Such precipitation patterns are best described as having low constancy (sensu 40) and high predictability (36, 40, 126). Relatively long-term dry and wet cycles (>10 years) have been detected in mediterranean-climate regions (e.g. 48, 145), but the pattern

is far from being consistent and underscores that short-term and year-to-year variations in rainfall are unpredictable.

Because annual precipitation usually ranges between 275 and 900 mm (5, 102), certain mediterranean-climate regions fall into the category of semi-arid regions (200 and 500 mm annual rainfall; 73, 170); however, others may encompass regions with annual rainfall exceeding 1000 mm, including small amounts of summer rain (e.g. in Australia and South Africa—50, 148, 155). Similar to arid regions, mediterranean-climate regions are naturally water stressed because of high annual water losses by evapotranspiration relative to inputs from precipitation (71, 96, 170).

HYDROLOGIC REGIME

The discharge regime of mediterranean-type streams generally follows that of the rainfall pattern, and consequently exhibits both strong seasonal and annual variability (48, 140, 145). In mediterranean-type streams, the high flows abruptly commence in fall or early winter and floods occur during a few months in late fall, winter, and early spring. Subsequent drying and declining flow are gradual over a period of several months in summer, ending abruptly in fall or early winter when the next year's rains commence (see also "extreme-winter" category in 77, and the "perennial" and "intermittent" seasonal winter categories in 171). This seasonal pattern of high discharge coinciding with cool temperatures, which is followed by low discharges with warm or hot temperatures, greatly differs from that of temperate desert streams, which can be disturbed repeatedly and unpredictably by wetting and drying over an annual cycle (e.g. 59).

Deviations from the above-described pattern can occur in mediterranean-type streams. In regions of karst geology (e.g. Spain, Israel), large amounts of water may be stored in subterranean aquifers, which may moderate seasonal fluctuations in flow in mediterranean-type streams (e.g. 4). Furthermore, mediterranean-type streams that have part of their catchment in elevated areas with subfreezing winter temperatures and snow accumulation may exhibit a bimodal mean flow pattern, with highest discharges following the onset of rain (e.g. in fall) and after snow melt in spring (e.g. 4, 145).

Although the occurrence of floods during fall, winter, or spring is predictable in mediterranean-type streams, the intensity and frequency of the floods vary greatly from year-to-year depending on the frequency and intensity of rainfall. Low rainfall may eliminate significant floods and extend the drying period; we refer to these years as drought years. Fluctuations of the mean monthly discharge ranging from 100% above to 50% below the multiannual average have been reported (145), and this is not atypical of other mediterranean-type streams (e.g. 140).

The often brief and sometimes intense rainstorms that occur in mediterranean climates produce flashy hydrographs. The streams flood and attain peak discharges shortly after the rainstorm begins (possibly within hours in situations of a saturated

soil and/or a high gradient topography) and decline to normal seasonal flow shortly after the storm ends (e.g. Figures 2 and 5 in 43).

Local geomorphology may play a major role in hydrograph dynamics. Brief, violent floods (characterized by rapid onset and short duration) typically occur in high gradient constrained channels. Mediterranean-type streams are expected to be less "flashy" than desert streams, which are often restricted by steep bedrock canyons or alluvium, and more "flashy" than streams in mesic drainages of low relief that have extensive tributary networks and floodplains and where the floods build in intensity over periods of hours to days (e.g. 77, 109, 126).

In the wetter areas of mediterranean regions, streams usually maintain permanent flow or at least hold surface water throughout the year. In the drier ranges, mediterranean-type streams often have sections of the stream that lack continuous surface water and are composed of a series of isolated pools (e.g. 43, 56); we refer to this mosaic of isolated pools and dry areas as intermittent reaches. In Israel, for example, drying of the headwater tributaries is characteristic of many of the coastal streams, and the duration of intermittency and proportion of the channel that dries generally increases from north to south as rainfall decreases. Seepage of groundwater, return of agricultural water, and effluent discharge may maintain channel wetness in the lower reaches of some of these streams during the dry, summer period. Streams in areas that are intermediate in the wetness gradient of the mediterranean climate may alternate between perennial flow in rainy years and intermittency with surface water limited to isolated pools in drought years (e.g. some coastal mountain streams in California, 43, 140).

THE STRUCTURING ROLE OF FLOODING AND DRYING

Floods are characteristic disturbance events in streams in both mediterranean- and nonmediterranean-type rivers (139). Streams throughout the world also undergo a drying process (i.e. a gradual reduction in discharge and wetted area); however, drying in most mesic and temperate desert streams over an annual cycle is interrupted by rain, whereas drying in mediterranean-type streams is a continuous, gradual process over the dry summer period.

Floods have a variety of effects on the stream ecosystem, depending on their frequency, intensity, timing, and duration. These effects include scouring of accumulated sediment and debris, and redistribution of streambed substrate and organic matter in the channel; changing channel morphology and forming new erosional (riffles) and depositional (point and mid-channel bars, pools) zones; washing away in-channel and encroaching riparian vegetation; restoring channel connectivity; and homogenizing water quality conditions along the stream channel (48, 78, 90, 93, 145).

Watershed-stream interactions in mediterranean-type streams are most pronounced during the relatively short wet season. The first floods usually flush the tributaries of accumulated debris and carry a high load of dissolved and suspended

matter from the drainage basin into the stream. Following this and continuing throughout the wet season, the concentration of total dissolved solids is usually relatively low and that of suspended solids relatively high (e.g. 145), water quality conditions along the stream channel are least variable, and diurnal ranges in variables such as temperature and dissolved oxygen are usually lowest (e.g. 32).

Drying involves a gradient of events from reductions in flow, to formation of isolated pools, to complete drying of substrate; a temporal sequence of this is illustrated for a desert stream (160). The physical effect of drying involves habitat contraction, which is essentially the opposite of the habitat expansion that occurs during flooding. Depending on the severity of drying, the following conditions may occur in streams (55) and typically occur in mediterranean-type streams during the dry season: highly fluctuating oxygen concentrations caused by a combination of factors (elevated temperatures, high daytime photosynthesis and nighttime respiration, high biochemical oxygen demand associated with increased algal production and enhanced microbial respiration, reduced dilution of effluents in streams, and reduced turbulence); reduced dilution of nutrients; increased salinity; increased deposition of fine sediments; loss of connectivity with the hyporheic zone; encroachment of vegetation into stream channels (that further enhances siltation); and increased channel erosion because of the prolonged drying of banks.

Droughts can exaggerate the average drying sequence and not only result in the elimination or reduction of scouring flows but also result in an alteration of the temporal and spatial dynamics of habitat structure. Consecutive drought years may have an effect similar to that of water diversion in that accrual of fine sediments, expansion of deposition zones, bank erosion, and vegetation encroachment may produce major changes in channel morphology, including a complete choking of the channel (e.g. 78). There also may be an indirect response of flow to riparian vegetation through changes in geomorphology; this may be of greater consequence to the vegetation than the direct effects. In regions where beaches build, coastal mediterranean-type streams may become seasonally or annually disconnected from the sea during drought years because there is insufficient water to wash away the deposited sand (e.g. 85); this turns the lowermost reach into an elongated, closed lagoon (67).

An increase in evapotranspiration in summer may result in an increase in concentration of dissolved minerals (16, 32, 145). The diurnal fluctuations in water quality condition are highest during this period (32), and a spatial gradient in water quality conditions can develop along the stream, particularly in streams where the surface flow is fragmented into isolated pools. The changes in water quality conditions that occur during the drying process in mediterranean-type streams extend over a period of several months and thus have a more gradual impact on the biota than is typical of more arid streams. As in other streams, water quality conditions in mediterranean-type streams are influenced by stream-specific attributes such as local geomorphology, edaphic features, and human impact, and thus may vary spatially irrespective of climatic conditions (e.g. 139).

RIPARIAN VEGETATION AND INPUT OF ALLOCHTHONOUS ORGANIC MATTER

Riparian Vegetation

The vegetation in mediterranean climates is typically sclerophyllous and ever-green, adapted to water stress during the dry summer period, and able to grow on infertile soils (22, 25, 50, 83, 91, 103, 156, 163). The availability of year-round moisture near streams enables deciduous woody vegetation to occur in the riparian zone as seen in mediterranean-type streams in the Northern Hemisphere (86), with equivalent species pairs occurring in different mediterranean regions (e.g. Israel and California, 150).

With increasing aridity, the riparian vegetation of mediterranean-type streams becomes shorter, more scattered, more restricted to the side of the active channel, and markedly different from the upland regions (58, 103). Because the riparian vegetation is also related to site-specific attributes such as elevation, slope, and lithology (e.g. 56, 111), it may exhibit spatial variability in species richness, composition, and density from the headwaters at high elevation to the lowland reaches (56). Shrubs and herbaceous plants often predominate on exposed banks, particularly in areas impacted by humans, and their richness increases in exposed streambeds of intermittent streams (56). Although riparian vegetation of humid regions cannot withstand even mild fires (121), vegetation along mediterranean-type streams is frequently exposed to natural and human-made fires (22, 23, 158, 168) and therefore may be more fire-adapted and show more rapid recovery after fire.

Inputs of Allochthonous Organic Matter

Riparian input may be the primary energy source to consumers in low-order streams worldwide (e.g., 110). Its role in stream ecosystems is well recognized, based mostly on studies in temperate forests (e.g. 3, 110, 174). Although far less is known about riparian inputs to mediterranean-type streams, canopy cover and organic matter input in low-order streams in the wetter range of the mediterranean climate are apparently as important as they are in temperate, forested streams (e.g. Table III in 103).

mediterranean-type streams differ from temperate deciduous-forest streams in the timing and dynamics of allochthonous detritus input. In the latter, the bulk of litter fall occurs in a short pulse in autumn (ca. 70%–80% in 1–2 months, e.g. 60), with additional material entering the streams by lateral movement over the re-mainder of the year (e.g. 10, 42, 112). The few studies that have measured organic matter input to mediterranean-type streams suggest a more protracted period of litter fall than in non-mediterranean-type streams, with peaks occurring at different times of the year in the Northern and Southern Hemispheres (autumn and spring cf. summer, respectively, 22, 91, 103, 163). In the Northern Hemisphere, the presence

of fall-winter or summer deciduous trees along with sclerophyllous evergreens in the riparian community of mediterranean-type streams (e.g. 43, 86, 103) can partially explain the autumn peak and the extended period of litter production. In the Southern Hemisphere, protracted litter fall results from evergreen phenology whereby new leaf growth is balanced by almost simultaneous leaf fall (157); perhaps the summer peak results from the relic phenology of the tropical-subtropical vegetation that occurs there (155, 157). In Northern Hemisphere mediterranean-type streams, most input occurs when discharge is high and the temperature is relatively low. In contrast, most leaf fall enters mediterranean-type streams in the Southern Hemisphere when discharge is low and water temperature is usually increasing.

Riparian litter that enters streams by lateral movement, i.e. blown by the wind, sliding in from the stream banks, or being carried in by receding flood water (10, 136), may vary considerably in quantity and quality, but it may be especially important in areas of low plant cover, such as in higher-order streams or mediterranean-type streams in drier regions. The lateral movement of the riparian litter, however, is expected to vary locally depending on geomorphology and the nature and density of the understory vegetation (34), and whether the litter fall is wind blown or floodwater transported.

Retention and Transport of Allochthonous Organic Matter

The availability of allochthonous detritus to consumers depends not only on inputs but also on the instream distribution of these inputs. The latter is a function of the retentive capacity of the stream, which is generally inversely related to discharge and positively influenced by retentive structures (i.e. rocks and debris dams) where coarse particulate organic matter (CPOM–>1 mm in diameter) accumulates (e.g. 133, 136, 149, 153, 154). During the wet season, spates scour the streambed and transport particulate matter downstream; therefore, low-order mediterranean-type streams in both hemispheres are likely to exhibit lowest standing stock of CPOM during the wet season. In mediterranean-type streams in the Southern Hemisphere, most of the allochthonous detritus is expected to be transported downstream several months after it enters the streams. In Northern Hemisphere mediterranean-type streams, the residence time of the allochthonous matter may be much shorter because it enters the streams shortly before or at the time of flooding. In streams with broad valleys, litter may either enter the stream or be deposited in the floodplain during the rise and fall of the hydrograph (44, 136, 151). Thus, fluctuating discharges during the wet period may sequentially accumulate, replace, or distribute CPOM in streams (47); however, the organic material is rearranged only during high discharge periods.

The retentive capacity of forested streams is markedly enhanced by accumulations of large woody material originating in the riparian zone (120), which forms debris dams (12). Because of sparser woody riparian vegetation (except for restricted headwater reaches in the more mesic mediterranean range), mediterranean-

type streams are likely to have fewer debris dams (on an areal basis), lower retention capacity, and less allochthonous detritus available than their temperate forest counterparts with similar physical structure (e.g. 91). Human interference that typically occurs in mediterranean regions (deforestation, grazing, fire, channelization, urbanization) further reduces riparian inputs of woody material and the likelihood of natural formation of debris dams and backwater habitats in mediterranean-type streams.

In the Northern Hemisphere where the largest amount of litter fall apparently enters mediterranean-type streams in autumn and winter (e.g. ca. 60% in a Moroccan stream; 103), CPOM is expected to be retained in low-order reaches for only a short period in autumn (1–2 months) until the rainy period commences and the seasonal successive floods occur. In short and steep gradient mediterranean-type streams with low retentive capacity, a significant portion of the CPOM that enters the stream during fall may be exported downstream and possibly even leave the system incompletely processed (energy "leakage" sensu 172). This loss may be partly compensated for later in the year by the influx of litter in spring and summer (e.g. ca. 40% of the annual input in a Moroccan stream, 103). In contrast, in the Southern Hemisphere where litter fall production peaks in late spring and summer at the time when the discharge in mediterranean-type streams is decreasing, CPOM can be effectively retained in low-order reaches for a period of 4–6 months (22, 92), but this CPOM may be reduced by high numbers of shredders that occur there (162, 163).

ECOSYSTEM AND AQUATIC BIOTA RESPONSE TO FLOODING, DRYING, AND HUMAN IMPACT

Expected Response

Based on the characteristics of the hydrograph of mediterranean-type streams, associated seasonal changes in habitat conditions and resource availability, the patterns of input of allochthonous organic matter, and the seasonal scarcity of water, we would expect that the biota of mediterranean-type streams should follow certain predictable trends. We propose 25 testable hypotheses (sequentially numbered in brackets) organized around (*a*) abundance and diversity, (*b*) richness, (*c*) abiotic and biotic pressures, (*d*) species coexistence, (*e*) riparian inputs and the importance of allochthonous organic matter compared to autochthonous production, and (*f*) competition for water and the impact of human activities. After presenting the hypotheses, we examine what the literature pertaining to flooding and drying, and the status of stream ecosystems in mediterranean areas, can tell us about actual influence of environmental and human factors.

[1.1] Unless the stream dries completely, the abundance of the biota is expected to be lowest during the wet season when flooding occurs. [1.2] In spring, following the cessation of flooding, the biota will rapidly increase in abundance from individuals recolonizing from refugia (e.g. fish) or from individuals migrating from

nearby aquatic habitats (e.g. insects, amphibians). [1.3] The most flood-resistant species will remain, and the resilient species (the "pioneer species" that are effective colonizers after disturbance) will be the first to colonize after floods cease. [1.4] These are gradually augmented with other species that are less resistant to flooding and slower to recover but that can use the window of opportunity present during late spring and early summer, when habitat and resource availability are high and habitat conditions are relatively moderate, to become established, grow, and reproduce. [1.5] Correspondingly, the abundance of the biota in mediterranean-type streams is expected to be highest at the end of the intermediate period between flooding and extreme drying.

[1.6] With the progression of drying in late summer and fall, and the associated decline in habitat availability and deterioration of water quality, the biota gradually becomes dominated by species that tolerate low discharge, warmer water, and poor water quality. [1.7] Correspondingly, diversity (i.e. the interaction of richness and evenness) should differ between winter and summer assemblages, reflecting temporal changes in species dominance that result from changes in resource availability and habitat conditions; evenness should be lowest at the end of the drying period when extreme physical and physicochemical conditions prevail. [1.8] Depending on the extent of drying, overall abundance can remain high, increase even further when drying is slow and isolated pools maintain water, or decline when drying is rapid and habitat conditions deteriorate or pools dry. [1.9] Furthermore, the species composition and abundance of the biota in mediterranean-type streams is expected to shift rapidly from the late summer-fall assemblage to that of the winter assemblage with the onset of floods; this is in marked contrast to the gradual transition that occurs from the end-of-flood winter faunal assemblage to the summer assemblage. [1.10] The change from the winter assemblage to that of the summer assemblage occurs earlier in drought years as a result of the earlier decline of the hydrograph. [1.11] Correspondingly, the community succession for macroinvertebrates in mediterranean-type streams occurs over the scale of one year, whereas that of temperate humid streams can be longer and that of temperate desert streams can be shorter.

[2.1] Although faunal composition changes occur, species richness is expected to be relatively persistent, reflecting the evolutionary adaptation of the biota in mediterranean-type streams to flooding and drying. [2.2] Moreover, species that evolved in streams that are disturbed predictably, as mediterranean-type streams are, may be expected to have life-history adaptations that maximize growth and reproduction during the period of moderate habitat conditions and minimize exposure of vulnerable stages to extreme conditions of flood or drought.

[3.1] Within an annual cycle, the regulation of assemblage structure in mediterranean-type streams is expected to temporally alternate between mostly abiotic controls during flooding ("reset" periods) and toward the end of the drying period (e.g. extreme physical-chemical conditions, such as high temperature, low dissolved oxygen, loss of flow), and biotic controls (e.g. predation, competition) that occur when isolated pools form. This pattern correlates with the hydrograph

of mediterranean-type streams, where extreme forces of mechanical stress and abrasion drastically alter the physical and biological nature of the stream during flooding (high abiotic pressures), which is followed by a period of high resource availability combined with moderate habitat conditions (low abiotic pressures) and then the gradual transformation of the lotic into a lentic habitat. [3.2] During the latter period, the biotic interactions peak (high biotic pressures) but then may decline when extreme conditions prevail.

[4.1] Species in mediterranean-type streams differ in their resistance and resiliency in coping with the sequential abiotic and biotic pressures that occur in these systems. Consequently, the competitive advantage of different species varies with the temporal changes in intensity of abiotic conditions and biotic interactions, and so facilitates species coexistence.

[5.1] The importance of allochthonous organic matter in mediterranean-type streams is generally expected to decrease along increasing gradient of aridity; in contrast, the importance of autochthonous organic matter increases along this gradient. [5.2] Although in both hemispheres the input of leaf litter to mediterranean-type streams is temporally protracted, in the Northern Hemisphere it enters the streams shortly before or at the time of flooding when discharge is high, and temperature and autotrophic activity are relatively low; in the Southern Hemisphere, more of the litter fall enters streams in late spring and summer when discharge is low, temperature is increasing, and autotrophic activity is high. [5.3] As a result of the short contact time between shredders and other decomposers with the leaf litter, a relatively larger portion of the CPOM is likely to be washed downstream (and possibly out of the system), not completely processed in mediterranean-type streams in the Northern Hemisphere than in their counterparts in the Southern Hemisphere (assuming streams with similar retention capacity). [5.4] However, in drought years when extreme habitat conditions develop early in the drying season, shredder activity may be inhibited, and the remaining incompletely processed CPOM in mediterranean-type streams in the Southern Hemisphere may be washed downstream by the next year's floods. [5.5] Overall, shredders may be expected to play a smaller role and filter feeders and scrapers a larger role in mediterranean-type streams relative to the role they play in streams in more humid regions. [5.6] Riparian vegetation of mediterranean-type streams should be more adapted to fire (i.e. able to recover rapidly after fire) than riparian vegetation along temperate, forested streams.

[6.1] The seasonal availability of water in mediterranean-climate regions leads to a competition between human needs for water and the needs of water in the normal functioning of mediterranean-type streams. The impact of this competition is strongest in drought years when discharge is naturally reduced; then even a small diversion of water may have a disproportional large adverse effect. [6.2] Moreover, increases in diversion of water for human use exacerbates the impact by the combined effect of reduced dilution capacity and increased pollution of return water. [6.3] Given the present trend of population increase and increasing demand for fresh water, the competition for water among different users will intensify

and result in most mediterranean-type streams having little chance of surviving as sustainable, self-regulating ecosystems.

Assemblage Response to Flooding and Drying

The role of flow in determining the distribution and abundance of aquatic organisms has been of interest to ecologists since early this century. Numerous examples of behavioral (161) and morphological (Table 8A in 141) adaptations and responses of stream organisms to flooding have been proposed. The survival of many organisms depends on finding a refuge from severe hydraulic stresses (e.g. 98); however, even the most effective instream refuge can become ineffective when flood intensity is high (e.g. in constrained channels).

For benthic macroinvertebrates, floods in all stream types consistently reduce population densities (because of reduced abundance and/or an increase in wetted area), but floods have a less consistent effect on reducing richness (for mediterranean-type streams: e.g. 6, 32, 93, 107); lower densities can result from drift (catastrophic drift in the sense of 177) and substrate disturbance (e.g. 39). Macroinvertebrates typically occurring in the wet season can persist into the dry season following wet winters, whereas typical dry-season taxa may appear earlier following drier winters (43). Severe floods greatly reduce population size of organisms that are entirely aquatic (e.g. snails, ostracods, some hemipterans), while those with terrestrial aerial stages (e.g. most aquatic insects) rapidly recolonize these streams (43). Density reductions in the populations with terrestrial aerial stages are not reflected in densities of the following generation (e.g. 57, 107), but in entirely aquatic organisms they are (43). Typically, benthic macroinvertebrate faunal assemblages differ before and after the flood period in mediterranean-type streams (e.g. 32, 107, 140); in part this is because flow-dependent taxa (e.g. filter feeders) are affected when flow is eliminated in isolated pools.

Relative to flooding, the effects of drying on biota have been little studied, and most studies have been descriptive accounts of physiological or behavioral responses, or lists of taxa collected (14, 20). For biota of temporary streams in both mediterranean and other climates, drying is a key environmental factor influencing their distribution, abundance, and life histories (159, 164, 173). While flooding reduces number of individuals, drying may increase numbers locally (from concentration of individuals into smaller areas), decrease (from predation or oxygen stress), or leave densities of individuals unchanged (159).

Although flooding affects stream organisms through a direct abiotic effect (e.g. the scouring of substrate) that results in their displacement, drying can produce a combination of abiotic and biotic effects. Flow and consequent oxygen reductions may result when isolated pools form, and these severe abiotic conditions can exclude some taxa. Moreover, biotic interactions related to food availability may occur as well. Predation has been shown to increase in isolated pools (17, 38, 109, 159), and intraspecific competition has been shown to result in reduced fecundity among macroinvertebrates (e.g. 57). In the latter study of a

caddisfly population in a northern California mediterranean-climate stream, the authors used long-term weather records to suggest that dry years that result in food limitation occur about every ten years, droughts that result in reductions of population fitness occur about 4/100 years, but during normal rainfall and wet years (which include most years), population densities are sufficiently reduced by floods (97) so that neither food limitation nor reductions in fecundity typically occur (57).

The effect of drying is most severe when the stream bed becomes completely dry. Under these conditions, taxa lacking desiccation-resistant stages or those unable to find refugia are eliminated until recolonization occurs. In a coastal California springbrook, a severe drought resulted in loss of habitat for over 3 months; the caddisfly population present shifted from one with an age structure typical of a multi-cohort population to one typical of a single-cohort population (137); perhaps even more striking was that age structure did not return to the pre–loss-of-habitat condition until 10 years later (138).

As the temporal sequence of drying in mediterranean-type streams progresses, a gradual shift occurs from macroinvertebrates typical of lotic systems to those that are typical of lentic systems in the isolated pools that form (e.g. 1, 38), to semi-aquatic taxa (e.g. higher Diptera) that colonize when only moist substrates remain, to completely terrestrial taxa (e.g. carabid beetles) that occur on the dry substrate surface as in any other cleared terrestrial habitat. Complete drying of stream bed channels occurs with some regularity in the drier parts of mediterranean-climate areas and less frequently in more moist areas; drying will eliminate all species that lack either resistant stages or the ability to find refugia (e.g. the hyporheic zone, 108). With the initiation of floods a rapid shift occurs from summer macroinvertebrate assemblage to a winter one.

The responses of fish communities in mediterranean-type streams to the sequential pattern of flooding and drying are less well known than the responses of macroinvertebrates to these stresses. Studies in streams with contrasting flow regimes suggest that variability in flow can temporally change the structure of stream fish assemblages by affecting mortality and recruitment rates of species differently (e.g. 72, 124). Moreover, the impact of flow variability on both assemblage structure and habitat use is much stronger than the impact of resource limitation and biotic interactions (e.g. 72). However, the relatively long flood-free period during the dry season that is typical in mediterranean-type streams suggests that the significance of density-dependent biotic interactions may play a greater role in fish communities in mediterranean-type streams than in temperate desert streams affected by repetitive, unpredictable disturbances of flooding and drying. For example, the characteristics of the fish assemblage in a small California stream with a hydrologic regime similar to that of mediterranean-type streams place this stream toward the deterministic end (i.e. mainly competition and predation regulation) of the deterministic-stochastic (i.e. flow-variability regulation) continuum of community structure (118; see also 165).

Fish can avoid the impact of high velocities by moving toward the stream bottom or edge where the shear stress is minimal (101), or they can escape and assume

a proper orientation to high flows, which allows them to persist during floods (109). Fish may also migrate into tributaries prior to or during the flood to avoid drifting downstream (e.g., 54) where they may get stranded in isolated reaches and markedly reduce their chance for recovery.

Floods have variable effects on fish populations. Several studies have shown a decline in abundance following intense floods (e.g. 36, 54, 109), but physically (and thus hydraulically) complex reaches lost proportionally fewer fish than hydraulically simple stream reaches (e.g. 124). Studies show that fish densities can rapidly recover after intense and even catastrophic flood events (e.g. 38, 101). Others found persistence of the fish assemblage (e.g. 101, 118), which may be attributed to the timing of flooding with respect to life cycles (i.e. absence of early life stages that are more vulnerable to mechanical stress; 106, 124), or the different intervals of recovery after flooding that were considered (106). Likewise, site-specific features such as pool size and depth, availability of floodplain habitat, and presence of stable substrate have been shown to significantly influence the ability of fishes to survive flood events (e.g. 106). Differences in these features may account for contrasting observations. Persistence of fish populations after flooding could also result from reduction in number of early stages (e.g. eggs or embryos), which could reduce competition and increase the survivorship of young fish (e.g. 101).

Fish in mediterranean-type streams are expected to be highly adapted to drying (e.g. 117, 135). Cessation or reduction of high flows in drought years might increase survivorship of pool-dwelling fish by reducing direct mortality, lowering energy expenditure, and increasing foraging success (72), but this response has not been consistently reported (e.g. 62). Fish may avoid drought effects by migrating upstream to inhabit remaining suitable habitats (72). Drying may differentially reduce survivorship depending on the species and, like with macroinvertebrates, intraspecific competition may occur within populations of tolerant species. This may be particularly important in fish populations that are stranded in isolated pools.

Species Traits Related to Flooding and Drying

In geological terms, the climate of the mediterranean basin is very young, appearing in the Pliocene approximately 3.2 million years ago (167). Many of the extant plant taxa in the mediterranean existed prior to the appearance of this climatic type (83). Certainly, many inhabitants of mediterranean-type streams are widespread in their distribution in different climatic regions, but the levels of endemism found for lotic fauna in mediterranean-type streams can be extremely high. For example, the highest rates of endemism in Europe occur in the mediterranean-climate areas of Italy and Greece for the insect orders Ephemeroptera, Plecoptera, and Trichoptera, all of which occur predominantly in lotic environments (data from Tables in 89), and for fish as well (113). Others have also noted that ecologically distinct taxa occur in mediterranean-type streams throughout the world (e.g. 21). However, at a broad taxonomic level and after removing endemic taxa, the macroinvertebrate

fauna collected when flow resumes after drying was similar among desert streams and intermittent streams (including mediterranean-type streams) in Africa, Australia, and North America (20). The species richness of biota that occur in mediterranean-type streams is also related to a variety of historical (e.g. climatic history; 30) and local factors such as vegetation type (e.g. 104), recent land use (e.g. 80), salinity (e.g. 70), and of course permanence of water.

Disturbance regimes are a strong component in the evolutionary history of biota (59, 139). Although both flooding and drying occur in streams in almost all climate types, the high seasonal predictability of the hydrograph of mediterranean-type streams should select for life-history features that favor resistance from being removed by floods, and survival during periods of no flow and high temperatures (or even loss of habitat from drying during droughts). Accompanying or in lieu of these solutions, organisms may have evolved responses that allow them to recover rapidly from disturbance, i.e. that emphasize resilience.

From the perspective of an organism with less than a one-year life cycle (e.g. most benthic macroinvertebrates), the annual predictability of a wet season with floods and a dry season with gradual reductions in (or cessation of) flow in mediterranean-type streams is very high. For an organism with a multiple-year life cycle (e.g. fish and amphibians), the year-to-year variation in the timing, intensity, and frequency of floods, and the rate of drying, are of critical importance to survival but are much less predictable. In the long term (more than 10 years), the likelihood of wet years with extremely high flows and drought years with extreme drying are somewhat predictable, but the timing within that cycle is not. As a result, short-lived and long-lived organisms would be expected to have evolved different adaptive strategies to these conditions. The short-lived organisms (e.g. macroinvertebrates) will maximize recovery rates through short life cycles and high reproduction; the long-lived organisms (e.g. fish) will maximize resistance by behavioral, morphological, and physiological adaptations.

The survival of benthic macroinvertebrates during the drying period in a mediterranean-type stream may involve resistance mechanisms, such as tolerance to abiotic stresses in isolated pools (e.g. 64, 65), having desiccation resistent stages (e.g. 15, 20), finding refugia such as entering moist substrate or the hyporheic zone (e.g. 15), or recolonizing from nearby permanent sources (e.g. 21, 137, 138). Life cycles may also be tied to the sequential predictability in mediterranean-type streams by seasonal breeding patterns (31), or flexible life cycles (21, 142) such as alternating short and long generation times to produce three generations in two years (29). Macroinvertebrates of highly seasonal waters such as some mediterranean-type streams and desert streams exhibit unique adaptations in that: (*a*) egg-hatching coincides with the historically optimum time that water reappears; (*b*) there are predictable, seasonally adjusted growth rates; (*c*) there is some specialization of feeding on predictable food types; and (*d*) there is a high correlation between life history stages and environmental factors (179).

Macroinvertebrates living in some mediterranean-type streams show adaptations that represent trade-offs between resistance to flooding and drying, and

avoidance of predators (129). Mobile invertebrates are exposed to predators but may have a better chance of finding refugia that enable them to avoid being washed away or stranded in a drying reach and may be more efficient in locating and gathering food, thus growing and recovering faster. Sessile, armored, and sedentary organisms may be less vulnerable to predation than mobile species but may grow slower and be at a greater risk in areas of scour or desiccation. Therefore, more mobile species that are less vulnerable to high discharges are expected to dominate in spring, shortly after the cessation of floods, and predator-resistant species will do best under the low flows that occur in summer (129).

The recovery rate of fish (i.e. their resilience) is constrained by relatively long life cycles, but they can have greater resistance to flooding and drying than macroinvertebrates because of their greater mobility compared to the passive mobility (i.e. via drift) of most macroinvertebrates. Given the high seasonal predictability of floods and drying, we would expect fish inhabiting mediterranean-type streams to exhibit life cycles that are synchronized with times of moderate flows, increasing temperature, and increasing food availability in order to maximize the growing season and population recruitment, and to minimize exposure of vulnerable stages to extreme conditions. Indeed, most of the fish in mediterranean-type streams reproduce in spring during the declining stage of the hydrograph when temperatures are increasing (e.g. 144). In contrast, in temperate streams where flooding may occur at almost any time of the year, the spawning seasons of most species are protracted or staggered (118). Consequently, the composition of the fish assemblages in temperate streams may vary considerably from year to year, whereas that of mediterranean-type streams may be relatively persistent (118), except where exotic species have invaded disturbed streams (7, 115).

Abiotic versus Biotic Regulation of Assemblage Structure and Species Coexistence

Intensely disturbed streams (i.e. those with violent spates and/or a high degree of intermittency associated with harsh physicochemical conditions) are mostly regulated by abiotic factors (e.g. 38, 61, 87, 126). Biotic controls such as predation and competition may be more important under relatively more stable conditions (e.g. 147, 171). Biotic interactions generally correlate with density (e.g. 152); however, little is known about the importance of density in terms of some biotic interactions (131), as for example in mutualism and other types of symbiosis. The expected increase of populations in mediterranean-type streams during late spring to the middle of summer suggests that biotic interactions will peak at the end of this period.

As the dry season progresses, abiotic pressures increase, perhaps even culminating in a loss of habitat (e.g. 137). Biotic interactions can occur during drying as well. For example, increases in density of macroinvertebrates in isolated pools attract invertebrate predators (e.g. 17, 159) and increase the predation rate by fish (99), oftentimes on nectonic species (e.g. mosquito larvae and dytiscid beetles, 38).

Several authors have suggested that coexistence and high resource overlap for assemblages inhabiting a disturbed ecosystem are possible because intense environmental variation reduces species abundance to levels below which resource limitation occurs, or variation may shift competitive advantage from one species to another (e.g. 41, 72, 109, 176). Observations in an unregulated Northern California mediterranean-type stream have shown that invertebrates are the primary consumers in three- or four-level food chains that result because scouring floods reduce grazers; algae recover before grazers increase and provide the most important colonizable substrate. If scouring floods do not occur, a two-level food chain results, with high densities of grazers and low algal growth (129, 130). In a southern California mediterranean-type stream, spate-cleared areas were rapidly colonized by black fly larvae; in contrast, the substrate was increasingly dominated by a competitively superior caddisfly in the absence of high flow (81).

Heterotrophy versus Autotrophy

The late spring and summer peak of litter input to mediterranean-type streams in the Southern Hemisphere occurs when discharge is reduced, which allows relatively long contact (at least four months) of decomposers and detritivores with CPOM (unless the stream dries). Combined with elevated water temperature in summer, this should promote rapid and efficient processing of the organic matter (79, 166). However, the biotic response observed in Australian streams (including mediterranean-type streams) with bank vegetation of certain eucalyptus trees may contradict this prediction (28). Fewer shredders, poor colonization by aquatic hyphomycetes, and the subsequent slow breakdown of eucalyptus leaves in summer were attributed to the low nitrogen and high polyphenol concentrations that make senescent leaves of this species a low-quality food source (8, 9, 25–28, 35). Inhibited growth rate was also found for a detritivore feeding on eucalyptus leaves in a mediterranean-type stream (35). The inhibitory effects of the polyphenols of eucalyptus leaves dissipate with time and, thus, it is less apparent in leaves that are washed downstream (9).

Low flow, possibly higher concentrations of leached polyphenol compounds, and high water temperature that result in low oxygen level could also restrict microbial conditioning and eliminate some of the detritivores in summer, contributing to slow breakdown rates of CPOM observed in Australian mediterranean-type streams (25–27). This, however, appears to be a special case for Australian streams and possibly more so for those in a mediterranean climate because highly refractory, sclerophyllous species of eucalyptus dominate in the riparian zone and environmental conditions in summer are less conducive to metabolism by consumers (25).

Microbial processing of CPOM on land is directly influenced by the extent of soil wetness; as a result, different loads of dissolved organic carbon (DOC) are expected to enter mediterranean-type streams in wet and drought years (33, 105). Moreover, because semi-arid land leaches more refractory DOC than does soil in more humid regions, lower metabolic rates of biofilms result in the former (94).

The importance of autochthonous production of organic matter in streams is generally expected to increase downstream from the headwaters because of the widening of the stream channel, which allows more light to reach the water, production is expected to decline in high order reaches where turbidity increases (e.g. 172). This effect will be less pronounced in regions with infertile soils and low nutrient loading in streams (e.g. Australia). Because of sparser vegetation and thus greater light penetration, the importance of autochthonous production is expected to be higher in lower-order mediterranean-type streams than in similar order streams in more humid regions. Autochthonous production will also increase in importance further upstream in mediterranean-type streams that are in regions with increasing aridity and will be similar to that in desert streams. Environmental conditions typical to mediterranean-type streams, such as long periods of clear sky, large sunlit instream areas, mild winter temperatures, and low flows, promote algal growth such as that of the attached filamentous alga *Cladophora glomerata* (13, 43, 127–129, 178). In disturbance-controlled systems such as lakes undergoing water level fluctuations (63) and in a spate-scoured mediterranean-type stream, *Cladophora* has been shown to produce large biomass after the cessation of the flooding period, which provides substrate for colonization of epiphytes and invertebrates and serves as an important food source (11, 53, 127–129). Rapid colonization of spate-scoured substrate in riffles, first by diatoms and then by colonial algae, occurred as the time increased since the last disturbance in a southern California mediterranean-type stream (43). The establishment of colonial algae was thereafter significantly affected by macroinvertebrate grazing and perhaps sedimentation.

The prolonged low flow and high temperature during summer in mediterranean-type streams enhance primary production by allowing a massive biofilm matrix (composed of algae and heterotrophs) to develop on solid surfaces (e.g. 74, 75, 146). A different biofilm formed by microorganisms and invertebrates in the hyporheos during the period of low flow may be an alternative energy and nutrient source to mediterranean-type streams, in addition to the above mentioned allochthonous and autochthonous sources (47). High discharges in winter and upwelling of groundwater wash the biofilm into the stream where it becomes a utilizable resource for surface dwellers. Furthermore, this rich biofilm can enhance leaf litter conditioning and processing (47).

Competition for Water and the Associated Human Impact

Mesic regions generally have a surplus of river water, a predictable and relatively stable supply, and a per-capita water renewable volume that exceeds the demand. In contrast, mediterranean-climate regions (like arid regions) have a deficit of water resources (71, 96), which is typical of sub-humid zones (sensu 170) where the ratio of mean annual precipitation to mean potential evapotranspiration is <0.75 (76, 170). However, unlike arid regions where the shortage of water and harsh climatic conditions limit population growth and development, an abundance

of sunshine and mild winters make mediterranean-climate regions particularly suitable for human settlement and intensive agricultural production (e.g. 122). This results in a high demand for freshwater, particularly for irrigation, which often consumes water more than all other sectors of the economy combined (e.g., ca. 70% in California and Israel; 180). Consequently, mediterranean-type streams are particularly susceptible to human impact (46, 67, 145). Moreover, the seasonal availability of water in mediterranean-climate regions is a strong catalyst for flow regulation through water diversions and reservoir construction (e.g. 46, 47, 66, 129, 169).

When the ratio of renewable water to withdrawal volume is <1 (e.g., Israel; 180), the excess water demand for freshwater must be complemented by the use of reclaimed wastewater, desalinized water, or water imported from elsewhere. This produces a strong competition for water among consumer sectors. This competition is accentuated in drought years when the increased water deficit imposes further reductions on water consumption (e.g. 67). In practice, a greater proportion of water is abstracted from streams for human use during drought years, which leaves less for the biota at times when they need water the most (114).

Mediterranean-type streams, like other streams in semi-arid regions, are particularly susceptible to water diversion (directly or via groundwater withdrawal) and flow regulation. Diversions, like flow regulation in mediterranean-type streams, interfere with the fundamental mechanisms that structure the stream habitats: They reduce the intensity and frequency of scouring floods, alter the normal stream-floodplain interaction (18, 19), and change water quality conditions (e.g. 169).

Macroinvertebrates and fish are directly affected by dam construction in mediterranean-type streams (e.g. 113, 132, 169, 175). The elimination of eels from central Spain (66) and the drastic decline of Chinook salmon in California (181) are extreme examples of such effects on fish.

In summer, when flow in mediterranean-type streams is naturally reduced, even a relatively small diversion of water from the stream may drastically reduce the water surface and have an effect similar to that of extended drought. Long periods of reduced flow may also result in extinction of threatened species (e.g. 114). Furthermore, the dilution capacity of the stream is lowest during this period and, consequently, even small discharges of poor quality water into streams may have disproportionally large, adverse effects.

Although diversion of water from the stream may change a perennial stream to an intermittent one, the return of agriculture water, and the discharge of sewage effluents into streams may lengthen inundation time (e.g. 125) or even transform intermittent reaches to perennial ones (e.g. 24, 52). This supplementation may alter the distribution of the biota (e.g. favoring pollution resistant species; 69), life history cues, and the structure of the intermittency-adapted communities that occur there.

Riparian vegetation is especially sensitive to changes in minimum and maximum flows (123). Floods facilitate the recruitment of new plants and maintain heterogeneity within the riparian zone (120). In contrast, hydrologic alterations can result in shifts in riparian plant community composition as well as senescence

of woody communities (120). Reduced channel wetness for prolonged periods may also result in loss of riparian vegetation and in extensive bank erosion, particularly when combined with steep topography (78). A loss of vegetation and a ten-fold channel width increase were reported in a California mediterranean-type stream in response to local underground water withdrawal that lowered the water table and dried the river bed (95). Elimination of woody vegetation may result in overall reduction in shading, and inputs of allochthonus detritus and large woody debris.

The sensitivity of the riparian vegetation to water diversions is expected to be highest in streams that are within the intermediate wetness range of the mediterranean climate, where a relatively small reduction in the water balance can have a disproportionally large effect, transforming perennial reaches to intermittent ones. In contrast, loss of scouring flow combined with low but constant summer release from upstream dams may enable in-channel intrusion of riparian vegetation that reduces conveyance and increases shading and input of allochthonous detritus.

One major but rarely discussed consequence of water diversions is the change in salinity that puts the biota of mediterranean-type streams at risk. Reduced flow followed by an increase in salt content is expected in mediterranean-type streams during drought periods (e.g. 32). Moreover, reduced discharge also enables greater surface or subsurface intrusion of seawater into coastal streams, transforming freshwater habitats into brackish ones. Agricultural practices such as irrigation-water return and salt flushing increase salinity in mediterranean-type streams (e.g. 122). Lowering of the watertable can result in intrusion of seawater into coastal aquifers or seepage of salt water from inland salt deposits historically covered by sea (e.g. mediterranean Basin). Salinity increases in streams may also result from selective diversion of freshwater sources, whereby the proportion of water contributed by the brackish springs increases (e.g. 67), and by removal of native vegetation in areas where evapotranspiration exceeds precipitation and salts accumulate in the soil (e.g. Australia, SE Bunn, personal communication). mediterranean-type streams can therefore be subjected to salinity pulses in response to fluctuations in annual rainfall and human exploitation of freshwater, which in turn may significantly change the assemblage structure (e.g. from insects to crustacean predominance; 82) or riparian composition (e.g. an increase in salt-tolerant species such as tamarisk).

The competition for water in mediterranean-climate regions is often compounded by water pollution, which threatens the existing supply of water and exacerbates the damage to stream ecosystem. Israel, one of the most water stressed countries (180), has extensive water reclamation and reuse projects; nevertheless, less than 50% of the wastewater is reused and the remaining effluents end up in streams and the sea (67).

Pollution impacts of streams in mesic regions are often ameliorated by the high dilution capacity of receiving waters that have high stream discharges; however, mediterranean-type streams experience a relatively long period of natural low flow, resulting in reduced conveyance and lower dilution capacity. Consequently, efflu-

ent release criteria developed for receiving waters in humid regions are unsuitable for mediterranean type streams (68) and can result in extreme deterioration of water quality and elimination of most of the natural biota (67).

The above-mentioned factors put mediterranean-type streams at a greater risk of adverse human impact and thus make them inherently more difficult to rehabilitate than most other stream ecosystems. Can we "have our water and drink it too"? This question may describe a rehabilitation option in water stressed regions. To alleviate the effect of stream water abstraction, the release of high quality reclaimed wastewater is presently being considered for rehabilitation of streams in Israel. However, this solution is not without potential problems: The allocation of high quality effluent for stream rehabilitation is not guaranteed because in drought years the agriculture sector will strongly compete for the higher quality effluents; public health reasons may restrict recreational uses, such as swimming and fishing; and the addition of effluents of any kind may setback stream rehabilitation efforts anytime the wastewater treatment operation fails. Successful rehabilitation has occurred in mediterranean-type streams, particularly in urban environments (e.g. 37, 143), but streams chosen may have unique reasons for selection and the costs of rehabilitation may be high (e.g. 37, 116). Allocation of water for rehabilitation of aquatic habitats in the Sacramento River Basin (California's largest river system) is being considered as part of the implementation of the Central Valley Project Improvement Act (78). In addition to reversing the increasing trend of water pollution as required by the federal Water Quality Act, rehabilitation projects in California also focused on channel stabilization, flood management, fishery enhancement, and riparian floodplain revegetation (78).

CONCLUSIONS

Although streams in mediterranean-climate regions are less studied than their counterparts in temperate, forested regions, ecological information is available for four of the five mediterranean regions worldwide (i.e. not Chile). In Australia and South Africa, however, most information is available for headwater reaches and mountain streams. Important aspects of stream ecology such as nutrient loading and spiraling, algal dynamics and primary production, secondary production, and hyporheic communities were not included in this review and deserve special attention in future overviews of mediterranean-type streams.

First and foremost, mediterranean-type stream ecosystems are ecological reflections of the unique mediterranean climate; they are fluvial systems that are physically, chemically, and biologically shaped by sequential, seasonally predictable events of flooding (late fall-winter) and drying (late summer-early fall) that vary markedly in intensity on a multi-annual scale. Although the biota is under abiotic pressure from floods, there is a period that may last for several months (spring-early summer) during which moderate ecological conditions and high resource availability allow the biota to recover from floods. However, as den-

sities increase, biotic pressures such as competition and predation also increase. If there is extreme drying or desiccation, abiotic regulation returns. This seasonal sequence of abiotic, biotic, and abiotic regulation is a unique characteristic of mediterranean-type streams.

Second, in this review we have presented 25 testable hypotheses about the structure and function of mediterranean-type stream ecosystems, including predictions about structural responses of biotic assemblages, the long debated importance of abiotic versus biotic regulation in stream ecosystems, riparian inputs and the importance of allochthonous matter, and the ecological impact of water scarcity and the resulting severe competition for water. mediterranean-type streams are particularly well suited for experimental tests of the relative importance of biotic and abiotic controls on populations and communities.

Third, the significance of the protracted leaf litter input in terms of the timing of flooding and autotrophic production peaks requires further study. More measurements of allochthonous organic-matter input in streams of different sizes and in different locations are needed, as is an assessment of its effect on community structure and function. Special attention should also be given to the effect of fires, which are common in mediterranean regions, on nutrient and organic-matter input dynamics.

Fourth, the relatively sparse riparian vegetation and abundance of sunshine in mediterranean regions suggest that autotrophic processes may play a more important role in mediterranean-type streams than heterotrophic processes. Reductions in riparian vegetation or increases in nutrient loading further enhance autotrophic processes in mediterranean-type streams.

Finally, unlike the transitory characteristic of the natural disturbances, human disturbances in streams (e.g. water diversion, flow regulation, pollution) are often permanent and tend to increase as population size increases. Population increases in mediterranean-climate regions result in an intensification of the competition for water among different users (e.g. agriculture, domestic consumption, industry, nature conservation). Consequently, mediterranean-type streams (particularly in fertile regions) face major challenges in surviving as sustainable, self-regulated systems. Attempts to rehabilitate these streams must address the inherent problem of how to compensate users for the loss of water that is needed to reinstate the typical hydrological regime of mediterranean-type streams. Rehabilitation efforts in mediterranean-type streams, therefore, may best succeed in urban or unique conservation areas where citizen pressure can successfully outcompete agricultural withdrawal.

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