Journal of Mediterranean Ecology **vol. 4, No.1, 2003: 13-21**
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Exotic crayfish activity and its effects on water quality: preliminary implications for the alternative stable equilibria in Mediterranean wetlands

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Keywords: freshwater crayfish, water quality, charophytes, aquatic ecosystem health

Abstract

Charophytes can comprise the dominant submerged vegetation in highly fluctuating wetlands. However the exotic crayfish, *Procambarus clarkii* Girard, eradicated submerged vegetation in many shallow aquatic ecosystem, moving them between stable states. In this study we aimed at elucidating how such crayfish induced changes can impact abiotic ecosystem processes. Employing enclosures we provided snap shots of water quality characteristics (total phosphorus, total nitrogen, chlorophyll *a*, and total suspended solids) 1) in the presence of charophytes and absence of crayfish (simulation of the clear water state; charophyte treatment), 2) when crayfish herbivory eliminates charophytes (transition between alternative stable states; charophyte x crayfish treatment), and 3) when crayfish has eliminated entirely submerged vegetation (reflecting the turbid state; crayfish treatment). Results indicate that the synergistic action of crayfish bioturbation and feeding mode are involved in water quality decline. However the magnitude of the decline was correlated chiefly with crayfish feeding. Crayfish herbivory substantially decreased *Chara* beds in the charophyte x crayfish treatment enclosures, but had no effects on nutrient and chlorophyll *a* concentrations. On the other hand, crayfish detritivory in crayfish treatment significantly increased nutrients a likely result of translocation of sediment-bound nutrients to the water column. Water quality decline due to bioturbation, i.e., increased non-algal turbidity due to sediment resuspension, occurred whether or not charophytes were present in the enclosures. The potential implication of our results in the context of alternative equilibria in wetland ecosystems is discussed.

Introduction

Two alternative stable states have been described for shallow aquatic ecosystems (Moss 1990, Scheffer *et al.* 1993). The first is characterised by clear water and dominance of submerged macrophytes, including the charophyceaen macroalgae. Charophytes are often the dominant submerged vegetation in hydrologically variable systems because they can germinate, grow and reproduce quickly in response to inundation (summarized in Van den Berg 1999). Here they fulfil an important role in clear water maintenance, sediment consolidation, and habitat provision for an array of aquatic biota.

Loss of submerged macrophytes promotes a successive degradation of the aquatic environments. The systems become susceptible to either wind or animal induced sediment resuspension. This has an important repercussion on water quality and habitat structure. The consequences of such a loss are a manifest decline of water quality (in terms of increased nutrient and turbidity levels and reduced transparency), a loss of biodiversity, and a shift of energy flux through phytoplankton. This state has been considered as degraded, turbid, dominated by phytoplankton (Moss 1990, Scheffer 1998).

The shift between the alternative states is the result of cultural eutrophication (e.g., Hosper and Jagtman, 1990). On the other hand, severe damage to and loss of macrophytes can be caused by animals (e.g., carp, grass carp) resulting in an equivalent loss of aquatic ecosystem quality. Animal activity can mechanically damage submerged macrophyte vegetation (Crivelli 1983). Macrophyte growth may also be hindered by shading from high algal biomass (Brönmark and Weisner 1992) and elevated turbidity (Skubinna *et al.* 1995), both of which have been shown to increase in the presence of benthic animals (Meijer *et al.* 1990, Qin and Threlkeld 1990, Richardson *et al.* 1990, Breukelaar *et al.* 1994, Angeler *et al.* 2001).

Crayfish can trigger a shift from the clear water to the turbid state by consuming macrophyte biomass (Nyström 2002). Furthermore, negative impacts are related to non-consumptive destruction, and animal-mediated bioturbation which increases turbidity. A case in point is the Louisiana red swamp crayfish (*Procambarus clarkii* Girard), which has its natural habitat range in the southeastern United States. It has been successfully introduced to several continents (Hobbs *et al.* 1989, Holdich 2002) often to obtain socio-economic benefits. However, massive proliferation was disastrous from the ecological point of view. Large-scale vegetation loss and major changes in matter and energy fluxes through aquatic food webs have been reported (e.g., Feminella and Resh 1989, Montes *et al.* 1993). However, it remains largely unknown how such shifts affect water quality characteristics.

In this study, we employed a three treatment enclosure design, aiming to simulate the potential mechanisms involved in crayfish-induced shifts between alternative equilibria in charophyte-dominated wetlands, with special emphasis on water quality. We expected that mechanisms involved in water quality decline at the ecosystem level should change with degradation and should be related to crayfish feeding mode and bioturbation activity (Fig. 1). Hence our enclosure study was designed in a way to provide instantaneous pictures of water quality in the absence of crayfish, when crayfish herbivory eliminates charophytes and during crayfish detritivory, when charophyte meadows have been largely eliminated. In the presumably healthy ecosystem, submerged macrophytes should stabilise the sediment and reduce water column nutrient and chlorophyll *a* (Chl *a*) concentrations. In the transition from the healthy to the degraded state crayfish herbivory should reduce macrophyte biomass. A concomitant negative impact on water quality is expected as a result of macrophyte destruction (i.e. leaching from damaged plant tissues, plant biomass recycling by crayfish and subsequent nutrient release to the water column). Moreover, turbidity levels should increase owing to a loss of the sediment consolidation properties by macrophytes. Finally, in the degraded state where macrophytes have been eliminated by crayfish herbivory, *P. clarkii* should change to a detritivorous feeding mode contributing to further wetland water quality decline by translocating sediment-bound nutrients to the water column. Additionally, benthic activity (burrowing, walking, tail flipping) should increase non-algal turbidity.

Study Site

Las Tablas de Daimiel National Park (TDNP; central Spain “39º08’N, 3º43’W”; Fig. 2), a site included in the Ramsar convention, is a severely degraded riverine wetland infested with *Cladium mariscus* (L.) Pohl and *Phragmites australis* (Cav.) Trin. ex Steud. It covers ca 20 km^2 in a 13000 km^2 catchment that is heavily impacted by agriculture and contamination of nearby villages. Hydrology is highly fluctuating, water inputs being provided almost exclusively by erratic discharge of the Giguela river. According to nutrient levels the wetland can be classified as hypertrophic (Sánchez-Carrillo and Alvarez-Cobelas 2001). The wetland historically supported dense submerged vegetation and populations of the white-clawed crayfish *Austropotamobius pallipes* (Lereboullet). However, floristic changes have occurred during the last decades, resulting in a replacement of the diverse submerged macrophyte flora by phytoplankton. This is the result of eutrophication, and introductions of exotic benthivorous (carp and crayfish) and planktivorous (mosquitofish) animals (Alvarez-Cobelas and Cirujano 1996; Rojo *et al.* 2000). Submerged plants are currently restricted almost exclusively to *Chara* spp. which biomass therefore is manipulated in this study in order to assess the relative importance of macrophytes and exotic crayfish on water quality. *Procambarus clarkii* was introduced to TDNP in the 1980s and has completely replaced *A. pallipes*. Because of its broad ecological plasticity, declines of commercial fishing in the area and decreased abundance of important predators (e.g. *Lutra lutra* L., *Esox lucius* L., and birds), *P. clarkii* can reach frequently very

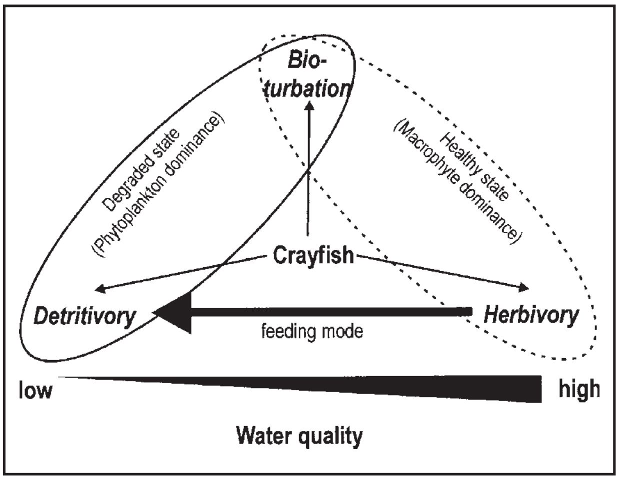

Figure 1. Conceptual model of shifts between alternative equilibria in Mediterranean wetlands with emphasis on water quality, associated with exotic crayfish (*P. clarkii*) activity (feeding behaviour and bioturbation). For details see text.

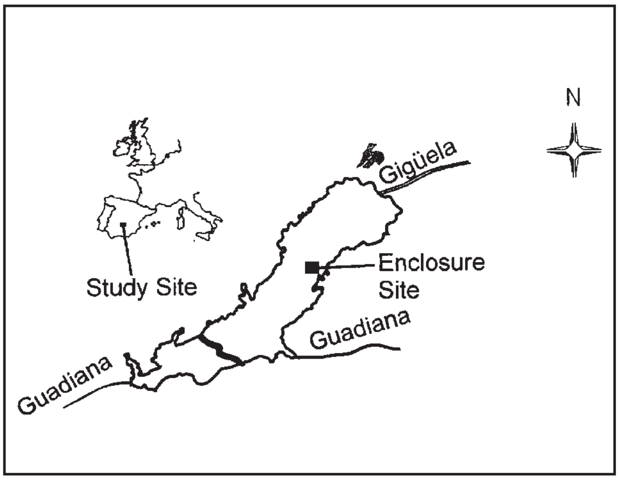

Figure 2. The study wetland, Las Tablas de Daimiel National Park (central Spain), with location of the enclosure installation site.

high biomass in TDNP. Nonetheless, its ecological impacts on the wetland ecosystem remain to be assessed fully. The fish fauna is actually dominated by non-native carp (*Cyprinus carpio* L.), pumpkinseed sunfish (*Lepomis gibbosus* L.) and mosquitofish (*Gambusia holbrooki* Gir.), which contribute significantly to wetland degradation (Angeler *et al.* 2002).

Material and methods

The experiment

Wetland enclosure studies can be faced with limitations when compared with lake mesocosm experiments. Space availability for enclosure installation can be limited because of biological (dense emergent vegetation stands) and/or hydrologic (decrease of inundated area, small open water spots) constraints. Such constraints allowed us to install only two replicates for each of the treatments and the control.

We acknowledge that the low level of replication could cause difficulty in assessing the effects of the experimental organisms. To overcome this problem our study was designed in a way to compare treatments and control, replicated in time, before and after crayfish stocking (see also Angeler *et al.* [2001] for a detailed explanation). This kind of design follows the principles of the BACI (Before-After-Control-Impact) analytical design, proposed by Stewart-Oaten *et al.* (1986), which is nowadays widely used in environmental impact assessment studies (e.g., Schroeter *et al.* 1993, Bradley and Ormerod 2002). The idea of the BACI design is to assess ecological impacts in ecosystems where replication is impossible. We believe that this design can be fruitfully applied to low-replicated mesocosm studies because one can 1) avoid extreme manipulation (i.e., unnaturally high density stocking) that are ecologically unrealistic (Crowder *et al.* 1988), and 2) reveal cause-effect relationships that may be indicative for processes taking place at the ecosystem scale. Even though responses may be subtle, they may be of theoretical and practical interest (Schindler 1987, Crowder *et al.* 1988).

Experimental and enclosure design

A total of 8 enclosures (polyethylene hose mesocosms) were established in a shallow area of the wetland (Fig. 2) prior to the onset of the vegetation period to allow for establishment of a natural submerged macrophyte community within the enclosures. This site, known as "el Tablazo" is only temporarily inundated and draws down completely during summer months. *Cladium*, *Phragmites* and also cattails (*Typha domingensis*) densely vegetate the study site. Two enclosures were assigned to the charophyte treatment (T1), 2 to the charophyte x crayfish treatment (T2), 2 to the crayfish treatment (T3), and the remaining 2 enclosures to the control which contained neither charophytes nor crayfish. The experiment started on 20/6/2000 and lasted until 8/7/2000 when the study site dewatered. A detailed description of the enclosure installation and design can be found in Angeler *et al.* (2001, 2002).

Stocking schemes and surveys

The naturally established macrophyte assemblage consisted of *Chara aspera* Deth. ex Willd. and *Chara hispida* L. Both species are lumped to *Chara* hereafter because a taxonomic discrimination was not of primary interest for this study. Young shoots of *Typha domingensis* (Pers.) Steudel occurred in negligible numbers and are not further considered. During the experiment we surveyed each enclosure for areal coverage of charophytes, by superimposing a grid with $9cm^2$ squares and counting the squares occupied by the plant. Percentage coverage proved fruitful because the highly branched growth form made it impossible to count shoot numbers. The entire macrophyte biomass was retrieved from the respective treatments as indicated in Figure 3 for subsequent determination of biomass (dry weight). Biomass of charophytes was well predicted by *Chara* cover estimates (g biomass = 1.697[%cover] – 20.71; $R^2 = 0.75$, $p = 0.006$).

The T2 and T3 enclosures were stocked with adult *Procambarus clarkii* Girard as is shown in Tab. 1. This stocking scheme is well within the natural procambarid crayfish density range in marshes (e.g., Feminella and Resh 1989, Angeler *et al.* 2001). Experimental individuals received enclosure specific marks with finger nail polish for identification against possible intruders. After termination of the experiment, animals were retrieved from enclosures, weighed and measured, and transferred to the laboratory for subsequent gut analyses. We quantified gut contents by estimating the percent cover of food items with the inverted microscope. The timing of stocking of crayfish is summarized in Figure 3. The treatment period for all three treatments commenced upon crayfish addition to the T2 and T3 enclosures. The period before is considered as the pretreatment period (Fig. 3).

Sampling and water quality variables

Field sampling was carried out two times a week during the whole experiment and included water quality and macrophyte surveys (see below). Water samples for nutrient analyses were collected in 2 L HCl-cleaned and distilled water-rinsed PVC bottles. Samples were preserved below 4 °C during the field trip and immediately analysed in the laboratory for contents of total nitrogen (tot-N), total

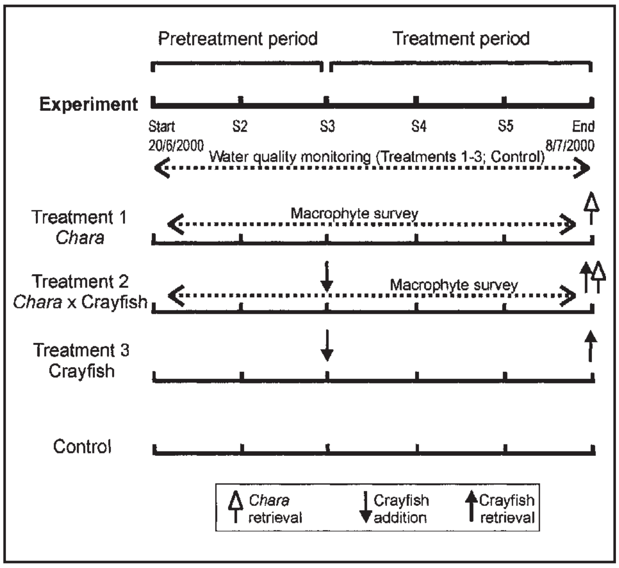

Figure 3. Graphical presentation of the experimental design, duration and methodological steps.

phosphorus (tot-P), chlorophyll *a* (Chl *a*), and total suspended solids (TSS). TSS and tot-P were analysed according to APHA (1989). Tot-N was measured employing the method of Bachman and Canfield (1996). Phytoplankton Chl *a* was measured spectrophotometrically after extraction with 90% methanol (Marker *et al.* 1980).

Statistical analyses

A repeated measures analysis of variance (RM-ANOVA) was carried out to compare the control and treatment trends in nutrient parameters, Chl *a* concentrations, and total suspended solids before (pre-treatment) and after (treatment period) crayfish stocking. All data were log-transformed to meet the criteria of normality. Given the low level of replication and limited number of observations it was reasonable to accept a relatively high type 1 error level ($\alpha = 0.10$) to reduce β (type II) errors (Winer, 1991). Such assumptions were made also in other enclosures studies (e.g., Vanni and Layne 1997, Matveev *et al.* 2000). All analyses were carried out employing the STATISTICA software package (StatSoft Inc. 1995).

Results

Nutrient and Chl *a* concentrations as well as levels of TSS were not significantly different comparing each of the treatments with the control during the pre-treatment period ($p>0.1$, Figs 4 and 5). In the treatment period several significant differences were found comparing the respective treatments with the control at a p-level ≤ 0.1

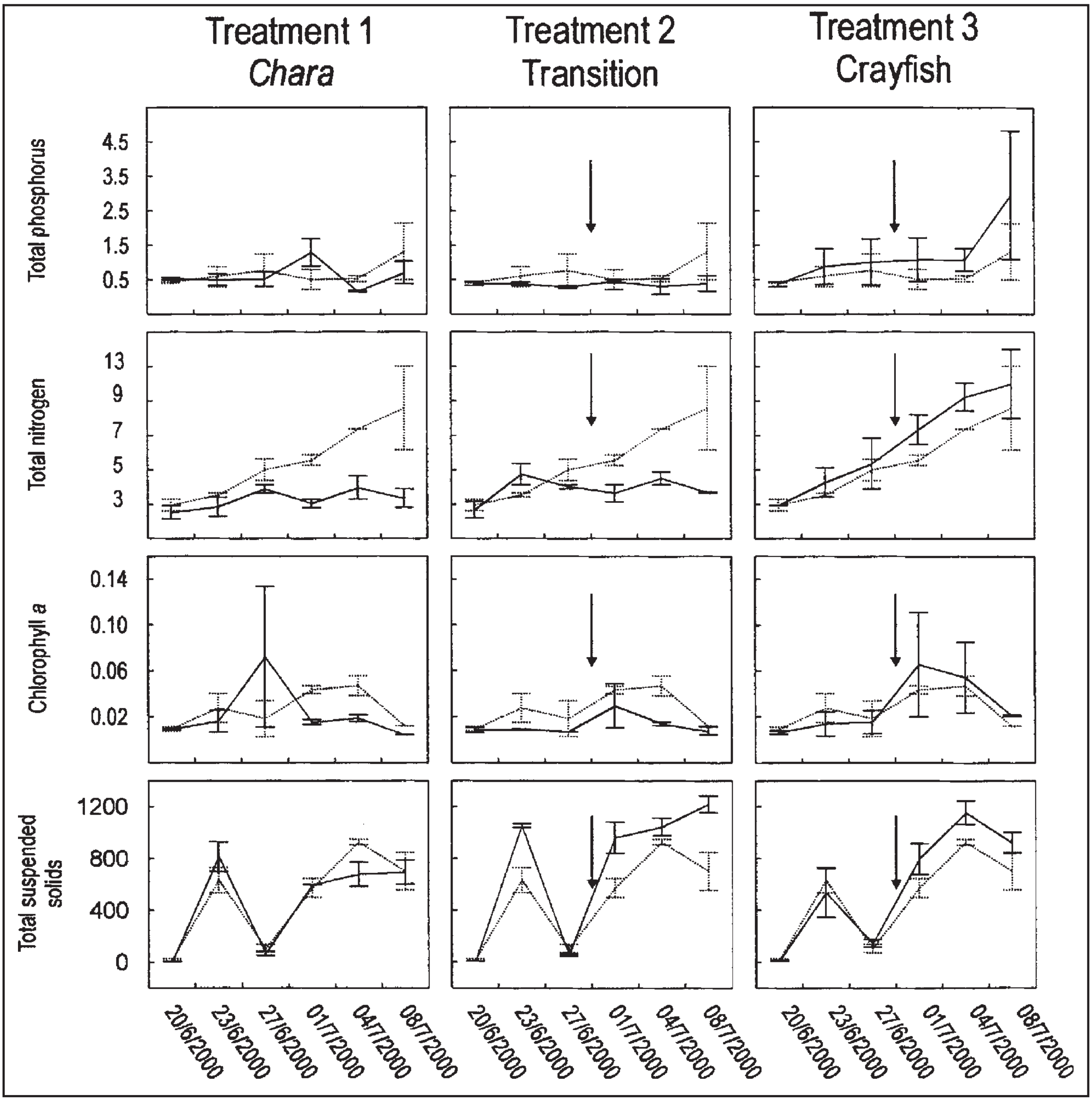

Figure 4. Comparison of time trajectories of water quality parameters in the experiment. Shown are the averages ± SEs. The addition of crayfish to the respective treatment enclosures is indicated (arrows). Full lines denote the respective treatments and dotted line the control.

(Figs 4 and 5). In T1, mean *Chara* cover increased steadily from 55% (72.6g dry weight) to 90% (132g dry weight) throughout the experiment (Fig. 6). This increase contributed to a water quality improvement in the treatment period. The charophytes reduced the levels of tot-N and Chl *a*, but no effects on TSS and tot-P were found in comparison with the control. When combining charophytes and crayfish (T2) we observed clear negative effects on macrophytes. Crayfish herbivory significantly reduced charophyte cover/biomass to 65% (91.08g dry weight; Fig. 6) and TSS increased significantly as a result of crayfish benthic activity (Figs 4 and 5). The concentration of nutrients and Chl *a* levels, however, remained in the same range as in the control. On the other hand, crayfish increased the concentrations of tot-P (p= 0.07), tot-N (p= 0.08) and TSS (p=0.04) in T3, indicating its deleterious effect to water quality (Figs 4 and 5). Interestingly, phytoplankton standing crop did not differ significantly comparing T3 with the control, even though Chl *a* was positively correlated with tot-P (Correlation analysis [CA], r = 0.63, p = 0.05) and tot-N (CA, r = 0.76, p = 0.05).

Trapping of crayfish at the end of the experiment revealed a loss in all enclosures because of mortality and escape from the enclosures (see Tab. 1). The results of the gut content analyses are summarized in Figure 7. Plants were preferred over detritus in the T2 enclosures, while detritus, as the only food source in the T3 enclosures, built up the major part of crayfish diet (Fig. 7). Crayfish scavenged on a dead conspecific in T2, resulting in a higher percentage of meat remains in the guts.

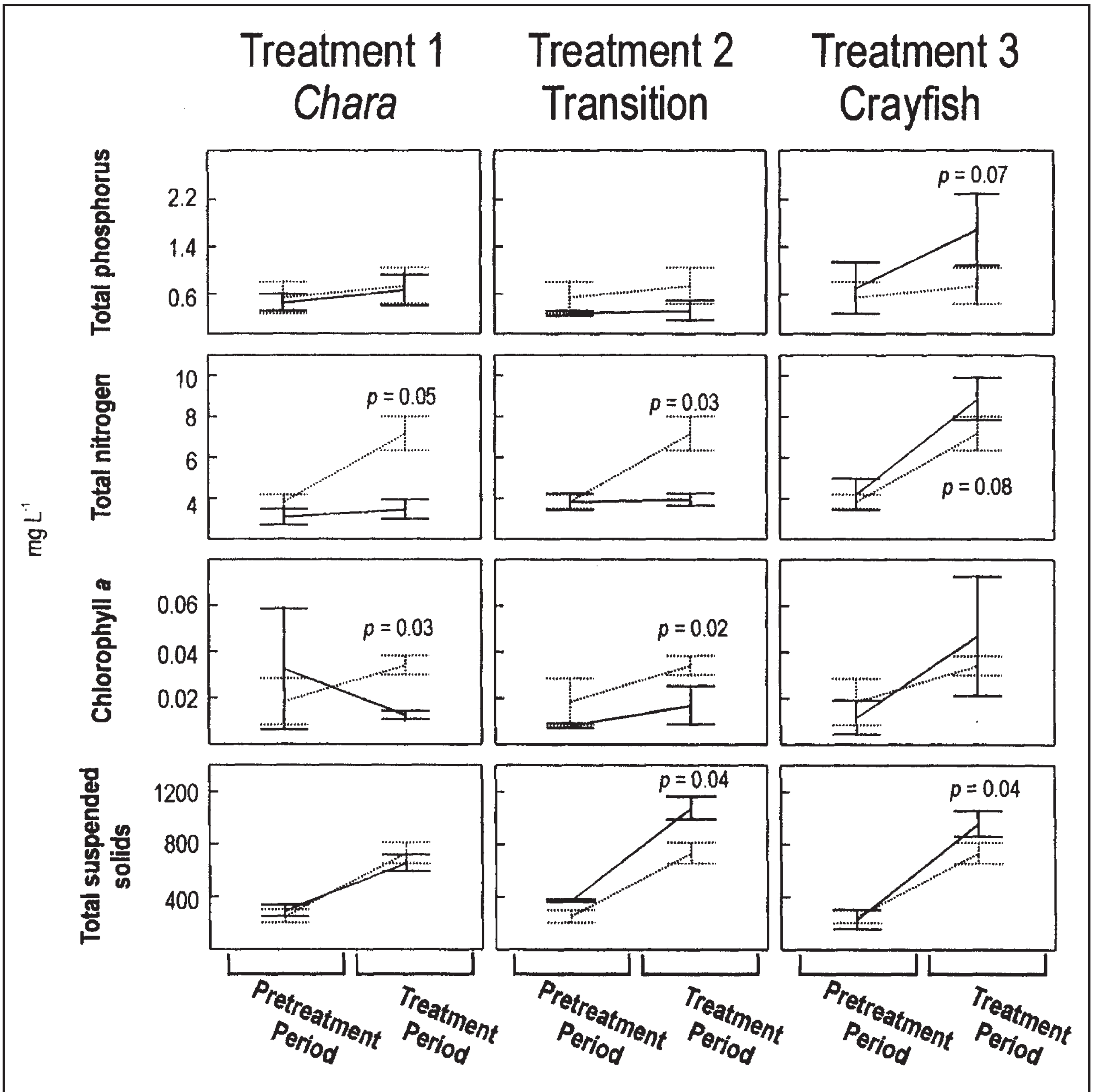

Figure 5. Comparison of water quality parameters (average ± SE) in the respective treatments before (pre-treatment period) and after (treatment period) crayfish stocking. Full lines denote the respective treatments and dotted line the control. Significant differences (revealed by RM-ANOVA) are highlighted by p-levels.

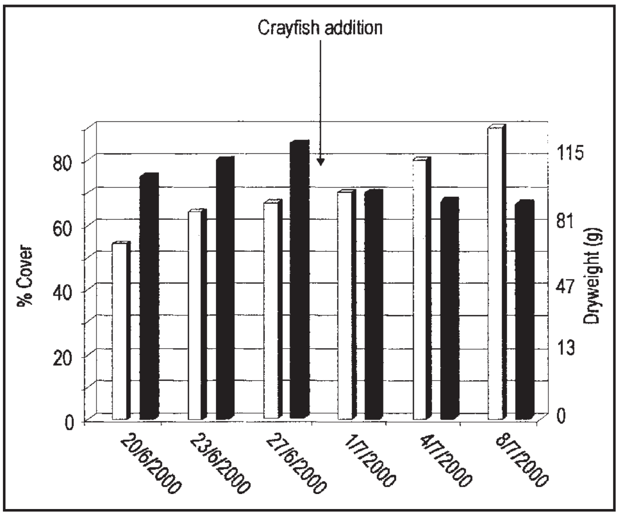

Figure 6. Time course of mean *Chara* cover/biomass in absence and presence of *P. clarkii*, i.e. in Treatments 1 (grey bars) and 2 (black bars).

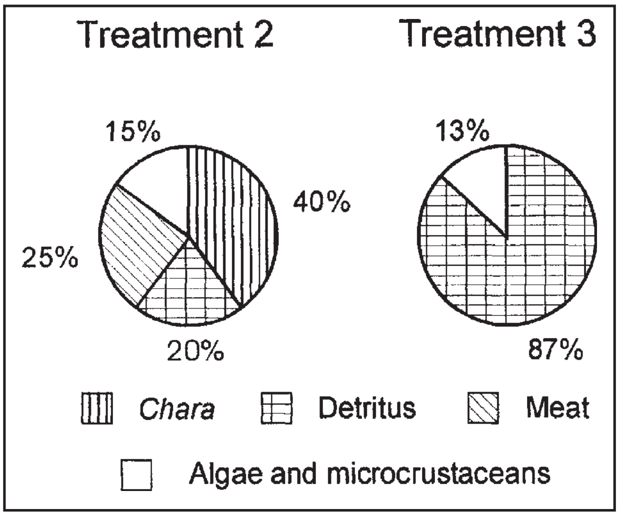

Figure 7. Relative percentage of crayfish gut contents.

Discussion

Our study was designed to assess how crayfish feeding mode affects water quality in wetlands. It is not possible to determine water quality trends along the degradation continuum with the present data set, but it provides us with snap shots of potential water quality characteristics that may be present in each of the alternative equilibria in wetlands. The duration of our study period was too short to extrapolate the results to the whole ecosystem, but several mechanisms were identified that could be indicative for ecosystem processes.

Results show that the water quality deteriorates despite the hypertrophic conditions of the wetland. The decline is a sequence of combined processes in which bioturbation and feeding activity are involved. The mode of the latter is considered as crucial in the strength of decline because crayfish herbivory was shown to be less detrimental to water quality than crayfish detritivory.

In relation to feeding mode herbivory is preferred over detritivorous nutrition in nature because of the low energetic quality of detritus (Lodge and Hill 1994, Momot 1995). This was confirmed by our gut content analyses because the percentage of detritus as food was greatly reduced when *Chara* was available. Based on this preference, herbivory can dramatically impact submerged vegetation within a short temporal scale shifting the systems from the clear water state to the turbid state relatively fast (e.g., Feminella and Resh 1989). Interestingly, we found an elevated percentage of animal remains in guts of crayfish instead of charophytes. Because proteinaceous prey best suits the energetic demands of crayfish (Momot 1995, Lodge and Hill 1994), carnivory can temporarily relieve submerged vegetation from predation. We argue that the *Chara* cover decline in our experiment would have been stronger if crayfish have not had scavenged on its conspecific.

Bringing herbivory and water quality in a context, plant damage can increase leaching processes that translocate nutrients stored in plant tissues to the water column (Denny 1980). Carpenter and Lodge (1986) state that over 75% of leached phosphorus is in a soluble reactive form. This phosphorus can be rapidly assimilated by phytoplankton leading to increased chlorophyll concentrations (Landers 1982). Even though we observed a dramatic *Chara* bed decline owing to *P. clarkii* plant consumption, our data set indicated that plant leaching negligibly affected water quality. Neither nutrient concentrations nor chlorophyll *a* levels changed significantly, suggesting that either the remaining *Chara* biomass can still substantially buffer the increase of nutrients in the water column via uptake, or that sorption of P to sediment particles may have taken place.

Table 1. Crayfish stocking scheme. Shown are the data for the initial stocking scheme (commencement of the treatment period) and those obtained upon termination of the experiment (final density).

	Treatment 2 (*Chara* x Crayfish)		Treatment 3 (Crayfish)	
	Enclosure 1	Enclosure 2	Enclosure 1	Enclosure 2
Initial stocking				
Density (ind. m^{-2})	3.8	5.1	3.8	3.8
Total wetweight (g)	79.8	64.9	64.3	73.0
Final density				
Density (ind. m^{-2})	1.3	2.5	2.5	1.3
Total wetweight (g)	33.1	30.5	47.2	31.8

Once charophytes are eliminated, crayfish can readily shift to detritus feeding (Momot 1995). Accordingly, gut content analyses found that detritus was the most abundant food source for crayfish in the absence of plants. In regard of water quality the detritus feeding mode may be most detrimental to water quality. Crayfish may act as an efficient nutrient pump that translocates sediment-bound nutrients stored in particulate organic debris and its associated microbial communities as well as those adsorbed to inorganic sediment to the water column. The excreted nutrients (mainly dissolved inorganic fractions [Andersson *et al.* 1988, Fukuhara and Yasuda 1989, Brabrand *et al.* 1990, Søndergaard *et al.* 1992]) can then be available to water column primary producers, which no longer suffer from biological interference with the charophytes.

Besides crayfish feeding mode, bioturbation can contribute to a water quality decline in terms of increased turbidity levels. Crayfish as benthic dwellers can disturb the sediment by their moving and burrowing behaviour, which increases non-algal turbidity. We observed a significant increase of TSS associated with *P. clarkii* activity independent of charophytes presence or absence, indicating that the sediment consolidation properties are lost even when charophytes are still present. The increase of TSS seems to be correlated with shelter construction in our study. We observed between two and three burrows along the walls of all enclosures which were stocked with crayfish. Such an activity was also reported by other authors and interpreted as a strategy to withstand unsuitable environmental conditions (dry periods) and to reduce predator-imposed mortality (e.g., Penn 1943, Sommer and Goldman 1983, Gutiérrez-Yurrita and Montes 1999).

In summary, water quality decline in charophyte-dominated wetland systems due to crayfish activity can be seen as a sequence of synergistically acting processes. As long as sufficient plant biomass is available, it is the combination of bioturbation and herbivory that affects water quality. It is however only the increase of non-algal turbidity that degrades water quality because nutrient levels and phytoplankton biomass may be likely kept in check by the remaining *Chara* biomass. Once charophyte biomass falls below a certain threshold water quality decline is the result of an increase of water column nutrients, in addition to non-algal turbidity caused by bioturbation. In addition, the water quality decline seems to be fueled by crayfish detritivorous feeding which translocates sediment-bound nutrients to the water column.

These combinations and sequences of mechanisms could indicate ecosystem processes when *P. clarkii* is introduced to pristine charophyte-dominated wetland habitats, thereby inducing a shift from the clear water state to the turbid water state. However, we must acknowledge that such processes may be different for wetlands with other dominant submerged vegetation because chemical and structural defenses of macrophytes may deter crayfish herbivorous feeding (Bolser *et al.* 1998) forcing it to shift to detritivorous feeding even in the presence of extensive beds of submerged vegetation. Hence, the structure of submerged vegetation could be deterministic for crayfish behaviour, which in turn, dictates the animal-related processes involved in water quality decline. The combination of plant and animal traits seems to be promising for assessing processes involved in aquatic ecosystem health deterioration.

We must acknowledge that *P. clarkii* is most likely only a piece of the whole degradation puzzle in TDNP, and that the synergistic action of other forces such as exotic fish (carp, sunfish, mosquitofish) and the discharge of water with poor quality may maintain the wetland in its degraded state (Fig. 8). Returning TDNP to the clear water, macrophyte-dominated state may likely need to consider interventions in the food web, besides other internal and external remedial actions.

Acknowledgements

Thanks go to J. Escuderos, J. Sánchez and P. Riolobos for assistance with field and laboratory work, and to C. Rojo (Univ. Valencia) for providing helpful comments that improved the paper. Financial support by 4th Framework Programme of the European Community is gratefully acknowledged.

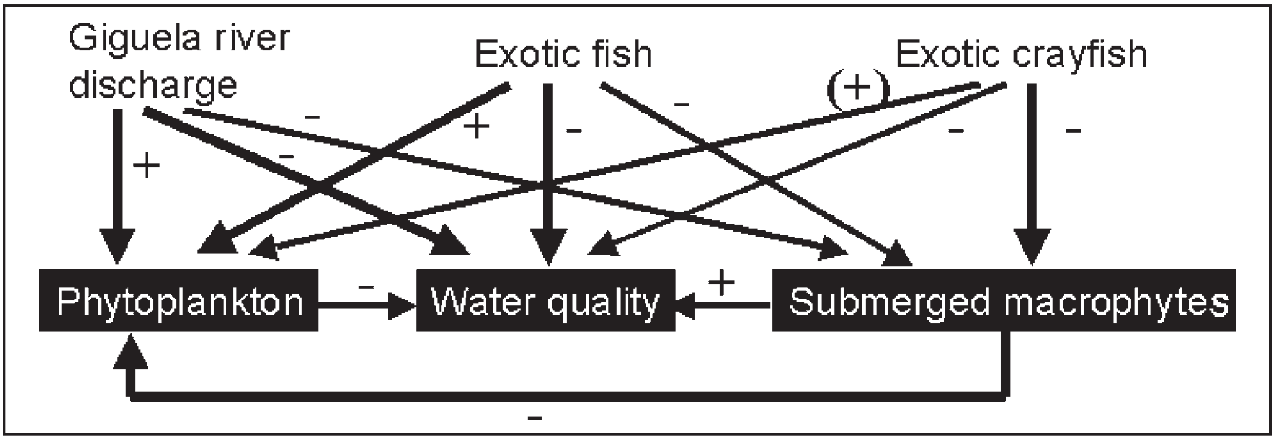

Figure 8. Conceptual model of forces that maintain Las Tablas de Daimiel in the degraded state. The model is constructed in part on the basis of results from enclosure studies of Angeler *et al.* (2001, 2002), information of Alvarez-Cobelas & Cirujano (1996) and results of this study. The thickness of arrows reflects the likely importance of each effect. + and – indicate positive or negative effects on a specific compartment. (+) signifies potential importance at the ecosystem scale, but not confirmed in our microcosm assessment studies.

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