

Submersed macrophytes and grazing crayfish: an experimental study of herbivory in a California freshwater marsh

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Feminella, J. W. and Resh, V. H. 1989. Submersed macrophytes and grazing crayfish: an experimental study of herbivory in a California freshwater marsh. - *Holarct. Ecol.* 12: 1-8.

Grazing by the crayfish *Procambarus clarkii* (Girard) on the abundance of submersed sago pondweed, *Potamogeton pectinatus* (L.), was quantified during 1984 through 1986 at Coyote Hills Marsh (Alameda County, California, USA). Annual marsh surveys indicated that *P. pectinatus* abundance declined (from 70% to 0% of the marsh surface), whereas *P. clarkii* abundance increased (from 1.6 to almost 3.0 crayfish trap⁻¹ week⁻¹). Crayfish in a 1425 m² trapping grid were non-aggregated when pondweed was abundant but became aggregated in the remaining pondweed beds as pondweed abundance decreased. In situ exclusion and enclosure experiments using crayfish densities of 0 to 3 individuals m⁻² were used to determine if crayfish reduced pondweed. Exclusion of crayfish from areas without pondweed, beginning in midsummer 1984, resulted in plant regrowth; addition of crayfish to these enclosed plots reduced pondweed. Exclusion of crayfish for the entire growing season in 1985 resulted in pondweed persistence in exclusion plots until August; in contrast, pondweed within adjacent, open control plots was eliminated by mid-June. Enclosure experiments showed a strong positive relationship between crayfish density and pondweed clearance. This study demonstrates that grazing crayfish can reduce and, in some cases, eliminate macrophytes from freshwater marshes.

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Introduction

In recent years, the ecological consequences of crayfish (Crustacea: Decapoda) invasions have become a serious concern in freshwater ecosystems. Reductions in the abundance of native, sympatric crayfish have been reported (e.g. Smith 1981, Capelli 1982, Butler and Stein 1985, but see Lodge et al. 1986), as have decreases in littoral invertebrate populations because of epiphytic habitat loss or from direct predation (Lodge et al. 1985, Lodge and Lorman 1987).

Crayfish are the most important invertebrate consumers of macrophytes in some lentic systems (Carpenter and Lodge 1986). They may reduce macrophyte biomass within lake littoral zones (Abrahamsson 1966, Flint and Goldman 1975), the extent of which varies

with crayfish food preferences and plant architecture (Lodge and Lorman 1987).

The red swamp crayfish, *Procambarus clarkii* (Girard), native to mid-southeastern North America (Hobbs 1982), was introduced into California for aquaculture in the early part of this century (Riegel 1959). *P. clarkii*'s burrowing activity (Penn 1943) and broad environmental tolerance (Huner and Barr 1984) have made this species a pest in commercial rice fields (Sommer and Goldman 1983) and irrigation canals (Goldman 1973), although macrophyte grazing by this crayfish may benefit vector control programs by reducing the amount of larval mosquito habitat (Feminella and Resh 1986). Despite its potential impact on aquatic plant and epiphyte assemblages, the degree to which macrophytes are regulated by *P. clarkii* has not been quantified.

Accepted 18 July 1988

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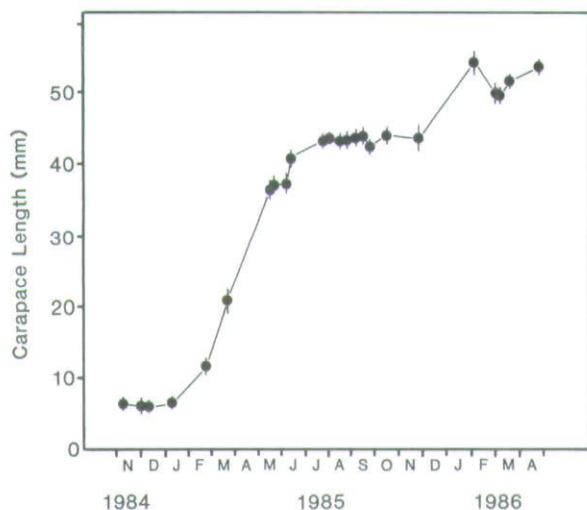


Fig. 1. Growth of the 1984 cohort of *Procamburus clarkii* at Coyote Hills Marsh during 1984 through 1986. Discrimination of this from other cohorts was possible because cohorts grew synchronously, and distinct size classes were apparent over most of the year. Sexes of crayfish (although collections were mostly males) were combined on all dates ($\bar{x} \pm S.E.$). Mean sample size = 48 individuals per date.

Similarly, population responses of crayfish to changes in macrophyte abundance, such as shifts in spatial distribution or changes in density, have not been examined.

Since 1981 a population of *P. clarkii* has occurred at Coyote Hills Marsh, a freshwater/brackish wetland near San Francisco Bay, California, USA. The aquatic plant community at this marsh has been dominated by sago pondweed, *Potamogeton pectinatus* (L.), a submersed macrophyte that forms a dense surface canopy across the marsh interior. In this paper we report the results of studies conducted at this marsh that demonstrate the influence of herbivory by *P. clarkii* on the abundance and distribution of *P. pectinatus*. By using a combination of field experiments and observations, we examined (1) the effects of different crayfish densities on plant abundance, (2) year-to-year variability in crayfish abundance, and (3) the seasonal movement patterns of *P. clarkii* in response to herbivore-induced variation in pondweed distribution.

Materials and methods

Study area

Coyote Hills Marsh (Alameda Co., California; 37°32'50''N, 122°04'30''W) is a 1.4-ha man-made wetland (maximum mid-summer depth 3–4 m) that was originally a tidal salt marsh before the construction of dikes and diversion of local streamwater (described further by Collins et al. 1983). Because the basin has saline

soils, water salinity typically ranges from 2–9‰, depending on water level and season. Most (>90%) precipitation occurs during October through March. Annual water temperatures range from 7–29°C. Emergent cattails *Typha angustifolia* L., *T. latifolia* L., bulrushes *Scirpus* sp., and spike-rushes *Eleocharis* sp. grow along the shallow marsh edges; submersed *Potamogeton pectinatus* occurs in the deeper (>0.5 m) marsh interior. Because public access to the study sites is restricted, loss of crayfish from fishing is minimal.

Phenology and distribution of *Potamogeton pectinatus*

Potamogeton pectinatus shoots first appear at Coyote Hills Marsh in early February; pondweed plants usually reach the water surface by late March or early April. By May, growing plants intertwine at the surface and form a dense floating canopy that persists until mid-October, when normal senescence occurs (Balling and Resh 1984). During August, pondweed beds normally reach their highest biomass and support a diverse and productive epiphytic invertebrate fauna (Lamberti and Resh 1984). In 1984, *P. pectinatus* usually did not occur within several meters of the marsh edge. This pondweed-free region, which we termed the "halo zone," gradually expanded inward toward the marsh center as the growing season progressed. We hypothesized that grazing by *P. clarkii* caused this peripheral halo zone and that its width varied with crayfish density.

Biology of *Procamburus clarkii*

At Coyote Hills Marsh, *Procamburus clarkii* has a 1-yr life cycle, although some individuals live for 2 yr. Eggs hatch in summer and growth is slow until the following spring, when individuals grow rapidly (Fig. 1). High spring growth and frequent molts of young crayfish (Huner and Barr 1984) coincided with the appearance of young pondweed shoots and early development of surface canopy. Crayfish growth and molts are reduced during the breeding season (July–October), and for those individuals that lived 2 yr a second growth phase occurs during the following winter and spring (Fig. 1). Most crayfish apparently die naturally after the first year or are consumed by predators during the low-water period in late summer; raccoon *Procyon lotor* L. scats containing mostly crayfish parts occurred commonly along the marsh shoreline at this time. Crayfish burrows, which enable individuals to survive drying conditions (Sommer and Goldman 1983), were rarely found in this marsh.

Descriptive studies: crayfish sampling methods

High turbidity and dense plant growth in the marsh prevented direct observations of crayfish. Instead, abundance, distribution, and movements of crayfish were assessed using cylindrical, hardware-cloth minnow

traps (length 51 cm, diameter 21 cm; mesh size 6.4 mm) at fixed stations within the marsh. To capture crayfish in all size classes except those less than 4-mm carapace length, traps were modified by increasing the entrance-way diameter to 6 cm.

In mid-July 1985, we established a 1425 m² sampling grid (~20% of the total basin) containing 70 permanent crayfish trapping stations, delineated with numbered stakes. Stations were set at fixed increments of 5 m, with one trap per station. The grid consisted of a 600 m² central zone of dense pondweed (>150 stems m⁻²), which contained 28 trapping stations, and a peripheral halo zone of sparse pondweed (<20 stems m⁻²), which contained the remaining 42 stations. Distribution of crayfish was monitored on 14 dates over a 36-d period (every 2–4 d), from 18 July to 22 August 1985. Crayfish spatial dispersion was analyzed during each sampling date (using the χ^2 variance to mean test, Elliott 1977). Because pilot studies had indicated that crayfish entered traps whether or not bait was used, traps were left unbaited to prevent bait-induced crayfish movement. To reduce disturbance of crayfish and rooted plants during trapping, we used a small boat propelled through the grid with wooden poles.

Date- and trap-specific marks were applied to the carapace of each crayfish collected. Individuals were then returned to their point of capture. All crayfish were marked with quick-drying metallic paint; immature individuals (carapace length <40 mm) also were marked using cauterization (see Abrahamsson 1965 for method) to circumvent the loss of paint marks after molt.

To assess movement activity of individual crayfish within pondweed and halo zone habitats, we determined the Euclidean distance (i.e. the straight path distance) between the trapping station where each male crayfish was marked and the station where it was recaptured. Estimates of crayfish movement rate within both habitats were compared using log ($X_i + 1$) transformation and Student's *t*-test.

Year-to-year variation in crayfish abundance was determined using a second, small (50 m²) sampling grid consisting of 10 unbaited traps, located about 50 m from the large grid. This second grid was established so that year-to-year abundance estimates in the small grid could be made independently of efforts to quantify habitat use and movement patterns in the large grid. All ten trapping stations were located within 3 m of the marsh margin, where no pondweed occurred. Traps were checked weekly from early August through mid-September 1984–1986.

Descriptive studies: crayfish grazing activity

To assess habitat-specific grazing intensity by *P. clarkii*, we examined pondweed stem damage across several marsh zones within the 1425 m² grid. Because high turbidity precluded direct visual assessment of sub-

mersed pondweed density and condition, these determinations were made by touch. Pondweed stems usually were snipped cleanly by foraging crayfish, which left a stump 2–5 cm high. On 11 August 1985, we estimated the relative abundance of intact pondweed plants (wholestems) and stumps at 24 locations along a 45-m linear transect that connected the *Typha* zones on either side of the grid and bisected the central pondweed bed.

Field experiments: general methods

To determine if the pondweed-free halo zone resulted from crayfish grazing and varied in size with grazer density, we (1) excluded crayfish from plots within the halo zone, and (2) held crayfish at different densities within enclosures containing dense pondweed.

We used submersed, rectangular plywood pens (2.5×1.2×1.2 m; area 3 m²) to exclude or enclose crayfish during summers of 1984 and 1985. Pens were embedded into the sediment at least 15 cm to reduce immigration or emigration; individuals that entered pens during installation were removed using baited crayfish traps. Hardware-cloth baffles (20-cm wide, mesh size 13 mm) were attached along the tops of pens, which were directed away from (i.e. for enclosures) or toward (i.e. for enclosures) each pen center at a 90° angle to the sides; these baffles were used to discourage swimming crayfish from entering the enclosures or from emigrating. Pens and baffles usually were submersed at the start of each experiment; however, the decline of the water level during summer caused the upper walls of pens to rise slightly (10–30 cm) above the water surface.

Pondweed density in experimental plots was estimated by touch, using counts of the number of basal stems within either of two quadrat sizes: 45 cm² for high stem density plots, and 500 cm² for low-density plots.

Crayfish exclusion experiments, 1984–1985

Experiments in which crayfish were excluded from areas within the halo zone were conducted in 1984 (11 June–16 August) and 1985 (8 March–27 July). In the 1984 experiment, three enclosures were installed about 1–2 m from the *Typha* zone along the marsh edges. Control plots of equal area (3 m²) in which crayfish had complete access to pondweed also were established contiguous with exclusion plots. This experiment began after a well-defined pondweed surface canopy and halo zone had developed.

In the 1985 experiment, crayfish were excluded from treatment plots before the pondweed canopy (and corresponding halo zone) could form. For this experiment, three additional exclusion/control pairs were established in March before extensive pondweed growth, and were used with those pairs left in place from the 1984

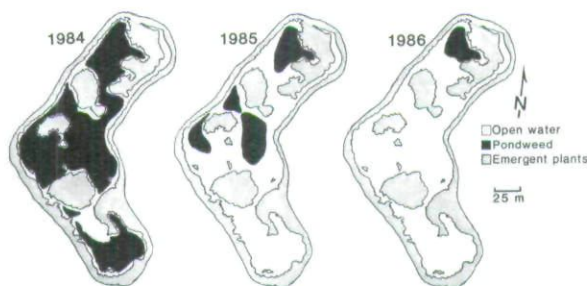


Fig. 2. Map of the study area at Coyote Hills Marsh showing amount of pondweed (*Potamogeton pectinatus*) surface canopy present in early August, 1984 through 1986. Emergent plants were *Typha angustifolia*, *T. latifolia*, *Scirpus* sp., and *Eleocharis* sp.

experiment; this increased the number of replicates from three (1984) to six (1985). Trapping of crayfish within exclosures was continued over both experiments to ensure that exclosures were maintained.

Crayfish density manipulation, 1985

Enclosures used to contain crayfish at different densities over a 45-d period (17 July–31 August 1985) were installed during June 1984 in a central region of the marsh that contained a high pondweed surface canopy. Plants were allowed to senesce naturally for the remainder of 1984, and a dense growth of pondweed (> 200 stems m^{-2}) developed within each enclosure in 1985 before crayfish were added.

Treatment densities of crayfish were assigned randomly to individual enclosures and consisted of 0, 1, 3, and 9 crayfish per enclosure; these levels were comparable with ambient crayfish density estimates, determined using the Lincoln-Peterson index (Davis 1963) in the 1425 m^2 grid (e.g. average estimate over 8 trap dates = 3 ± 1.6 individuals m^{-2} , $\bar{x} \pm 95\%$ C.I.; $N = 70$ traps d^{-1}). To avoid potential sex- and development-related differences in feeding behavior during the enclosure experiment, we used only sexually mature (Form I) males, ranging in carapace length between 41–49 mm (14.4–29.5 g as wet weight, respectively). Cylindrical PVC tubes (length 15 cm; diameter 2.9 cm), used as crayfish retreats, were placed in each enclosure to reduce intraspecific encounters that might lead to crayfish emigration or death. Crayfish were collected from Coyote Hills Marsh 1–2 d before the experiment began.

Individuals were given enclosure-specific marks to identify experimental animals from intruders; periodic assessment of effective treatment density in each enclosure was made throughout the study using crayfish traps set for 1–2 d intervals. At the end of the experiment pondweed stem density and distribution (i.e. spatial arrangement within enclosures) were estimated.

Results

Changes in *Potamogeton pectinatus* abundance

Based on aerial photographs (elevation 120–300 m) and shoreline surveys, pondweed surface canopy varied widely across the marsh from 1984–1986 (Fig. 2). In mid-August 1984, the pondweed canopy extended across 70% of the marsh surface (i.e. the halo zone composed about 30% of the total area). At the same time in 1985, surface canopy was found over only 20% of the marsh, with an 80% halo zone. In mid-August 1986, only 5% of the marsh had pondweed canopy, and no canopy formed in the basin in either 1987 or 1988. Surface canopy measurements produced reliable approximations of stem density: within surfacing pondweed beds, stem densities always exceeded $150 m^{-2}$; within the halo zone, densities usually were < 20 stems m^{-2} .

We also observed marked decreases in *P. pectinatus* abundance from July–August 1985 in the 1425 m^2 trapping grid. On 24 July, the pondweed bed measured 565 m^2 and formed a dense canopy over one-third of the 70 trapping stations in the grid. By 15 August, the canopy declined to about 240 m^2 and was found in less than 15% of the trapping stations. In contrast, observations made in this marsh during 1983 (Balling and Resh 1984) indicated that annual biomass of pondweed was highest at this time. Pondweed canopy disappeared entirely by 31 August 1985, about 7 wk earlier than plant senescence and canopy decline were observed in 1983 (Balling and Resh 1984).

Changes in *P. clarkii* abundance, distribution, and movement patterns

Crayfish abundance, as indicated by catch per effort within the 50 m^2 sampling grid, showed considerable within-year variation during summer surveys made from 1984–1986. Catch was consistently higher during the first half of each survey (August), and usually declined sharply in September, possibly from post-reproductive quiescence or mortality. Because of these seasonal differences, we used only the first three dates within each year (i.e. catch from dates in August only; total no. of traps = 30) to represent crayfish abundance during times when annual pondweed biomass was highest.

Crayfish abundance increased steadily during each year of this study: in 1984, crayfish catch was lowest (1.64 ± 0.32 individuals $trap^{-1}$, $\bar{x} \pm 2$ S.E.); in 1985, catch increased to 2.09 ± 0.40 individuals $trap^{-1}$; in 1986, catch reached a peak of 2.95 ± 0.50 individuals $trap^{-1}$. A 1987 crayfish abundance estimate was not possible because drought caused the marsh to dry well below normal August water levels.

Based on trapping data from the 1425 m^2 grid in 1985, we observed temporal shifts in the spatial distribution of crayfish that were associated with changes in habitat use. Crayfish distributions were non-aggregated (χ^2 var-

Tab. 1. Relative abundance and spatial distribution of *Procambarus clarkii* on 14 dates in a 1425 m² trapping grid, 1985. Population dispersion was analyzed using the χ^2 variance to mean test for $N > 31$ (see Elliott 1977). Crayfish were significantly aggregated on dates where $d > 1.96$. $N = 70$ traps for 18 July–4 August samples; $N = 64$ traps for all remaining dates. * = $P < 0.05$.

Date	Abundance		Dispersion		
	No. crayfish per trap		χ^2	d	
	\bar{x}	S.E.			
July	18	0.97	0.11	58.9	-0.85
	19	0.71	0.09	53.9	-3.15
	22	0.94	0.10	52.9	-1.41
	24	1.03	0.12	70.3	0.16
	27	1.21	0.12	57.7	-0.96
	30	1.37	0.15	73.6	0.43
August	1	1.36	0.14	70.6	0.19
	4	1.51	0.20	128.0	4.27*
	6	0.93	0.16	136.3	4.98*
	8	1.19	0.20	137.6	5.41*
	11	1.30	0.25	195.0	8.55*
	15	1.08	0.15	94.8	2.60*
	19	0.89	0.16	38.7	3.61*
	22	1.03	0.18	126.5	4.72*

iance to mean test, $P > 0.05$) on the first 7 sampling dates (18 July–1 August), and no obvious habitat preference occurred. At this time, sparse patches of pondweed (e.g. density range 0–55 stems m⁻² in mid-July) and submersed pondweed detritus occurred throughout the peripheral halo zone, as did dense plant growth within the central pondweed bed. On all subsequent dates (4–22 August) during the decline and inward re-

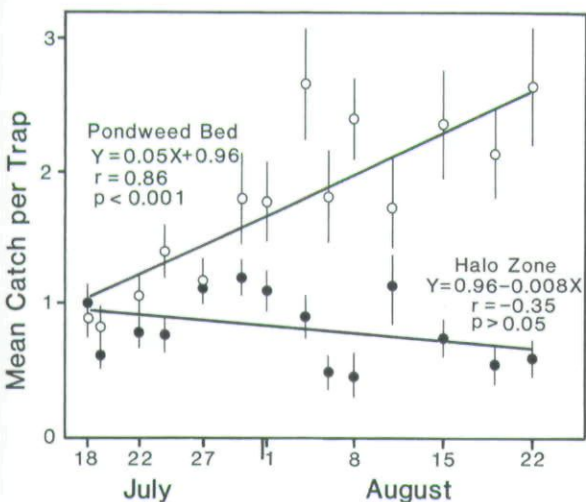


Fig. 3. Relative abundance of *Procambarus clarkii* (as catch per effort) associated with the central pondweed bed and peripheral halo zone in the 1425 m² trapping grid. Plotted points are mean catch per date (\pm S.E.); regression equations were based on means. Slopes of the regression lines for the two habitats were significantly different ($t = 4.62$; $df = 24$; $P < 0.001$).

Tab. 2. Evidence for habitat-specific crayfish grazing as indicated by pondweed stem damage. Whole stems are intact plants; stumps are those plants clipped 2–5 cm above the sediment surface.

Distance (m) from pondweed margin	Density (no. stems m ⁻²) ($\bar{x} \pm$ S.E.)		Ratio of whole stems : stumps
	Whole stems	Stumps	
0–4	161 \pm 117	26.6 \pm 20.4	6.1 : 1
5–8	196 \pm 177	10.1 \pm 21.3	19.4 : 1
>8	31 \pm 23	1.2 \pm 3.5	25.8 : 1

cession of the pondweed bed, crayfish were aggregated ($P < 0.05$; k range 0.61–2.2, Tab. 1); at this time, individuals became more concentrated within or near (defined as < 1.5 m from) the pondweed bed compared to the halo zone (Fig. 3). This shift to an aggregated distribution, and the movement by crayfish into the pondweed bed habitat, was coincident with the clearance of residual pondweed and detritus from most of the halo zone.

Between-habitat comparisons of movement rates by marked male crayfish revealed higher (Student's t -test, $P < 0.05$) movement within the halo zone (2.61 ± 0.39 m d⁻¹, $\bar{x} \pm$ S.E., $N = 30$) than in the pondweed (1.79 ± 0.30 m d⁻¹, $N = 36$). Thus, higher crayfish captures associated with the pondweed bed did, in fact, indicate higher abundance (cf. activity) in the pondweed bed habitat than in the halo zone.

Habitat-specific grazing by crayfish

Evidence of feeding by *P. clarkii*, as indicated by the presence of grazed pondweed stumps, occurred throughout the 1425 m² grid. However, the proportion of whole stems to stumps, used as an index of grazing

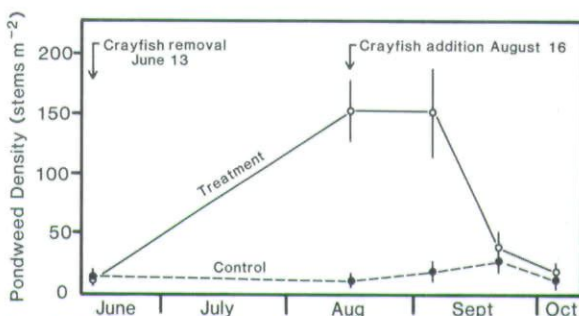


Fig. 4. Results of summer 1984 experiments on the effects of crayfish exclusion (= removal) and introduction (= addition) on pondweed density. Treatment = caged plots where crayfish were removed and then later introduced; control = open plots that were always accessible by crayfish. Plotted values are means (\pm S.E.) taken within 2 treatment and 3 control replicates.

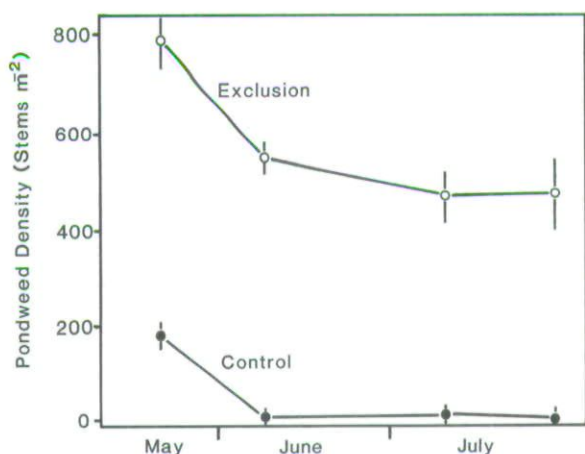


Fig. 5. Results of spring–summer 1985 crayfish exclusion on pondweed density. Exclusion = caged plots where crayfish were denied access; control = plots where crayfish had access. Plotted values are means (\pm S.E.) taken within 6 treatment and 6 control replicates.

intensity, varied considerably across open water (i.e. halo zone), the pondweed bed margin, and pondweed bed interior habitats. Grazing was highest in areas nearest the margin of the pondweed bed (6:1, plant:stump ratio) and lowest in areas furthest from the margin (26:1 ratio) (Tab. 2). Such high plant:stump ratios and associated low grazing rates away from the pondweed margin occurred whether sampling locations were in the halo zone or in the interior of the pondweed bed.

Crayfish exclusion and introduction

The exclusion of crayfish from plots within the halo zone in 1984 resulted in pondweed regrowth. Within 21 d after crayfish exclusion, pondweed shoots and some surface canopy appeared in exclusions; by 16 August (64 d after exclusion) mean pondweed densities were 151 stems m^{-2} in exclusions and only 11 stems m^{-2} in adjacent control plots (Fig. 4).

Three mature (Form I) males (C.L. range 43–51 mm) were added to each enclosure on 16 August 1984 (density = 1 individual m^{-2}) to confirm that the absence of crayfish was responsible for the appearance of plants. By 21 September (36 d after addition), pondweed densities in those pens to which crayfish were added were reduced to the levels found in control plots (Fig. 4), whereas plant densities in cage control plots (i.e. pens installed in dense pondweed without crayfish additions) remained high (323 ± 33 stems m^{-2} , $\bar{x} \pm$ S.E.; $N = 2$). Therefore, we attribute this reduction in pondweed density to crayfish grazing and not to plant senescence.

Exclusion of crayfish from plots in the halo zone for the entire growing season in 1985 led to the development and persistence of high pondweed biomass when compared with that of the heavily grazed control plots (Fig. 5). By mid-June, the pondweed-rich exclusion plots were isolated completely from the receding

pondweed beds at the marsh interior by the expanding halo zone. Stem densities in exclusions were higher in this experiment (cf. 1984, Fig. 4) because pondweed growth could proceed without any interference from grazing crayfish; alternatively, stem densities in the 1984 experiment represented late-season, less vigorous growth that could occur only after crayfish were removed.

Crayfish density manipulation

Examination of pondweed response using random sampling within enclosures showed no effect of crayfish density on pondweed abundance. However, strong density effects were found when sampling was stratified along inner enclosure perimeters. Conspicuous halo zones devoid of pondweed were discovered along the inner perimeter of those enclosures that contained crayfish 36 d after the experiment began. Measurement of the average width of these grazed areas (i.e. the distance between the enclosure wall and closest intact pondweed stems) on 31 August (after 45 d) indicated that the halo zone width was related directly to crayfish density (Fig. 6). In pens containing no crayfish, plants commonly grew in close proximity to the enclosure walls.

Discussion

The results of our studies indicate that *Procambarus clarkii* reduced *Potamogeton pectinatus* biomass at Coyote Hills Marsh. Lodge and Lorman (1987) observed similar reductions in mixed, macrophyte assemblages by manipulating densities of the crayfish *Orconectes rusticus* (Girard) in several northern Wisconsin

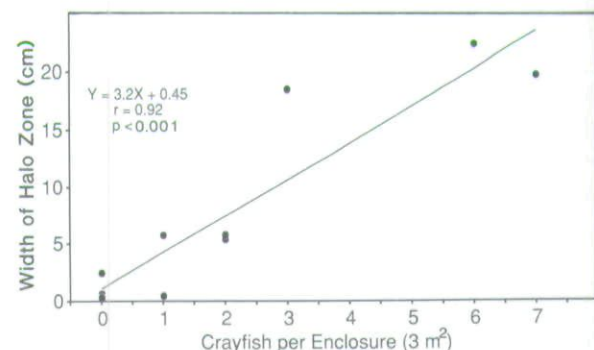


Fig. 6. Relationship between crayfish density and width of halo zone (area along inner perimeter of enclosure bottom devoid of pondweed stems) 45 d after crayfish were introduced, 17 July–31 August 1985. Effective crayfish densities (x-axis) were based on 1–2 d trapping surveys that were run throughout the experiment; an assessment of final crayfish density was not possible because of predation by raccoons.

lakes. They concluded that macrophyte destruction by crayfish resulted from a combination of direct (e.g. herbivory) and indirect (e.g. predation on epiphytic snails) effects. In our study, indirect effects (such as predation) apparently did not contribute to pondweed reductions. For example, at least two species of snails, *Physella* sp. and *Gyraulus* sp., occurred at high densities in pondweed (up to 400 snails per g pondweed, as dry weight) at Coyote Hills Marsh. However, we detected no significant relationship between snail and crayfish density ($r^2 = 0.07$; $P > 0.05$) in the enclosures, a pattern that would be expected if crayfish were selectively consuming these invertebrates. In addition, stomach analysis of *P. clarkii* (ranging in size from 21–50 mm carapace length) indicated that animal matter composed a minor part (<15%, by volume) of the diet relative to plant detritus and living pondweed tissue. Thus, direct consumption of plants by this crayfish is apparently the mechanism that accounts for pondweed reductions. These findings concur with those reported in other studies regarding herbivorous feeding by this (Penn 1943, Avault et al. 1983) and other crayfish species (Norton 1942, Momot 1967).

Enclosure experiments, time-series changes in pondweed surface canopy, and crayfish movements all suggest that crayfish first eliminate plants at the marsh perimeter. Grazing then extends concentrically toward interior regions. The resulting halo zone, which is largely devoid of plants, varies in size with crayfish density. That grazing began at the perimeters of both enclosures and the marsh proper suggests that crayfish prefer edge (cf. interior) habitats, which may provide areas that are more easily defended by individuals against conspecific intruders. In the marsh, crayfish may avoid the interior of dense macrophyte beds because physical constraints, such as low dissolved oxygen, may prevent prolonged habitation. For example, diurnal benthic dissolved oxygen measurements made in August 1985 were lower in dense pondweed (range 0.2–1.3 mg l⁻¹) than in the halo zone (1.4–2.6 mg l⁻¹). Huner and Barr (1984) indicate that *P. clarkii* favors those habitats where oxygen concentrations consistently exceed 2 mg l⁻¹. Fish predation, which affects crayfish microdistribution (Stein and Magnuson 1976) and activity (Hamrin 1987) in other systems, is not a regulatory factor for *P. clarkii* at Coyote Hills Marsh; fish that are important consumers of crayfish in other lentic systems (e.g. ictalurid catfish, Penn 1950; centrarchid bass, Taub 1972, Rickett 1974, Stein 1977) do not occur in this marsh (Schooley 1983).

Shifts by crayfish from a non-aggregated to an aggregated distribution in the 1425 m² grid may have resulted from a behavioral response to a declining food resource. Non-aggregated crayfish distributions have been reported (Camougis and Hichar 1959, Abrahamsson 1966), although shifts to an aggregated distribution associated with decreased food availability have not been documented. Shifts in *P. clarkii* habitat use associated

with changes in aquatic vegetation abundance were observed in a pond by Witzig et al. (1983), although in their study crayfish had a "more even" (page 336) distribution as individuals occupied deeper, less preferred pond zones after vegetation had decreased. In our study, *P. clarkii* may have become more tolerant of crowded conditions as food availability decreased, despite their normally highly aggressive behavior (Ameyaw-Akumfi and Hazlett 1975, Huner and Barr 1984). However, in laboratory experiments Copp (1986) found that agonistic behavior of *P. clarkii* was reduced during repeated conspecific encounters, which eventually allowed the formation of stable dominance hierarchies. Such reductions in aggression may account for highly aggregated crayfish distributions observed at Coyote Hills Marsh. However, increased tolerance of conspecifics also may result from physiological changes associated with the waning of the reproductive season.

Census data for *P. clarkii*, in conjunction with the gradual disappearance of *P. pectinatus*, provided circumstantial evidence that the eventual elimination of pondweed from Coyote Hills Marsh resulted from steady population growth of crayfish. Other herbivores were present in the marsh during the study, although their influence on pondweed was probably secondary to that of crayfish. For example, migratory waterfowl, which can reduce *P. pectinatus* in shallow lakes and marshes (Anderson and Low 1976), can regulate this macrophyte at Coyote Hills Marsh (Collins and Resh 1984). In mid-August 1984, foraging by dabbling ducks (e.g. *Anas* spp.) caused widespread disruption of extensive pondweed beds and eliminated the plant surface canopy within 2 wk (Collins, unpubl.). Waterfowl were less abundant the following year (e.g. 400–500 individuals sighted d⁻¹ in 1984; 100–200 in 1985, Feminella, pers. observ.) and when they did arrive, extensive grazing by crayfish had already eliminated pondweed from most of the marsh.

In summary, this study provides direct evidence that herbivorous crayfish such as *Procambarus clarkii* can eliminate submersed macrophytes from freshwater marshes. This loss of macrophytes can lead to extinction of habitat for many epiphytic organisms, which could ultimately cause catastrophic reductions in overall marsh diversity and secondary production. Currently, *P. clarkii* is cultured worldwide, with aquacultural programs in North and Central America, Europe, and Asia (IAA 1987). Unless macrophytes in systems where this crayfish has been introduced are naturally resistant, or predators occur, macrophytes may be dramatically reduced, or even eliminated, when grazing pressures are high.

Acknowledgments – We thank the East Bay Regional Park District for providing access and facilities at Coyote Hills Marsh. We also thank H. H. Hobbs, Jr. (Smithsonian Institution) for confirming the identification of *P. clarkii*, D. M. Lodge, and W. T. Momot for their suggestions on the manu-

script, D. Edds, K. Feminella, K. Heins, G. Lamberti, E. McElravy, J. Phillips, and M. Power for field or laboratory assistance, and J. Collins and B. Orr for providing technical help over many phases of this study. Support for this research was provided by the University of California Mosquito Research Funds and the California Coastal Region Mosquito Abatement Districts.

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