# Spatial and temporal movement of the lined shore crab *Pachygrapsus crassipes* in salt marshes and its utility as an indicator of habitat condition

**S. G. Morgan[1,3,*], S. A. Spilseth[1], H. M. Page[2], A. J. Brooks[2], E. D. Grosholz[3]**

[1]University of California, Bodega Marine Laboratory, PO Box 247, Bodega Bay, California 94923, USA
[2]University of California, Marine Science Institute, Santa Barbara, California 93106, USA
[3]University of California, Dept. of Environmental Science and Policy, One Shields Avenue, Davis, California 95616, USA

ABSTRACT: The utility of the lined shore crab *Pachygrapsus crassipes* as an indicator of small-scale variation in the condition of salt marshes was determined by conducting detailed mark-recapture studies of the spatial and temporal patterns of movement in 2 marshes in northern and southern California, and by conducting a stable isotope study along a nutrient gradient at one of the marshes. Crabs (1158) were captured from creek bank and vegetated marsh habitats, tagged, and released. Most crabs were recaptured in the same trap where they were originally tagged, and on average, they traveled less than 5 m from the site of first capture. The mean distance traveled did not increase significantly with the time between captures. A high percentage of crabs (62.1%) tagged near the creek bank remained there; fewer tagged crabs moved between the creek bank and the marsh plain (18.2%) or remained on the marsh plain (12.6%). Crabs moved least along creek banks and farthest when crossing creeks, although few of them did the latter (6.2%). During spring tides, crabs moved from tidal creeks onto the marsh plain. The nitrogen isotope data mirrored the gradient in nutrient input, supporting the conclusion that *P. crassipes* remained and fed within a localized area. Thus, the lined shore crab can serve as an indicator of small-scale differences in contaminant exposure. Furthermore, semiterrestrial species that are readily sampled and move little are abundant around the world, making them ideal indicators of habitat condition.

KEY WORDS: Movement · Indicator species · Mark-recapture · Nitrogen stable isotope · Crab · *Pachygrapsus crassipes* · Salt marsh

## INTRODUCTION

Human populations continue to burgeon along coastlines, generating increasing contaminant loads in estuarine and marine habitats. Wetlands have historically been among the most productive coastal communities in temperate regions and are now among the most degraded habitats (Catallo 1993, van Dam et al. 1998). Considerable effort has been expended on evaluating the condition of salt marshes, and most recently, the integrity of salt marshes has been assessed using ecological indicators of stressor-specific, sublethal exposure and effects on resident species to provide early warnings of impairment (Mineau 1998, van Dam et al. 1998). Crabs may be particularly useful indicator species of salt marsh condition because (1) they are among the largest, most abundant and conspicuous invertebrates living there, (2) their burrowing activities make them important engineers of these communities (Bertness 1985, Fiorillo 1994), (3) embryos are brooded externally, providing an easy, nondestructive way of evaluating impairment of this sensitive life stage (Lee & Oshima 1998), and (4) many species remain near their refuges (Crane 1975). Over the years an excellent

understanding of crabs residing in salt marshes has developed in many parts of the world from studying ocypodid species, such as fiddler crabs (*Uca* spp.), which leave their burrows to forage during low tides (Crane 1975). However, our understanding of crabs occupying marshes along the west coast of North America is much more limited because the grapsid crabs *Hemigrapsus oregonensis* and *Pachygrapsus crassipes* primarily remain in burrows during daytime low tides (Hiatt 1942, Willason 1981, Ricketts et al. 1985), making them difficult to observe. The utility of crabs as an indicator of small-scale differences in habitat condition critically depends on the extent of their movements.

Movement is a fundamental part of animals' lives, being essential for foraging, reproduction, and avoiding predators and competitors. However, movement receives more attention on land than in the marine environment, where sessile and sedentary lifestyles are more common due to (1) the delivery of food, (2) removal of waste, and (3) transfer of gametes by currents (Strathmann 1990). In the case of crabs, many juveniles and adults rely on heavy exoskeletons coupled with burrows, holes and crevices for protection from predators, seemingly moving little throughout the day. Some crabs home, returning repeatedly to the same refuge after foraging (Hughes 1966), whereas others remain within a home range without returning to the same refuge (Hazlett & Rittschof 1975, Abele et al. 1986, Stachowicz & Hay 1999, Brousseau et al. 2004). More dramatic movements from refuges are evident when juveniles of some species leave nursery areas, and when adults migrate to breeding grounds and larval release sites (Wolcott & Wolcott 1982, Hicks 1985, Carr et al. 2004). Movements are often periodic, being associated with oscillations in the light-dark, tidal, tidal amplitude, lunar and seasonal cycles (Morgan 1995, Palmer 1995). The extent of movements may be expected to vary with terrain, physiological stress and predation pressure as well as the availability of food, refuges, mates and hatching habitat. Although behavioral variation does occur across the extensive species ranges typical of decapods and other marine organisms (Morgan et al. 1996, Cannicci et al. 1999, Stachowicz & Hay 2003), it may also occur when a species occupies distinct habitats.

*Pachygrapsus crassipes* is semiterrestrial, attains a carapace width of 48 mm, occurs from Alaska to Mexico along the coast of the northeastern Pacific Ocean and inhabits habitats ranging from rocky benches and cobble fields on exposed coasts to muddy marshes in protected bays and estuaries (Morris et al. 1980, Jensen 1995). Its movement patterns have been investigated on rocky benches (Hiatt 1942, Michaels 1988), but are not well known in marshes. Like other semiter-

restrial grapsids, *P. crassipes* are active during low tides at night when they leave the safety of cracks and crevices in the upper intertidal zone of rocky shores to scrape algae and scavenge other food from rocks around neighboring tidepools.

The purpose of this study was to evaluate the utility of *Pachygrapsus crassipes* as an indicator of small-scale variation in the condition of salt marshes. Detailed mark-recapture studies of the spatial and temporal patterns of *P. crassipes* movement were conducted at 2 marshes in California. Studies were conducted during the warmest months of the year, when crabs were reproductive and expected to be most active. Recapture distances and rates were measured to determine the extent of movements by size, sex and reproductive status across different habitats within the 2 marshes and relative to the tidal amplitude cycle. *P. crassipes* reportedly does not home (Hiatt 1942) or dig its own burrow (Willason 1981) and was expected to move short distances similar to those recorded for other grapsid crabs (Cannicci et al. 1997, Brouseau et al. 2004). Although some individuals have been observed to travel long distances across sandy shores adjacent to rocky benches (Hiatt 1942, Michaels 1988), it remains unknown whether movement of most crabs is affected by differences in habitat type within marshes, such as mud banks, vegetated marsh and tidal creeks. *P. crassipes* reportedly is not territorial, but males more often defend refuges than females (Hiatt 1942), raising the possibility that males may stay closer to burrows during the reproductive season. During maximum amplitude tides, burrows in the upper intertidal zone are flooded at high tide and more time is available for foraging at low tide, and for this reason we determined the effect of the tidal amplitude cycle on movement. Although movement was expected to be roughly similar at both study sites, differences in environmental conditions and population density might lead to geographical variation in distances traveled. A thorough understanding of the movements of this species is both of fundamental interest and provides the basis for the use of this species as an ecological indicator of small-scale variation in habitat condition at multiple locales.

The ability of *Pachygrapsus crassipes* to reveal small-scale variation in habitat condition was evaluated along a known gradient in nutrient contamination at the southern study site. Stable nitrogen isotope analysis of producers and consumers can be a useful approach for identifying anthropogenic nitrogen inputs to estuarine food webs (Page et al. 1995, McClelland et al. 1997, Fry et al. 2003). Anthropogenically derived nitrogen is often enriched in $^{15}N$ relative to marine sources and can be propagated up food chains. If *P. crassipes* individuals feed within a local-

ized area, then the nitrogen isotopic composition of crabs should vary in association with exposure to anthropogenic nitrogen inputs from the watershed, and it would not be apparent if crabs were to move and feed over a large area.

## MATERIALS AND METHODS

**Study sites.** The study site in northern California was located near the mouth of Walker Creek (38° 04.25′ N, 122° 55.32′ W), a primary tributary to Tomales Bay, in Sonoma County, California (Fig. 1). The 2500 m$^2$ study area encompassed a 10 m wide main creek channel, a 4 m wide side channel, as well as many smaller first and second order channels that were located within a 371 309 m$^2$ salt marsh. The marsh plain vegetation was dominated by *Salicornia virginica*, the soil on the creek bank consisted predominantly of sand followed by silt, and clay (60.3 % ± 14.3 SE, 22.7 % ± 9.6 SE, 16.9 % ± 4.6 SE, respectively), and the mean water temperature during the summer was 17.8°C ± 0.6 SE (authors′ unpubl. data).

The southern study site was located at Carpinteria Salt Marsh (34° 23.76′ N, 119° 32.76′ W) in Santa Barbara County, California (Fig. 1). Carpinteria Salt Marsh is influenced by extensive greenhouse operations and numerous open field farms to the northwest, a light industrial park to the north, and the city of Carpinteria to the north and east, as well as the adjacent US Highway 101 and the Union Pacific Railroad tracks. The study site of 2250 m$^2$ encompassed a single tidal creek (5 m wide) without notable side channels. As at Walker, the marsh plain vegetation was dominated by *Salicornia virginica.* However, the soil was slightly sandier (67.60 % ± 2.25 SE sand, 22.09 % ± 1.74 SE silt, 10.29 % ± 0.66 SE clay), and the water was warmer during the summer (20.9°C ± 0.6 SE; authors′ unpubl. data). Both sites are located in a semidiurnal tidal regime.

**Mark-recapture.** A mark-recapture study using pitfall and minnow traps was conducted in both marshes to determine movement patterns and to estimate crab densities. A detailed study was conducted at Walker and followed by a less exhaustive study at Carpinteria to determine whether fundamental movements and densities were similar. Pitfall traps consisted of black potting containers that were 15 cm in diameter and 15 cm deep. Vexar screens (5 mm) were staked over the pitfall traps to 5 cm above the ground in order to shade trapped crabs. A rock (~5 cm diameter) was placed at the bottom of each pitfall trap to provide additional shelter and escape from muddy and anoxic water remaining at the bottom of the trap during low
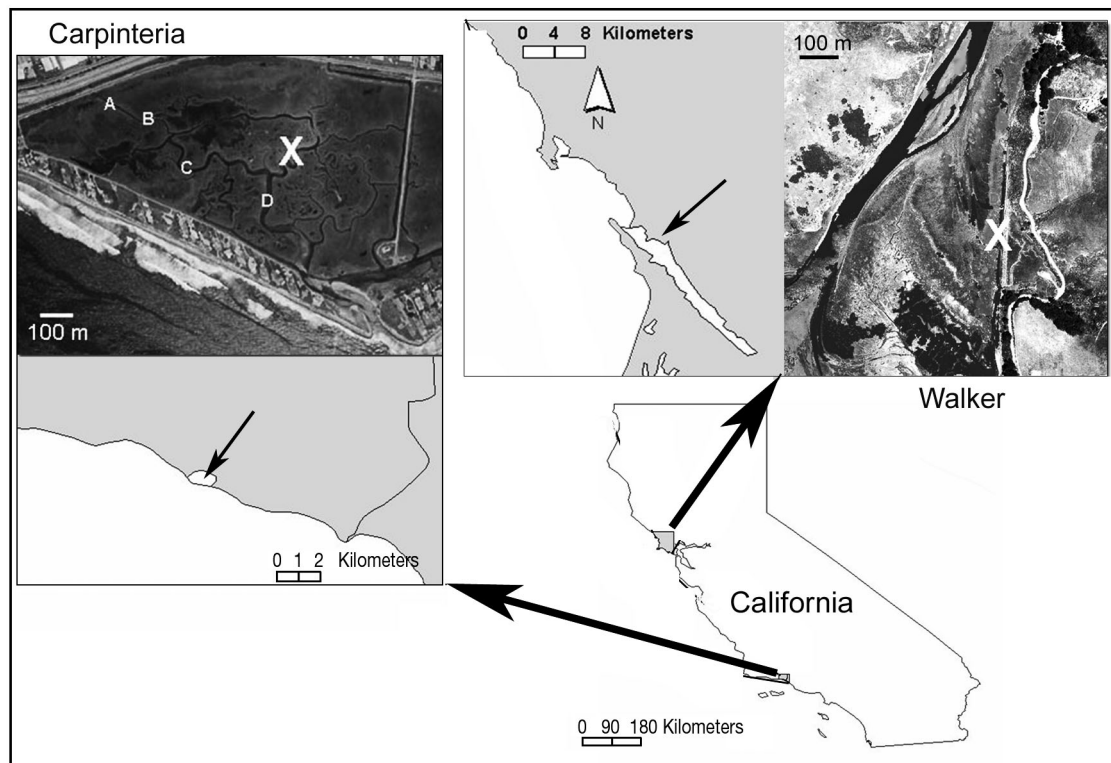


Fig. 1. Location map and aerial (Carpinteria) or LANDSAT satellite (Walker Creek) images of salt marshes. X: location of the mark-recapture studies conducted at both marshes; A–D: sampling locations for the nitrogen stable isotope study
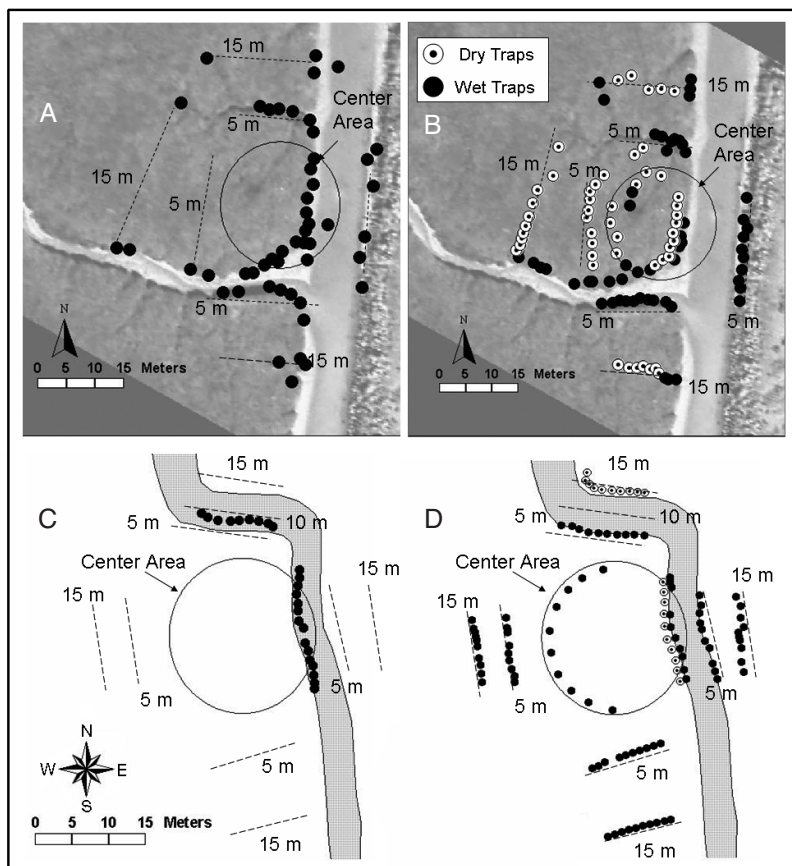
Fig. 2. Trapping arrays at (A, B) Walker Creek and (C, D) Carpinteria, indicating the locations of (A, C) minnow traps and (B, D) pitfall traps in dry and wet areas of the marsh

2500 m$^2$, including creek channels and areas that were not heavily trapped (Fig. 2a,b). At Carpinteria, most crabs were tagged and recaptured within the central area of approximately 475 m$^2$ (Fig. 2c,d). Fewer minnow traps were used at Carpinteria because there are fewer tidal creeks than at Walker.

Crabs were trapped and tagged for at least 3 mo at both sites. Crabs were initially trapped and tagged daily for 5 consecutive days, then weekly for the next 3 wk and monthly during the subsequent 2 mo. Crabs were trapped for 14 wk from April 12 to August 28, 2004 at Walker and for 12 wk from August 9 to November 9, 2004 at Carpinteria. Studies were conducted sequentially due to the logistical difficulty of conducting them concurrently at 2 widely separated locales. Traps were generally set for 24 h. The number of hours that each trap was set was used to calculate the catch per unit effort (CPUE) to standardize different trapping durations.

Carapace width was measured across the broadest dimension, and the sex and number of missing limbs were recorded. Crabs were marked with external tags to track the movements of individual crabs until they molted and with internal tags to track the movements of crabs that molted during the duration of the study. *Pachygrapsus crassipes* were tagged externally on the posterior carapace with numbered shellfish tags (Hallprint) and cyanoacrylate glue (Super Glue gel). *P. crassipes* were marked internally using Visible Implant Elastomer (VIE, Northwestern Marine Technology). VIE was injected into the joint between the basis and coxa of walking legs. A different combination of elastomer color and leg was used to identify crabs caught in different areas. Once tagged, crabs were released within 0.5 m of where they had been captured. A crab was not tagged if it had recently molted. Crabs less than 25 mm were too small to be injected with VIE and were only tagged externally. A companion validation study of VIE tags demonstrated that 91.5% of tagged crabs survived and that 95% of tags were still visible after many of the crabs molted during the 4 mo study (Spilseth & Morgan in press).

The total catch of crabs caught in traps was determined at the 2 study sites and population sizes were estimated using the Schnabel method (Schnabel 1938). The catch was categorized by sex, size, reproductive

tides. When traps were not in use, screens were staked down over the pitfall traps to prevent crabs from entering. Minnow traps were attached to numbered stakes and were baited with approximately 28 g of canned cat food. Minnow traps were deployed only during sampling, but the numbered stakes remained in place throughout the experiment to ensure that traps were returned to the same place.

The general design of the trapping array consisted of a central circular area (20 m diameter) that was surrounded by 4 transects situated 5 m distant in each direction from the perimeter of the central trapping area and 4 more transects that were situated 15 m away from the perimeter of the central trapping area (Fig. 2). The pitfall traps were located on the vegetated marsh plain and along muddy creek banks. Minnow traps were placed primarily in creek channels and along muddy creek banks, with some placed in wet depressions on the marsh plain. Traps were set at least 1 m apart from each other. The locations of traps were mapped using GIS Arcview (ESRI) software. At Walker, the total trapping area was approximately

status, trap type, and habitat for both marshes. The effectiveness of pitfall and minnow traps at capturing all crabs, large crabs, males, females and ovigerous females within each marsh was analyzed using *t*-tests. We calculated the distance (mean, median, mode) that individuals traveled between captures and the number of days between each successive recapture for each sex and habitat type. The effect of crab size (3 size classes) and sex on the distance moved per day within each site was determined using 2-way ANOVA. The distance that crabs moved between successive recaptures was analyzed using linear regression to determine whether crabs that had been free longer between successive recaptures traveled farther. For the subset of crabs that were recaptured multiple times, the distance moved after 1 recapture and the net distance traveled after multiple recaptures were compared using a *t*-test. For each trapping day in each marsh, the ratio of CPUE in pitfall traps that stayed dry to pitfall traps that filled with water was calculated and regressed with maximum high tide during the trapping period to determine the influence of tidal amplitude on capture location. Bartlett's and Levene's tests revealed that all data were normally distributed and homoscedastic before analysis.

**Nitrogen stable isotope.** To test the hypothesis that the nitrogen isotopic composition of *Pachygrapsus crassipes* varied with exposure to nitrate inputs from the watershed, crabs (25 to 35 mm carapace width) and the green macroalga *Enteromorpha clathrata* (attached to the substratum) were collected in March, and crabs were collected in September 2003 at 4 stations along a tidal channel in Carpinteria Salt Marsh, which receives runoff from a coastal plain that is highly developed for agriculture (Fig. 1). Stns A and B were separated by a distance of ~140 m, B and C by ~200 m, and C and D by ~300 m. Nitrate concentration decreases abruptly in this channel (Page et al. 1995, H. M. Page unpubl. data), suggesting that nitrogen isotope values of the macroalga and crab would vary over a scale of 100 to 200 m in the upper reaches of this channel (i.e. between Stns A and B). The nitrogen isotopic composition of *E. clathrata* is highly correlated with that of nitrate in this marsh ($r^2 = 0.58$, n = 17; H. M. Page unpubl. data). Crabs and macroalgae were placed in plastic bags, returned to the laboratory on ice, and frozen (–10°C). *E. clathrata* was not present in the September sample or at Stn D in the winter sample.

To provide a comparative measure of exposure of *Pachygrapsus crassipes* to nutrient inputs along the channel, salinity and dissolved inorganic nitrogen concentrations were measured at the stations and times that crabs and macroalgae were sampled for isotopic analysis. Nitrate and ammonium concentrations were measured in replicate water samples taken a few cm below the water surface in the center of the channel. The salinity of these samples was measured to the nearest 1 psu using a refractometer. Samples were filtered through GF/F filters into new 20 ml borosilicate glass scintillation vials, returned on ice to the laboratory, and stored frozen (–10°C) until analysis using a Lachat nutrient autoanalyzer.

Muscle tissue was dissected from the legs of 3 *Pachygrapsus crassipes* from each station and date. Several thalli of *Enteromorpha clathrata* were collected and composited to form a single sample from each station. Macroalgal samples were carefully inspected using a dissecting microscope, and cleaned of non-algal material. Samples of crab and macroalgae were rinsed in deionized water, dried at 60°C, and ground to a fine powder with a ceramic mortar and pestle. Stable nitrogen isotope values were measured on subsamples of the ground sample using a Finnigan Delta-Plus Advantage Isotope Mass Spectrometer with a Costech EAS Elemental Analyzer. The natural abundances of $^{15}$N are expressed in standard δ notation and calculated as follows: $\delta^{15}N = 1000[(R_{sample}/R_{standard}) - 1]$, where $R = {}^{15}N/{}^{14}N$ and expressed per mil (‰) relative to atmospheric $N_2$ for nitrogen, which has a $\delta^{15}N$ value of 0‰. Analytical precision, as determined by analyses of 15 replicate portions of the same ground sample was better than 0.5‰.

## RESULTS

### Mark-recapture study

The CPUE, size and sex ratio of crabs differed among trap types at the 2 study sites. First, more crabs were captured per unit effort in minnow traps than in pitfall traps at Walker (*t*-test: $t_9 = 3.38$, p = 0.008), whereas the opposite pattern was found at Carpinteria (*t*-test: $t_{10} = 2.989$, p = 0.014; Fig. 3). Second, larger crabs were caught in minnow than in pitfall traps at Walker (*t*-test: $t_{1213} = 7.39$, p < 0.001), and the opposite pattern was found at Carpinteria (*t*-test: $t_{424} = 22.08$, p < 0.001; Fig. 4). Third, more females than males were caught per unit effort in minnow traps at Walker (*t*-test: $t_9 = 2.908$, p = 0.017; Fig. 4), and the opposite trend was apparent at Carpinteria (*t*-test: $t_{10} = 2.187$, p = 0.054). The CPUE of males and females was similar in pitfall traps at Walker (*t*-test: $t_9 = 1.017$, p = 0.336) and Carpinteria (*t*-test: $t_{10} = 1.665$, p = 0.127; Fig. 3).

The percentage of tagged crabs recaptured once at Walker and Carpinteria was 22.2 and 13.8%, respectively. Crabs were recaptured as many as 3 times, and the percentages recaptured declined with each successive recapture at both sites (Table 1). A high proportion of males revisited the same pitfall trap at both sites,
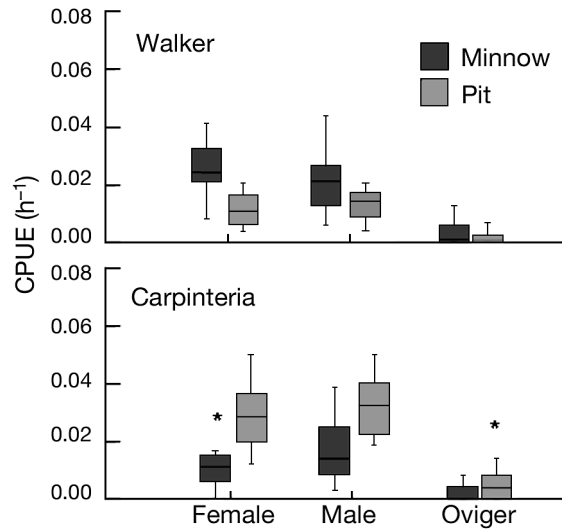
Fig. 3. *Pachygrapsus crassipes*. Median (horizontal line), lower and upper quartiles (bars) of catch per unit effort by sex and reproductive state of crabs caught in pitfall and minnow traps at Walker Creek and Carpinteria, outliers (asterisks) and minimum and maximum values (central vertical line)



Fig. 4. *Pachygrapsus crassipes*. Carapace width of crabs caught in pitfall and minnow traps at Walker Creek and Carpinteria. Lower and upper quartiles (bars) around the median (central horizontal line), outliers (asterisks), extreme outliers (circles) and minimum and maximum values (central vertical line)

whereas at Walker similar proportions of males and females were recaptured in the minnow trap in which they had initially been captured (Table 1). At Carpinteria, only 2 crabs, both males, returned to minnow traps. Few crabs were recaptured with visible internal tags but without external tags at both study sites (Table 1), and 43% of those without external tags were captured on the last trapping date at Walker.

Most crabs returned to the traps where they had previously been captured (Table 1), and traveled less than 5 m on average from the initial tagging location at both

study sites (Walker: 4.7 ± 0.48 m; Carpinteria: 3.6 ± 0.7 m). Crabs were recaptured at a mean distance of only 0.72 m d$^{-1}$ ± 0.15 SE from their previous capture site at Walker and even closer at Carpinteria (*t*-test: $t_{168}$ = 2.74, p = 0.007), although distances traveled were similar (*t*-test: $t_{81}$ = 1.30, p = 0.20) when considering the movement of crabs only within the target area at Walker (an area similar to the tagging area at Carpinteria). Distance moved per day did not differ by sex or carapace size at Walker (2-way ANOVA: Sex: $F_{1,193}$ = 1.436, p = 0.232; Size: $F_{2,193}$ = 0.162, p = 0.850; Sex × Size: $F_{2,193}$ = 0.259, p = 0.772) or at Carpinteria (2-way ANOVA: Sex: $F_{1,35}$ = 0.153, p = 0.860; Size: $F_{2,35}$ = 0.152, p = 0.860; Sex × Size: $F_{2,35}$ = 0.674, p = 0.516).

The distance traveled did not increase significantly with the length of time before crabs were initially recaptured at Walker (r$^2$ = 0.014, $y$ = 0.0289$x$ + 3.9353, $F_{1,200}$ = 2.87, p = 0. 092) or at Carpinteria (r$^2$ = 0.056, $y$ = −0.0559$x$ + 4.7133, p = 0.81; Fig. 5). Crabs that were recaptured more than once moved farther away from the initial capture location by the time of their final capture at Walker (*t*-test: $t_{29}$ = 2.86, p = 0.008) and at Carpinteria (*t*-test: $t_9$ = 3.21 p = 0.011; Fig. 6). Crabs spent a mean of 24 d ± 1.7 SE before recapture at Walker and even less time at Carpinteria (14.7 d ± 2.3). Although the mode before recapture was 1 d at both study sites, crabs that were free
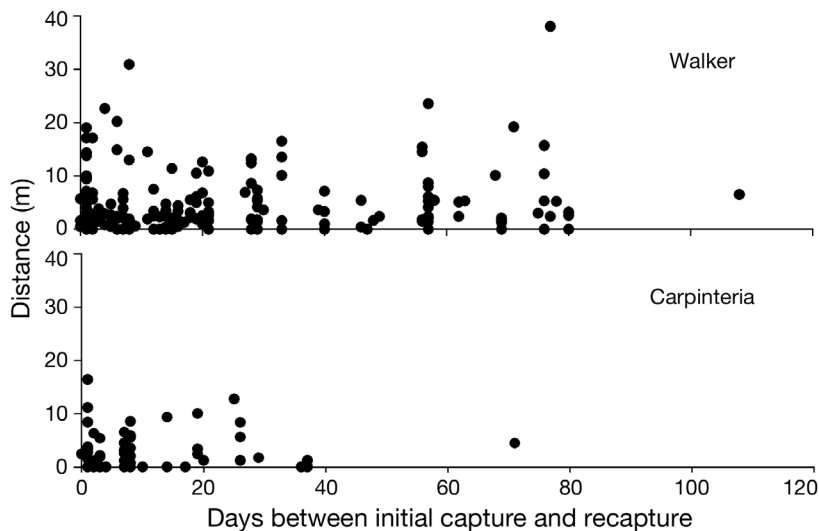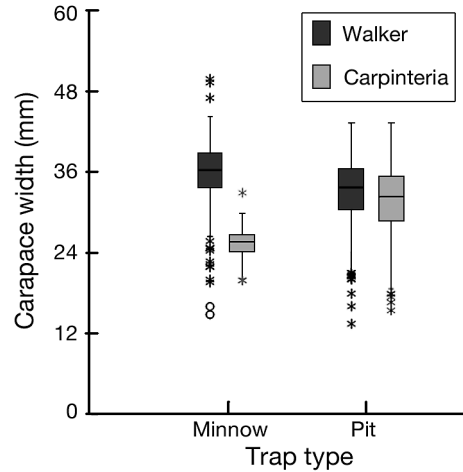


Fig. 5. *Pachygrapsus crassipes*. Relationship between the distance traveled and the number of days between initial capture, and between capture and recapture at Walker Creek and Carpinteria Marsh

Table 1. *Pachygrapsus crassipes*. Number and percentage of crabs captured, tagged and recaptured once, twice or 3 times at 2 salt marshes in California, USA, including a breakdown of crabs returning to the same trap and trap type (pitfall or minnow) by sex. Crabs were tagged with external and internal tags, and the number and percentage of external tags lost through molting is reported. Of the 984 crabs collected at Walker, 16 were juveniles

|  | Walker No. | % | Carpinteria No. | % |
|---|---|---|---|---|
| Captured |  |  |  |  |
| Males | 465 | 47.3 | 519 | 60.9 |
| Females | 503 | 52.7 | 332 | 39.1 |
| **Total** | **984** |  | **851** |  |
| Tagged | 752 | 76.4 | 406 | 47.7 |
| Recapture events |  |  |  |  |
| Once | 197 | 22.2 | 56 | 13.8 |
| Twice | 30 | 4.0 | 13 | 3.2 |
| 3 times | 6 | 0.8 | 2 | 0.5 |
| **Total** | **233** |  | **71** |  |
| Returned |  |  |  |  |
| Same trap | 40 | 17.2 | 16 | 22.5 |
| Same pitfall trap | 23 | 57.5 | 14 | 87.5 |
| Males | 17 | 73.9 | 11 | 78.6 |
| Females | 6 | 26.1 | 3 | 21.4 |
| Same minnow trap | 17 | 42.5 | 2 | 12.5 |
| Males | 9 | 52.9 | 2 | 100.0 |
| Females | 8 | 47.1 | 3 | 0.0 |
| Missing external tag | 14 | 6.0 | 16 | 22.5 |

for the longest time before they were recaptured did not travel far from their initial capture locations at either study site: 6.5 m over 108 d at Walker and 1.17 m over 71 d at Carpinteria. Furthermore, the 2 individuals that moved the farthest per day (17.1 and 19 m d$^{-1}$) crossed the main creek channel and were caught the following day. The crab that traveled the farthest since it was initially captured at Walker moved a net distance of 38 m from the marsh plain, across a creek and along a footpath on the opposite marsh plain over 77 d.

At Walker, most tagged crabs (62.1%) were first captured and were also later recaptured near the creek bank; however, 18.2% moved between the creek bank and the marsh plain (Fig. 7). Fewer crabs (12.6%) remained on the marsh plain, and only 6.2% crossed a creek channel. Those crossing a creek channel moved farther than those that moved along creeks or over the marsh plain, and those crabs that moved between the marsh plain and the creek bank moved farther than those that remained on the creek bank (ANOVA: $F_{3,157} = 14.74$, p < 0.001). Movement among habitats was not evident at Carpinteria because all recaptures were made along 3 parallel transects.

Of the 105 pitfall traps at Walker, 54 were filled with water during every tide, while the other 51 usually stayed dry, filling only during the highest amplitude tides. The ratio of CPUE of dry to wet pitfall traps was positively correlated with maximum tidal height at Walker ($r^2 = 0.83$, p < 0.001), and the same trend was evident at Carpinteria ($r^2 = 0.30$, p = 0.067; Fig. 8). The ratio was higher for females than for males in all but the final sampling period at Walker (Fig. 8). On the final day of sampling, only 11 females and 18 males were captured as compared to a mean of 127 crabs ± 11.74 SE for all other sampling periods. Like Walker, the ratio of CPUE of dry to wet pitfall traps tended to be greater for females than males, but the results were not significant at this site (*t*-test: $t_{20} = 1.11$, p = 0.28).

The Schnabel estimate of population size of *Pachygrapsus crassipes* in the tagging area at Walker was 2344 individuals (CI = 95%: 2065 to 2708). The mean net movement distance of Walker crabs of 4.6 m was used to calculate an effective trapping area of 1825 m$^2$. Using this estimate, the density of crabs was 1.3 ind. m$^{-2}$. Using the median movement of 2.4 m as the effective trapping distance, the effective trapping area was 998 m$^2$, and the resulting density was between 2.4 and 2.7 ind. m$^{-2}$. At Carpinteria, the estimated population of crabs within the 475 m$^2$ tagging area was 1164 individuals (CI = 95%: 939 to 1531). Depending on whether the mean (3.6 m) or median (2.1 m) distance traveled was used as the effective radial trapping distance, the density of crabs was estimated to be between 2.24 and 3.64 ind. m$^{-2}$ in a 420 m$^2$ trapping area or between 4.22 to 6.88 ind. m$^{-2}$ in a trapping area of 222 m$^2$.

## Nitrogen stable isotope

There was a strong gradient in salinity and nitrate concentration along the tidal channel at Carpinteria in both March and September. Salinity and nitrate concentration at low tide ranged from ~5 psu and 2000 μM at the upstream station (A) to ~30 psu and 71 (Septem-
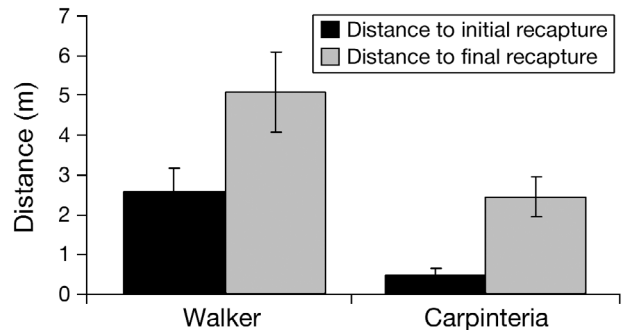


Fig. 6. *Pachygrapsus crassipes*. Mean distance (±1 SE) traveled between initial capture location and first point of recapture, and between the initial capture location and final point of recapture
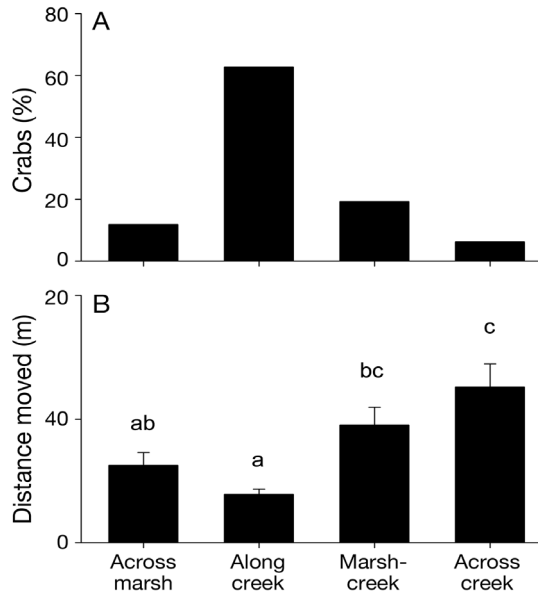
Fig. 7. *Pachygrapsus crassipes*.: (A) Percentage of crabs recaptured in each habitat, and (B) mean distance (±1 SE) traveled by crabs remaining within or traversing habitats. Substrate definitions are as follows: across marsh = movement along or across marsh plain; along creek = movement along creek bank; marsh-creek = movement between the creek bank and marsh plain; across creek = movement across a major creek channel. Different letters above bars indicate a significant difference in the distance moved among habitats

ber) and 220 µM (March) at the most downstream station (D) (Fig. 9a,b). Ammonium concentrations were much lower than nitrate, ranging from 2.5 to 38.9 µM, and are not shown.
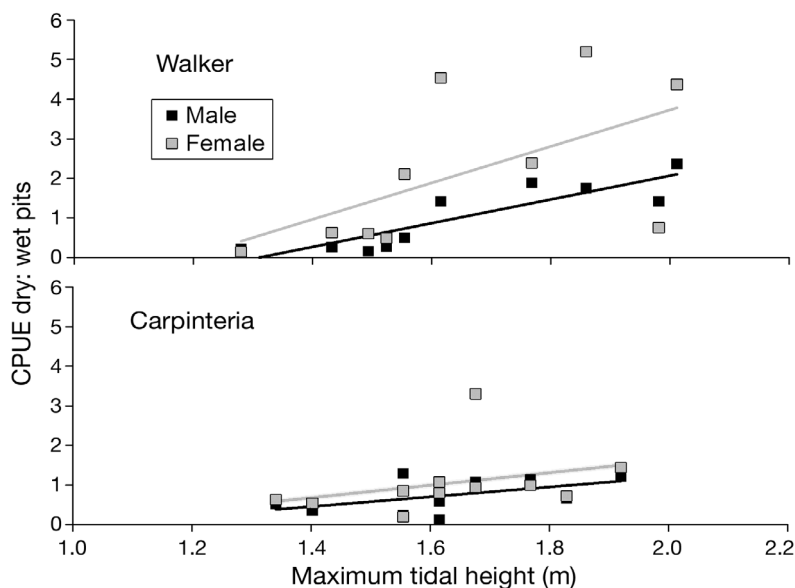


Fig. 8. *Pachygrapsus crassipes*. Ratio of crabs caught in dry and wet pitfall traps relative to maximum tidal height

The $\delta^{15}N$ values of *Pachygrapsus crassipes* and *Enteromorpha clathrata* decreased from Stns A to C in association with the decrease in influence of freshwater runoff (Fig. 9).

Values for both the crab and macroalga ranged from 14.5‰ at Stn A to between 10.6‰ (March) and 12.3‰ (September) at Stn D.

## DISCUSSION

The combined approaches demonstrated that *Pachygrapsus crassipes* is an effective indicator of small-scale variation in habitat condition. The mark-recapture studies provided direct evidence that crabs moved little, and the stable isotope study demonstrated that movement was sufficiently limited to indicate exposure to a gradient in nutrient contamination. A marked decline in isotope values of crabs was evident between the 2 upstream stations that were separated by only 140 m. The pattern of decrease in the isotope values for both macroalgae and crabs suggested the incorporation of anthropogenic nitrogen by producers and its transfer up the food chain to crabs. If crabs moved extensively along the channel, a gradient in crab $\delta^{15}N$ values from the upstream to downstream stations in association with the dilution of anthropogenic nitrogen inputs by tidal waters would not have been evident.

Several measurements taken during the mark-recapture study revealed that crabs typically dispersed only short distances, as previously found for other semiterrestrial crabs. First, the high percentage of *Pachygrapsus crassipes* recaptured suggests that crabs usually stayed within the central sampling area. The percentage of tagged crabs caught at least once during our study was 22.2% at Walker and 13.8% at Carpinteria, as compared with an average value of about 12% with ranges from 5 to 21% recapture rates in previous studies of other semiterrestrial crabs (Hill 1975, Ameyaw-Akumfi & Naylor 1987, Diaz & Conde 1989, Turner et al. 2003). Second, most *P. crassipes* were recaptured in the trap in which they were also initially captured. Third, the average dispersal rate (Walker: 2.06 m d$^{-1}$; Carpinteria: 3.07 m d$^{-1}$) of *P. crassipes* is typical of short-distance movements for semiterrestrial species that reside in burrows and other refuges. Fourth, the daily distance traveled declined over time, and although it may have

been truncated somewhat by the spatial limits of our trapping grid, it is evident that most *P. crassipes* did not travel far over the 3 mo studies. While some crabs return to specific refuges and move little outside of those refuges (Hughes 1966), *P. crassipes* and other semiterrestrial crabs that do not home, travel slightly farther from the site of original capture over time. In the case of 2 other grapsid crabs, *Pachygrapus marmoratus* in the Eastern Atlantic and Mediterranean remained within 2.2 to 3.64 m of the site of original capture over 24 to 33 d (Cannicci et al. 1997), and the Asian shore crab *Hemigrapsus sanguineus* traveled an average of 7.34 m over a 24 h period (Brouseau et al. 2004). Small subtidal and lower intertidal crabs also move little: *Mithrax forceps* (Majidae) traveled a mean of 0.5 m, *Libinia dubia* (Majidae) moved 2.3 m, and *Panopeus herbstii* (Xanthidae) moved 3.8 m over 48 h (Stachowicz & Hay 1999). In contrast, subtidal swimming crabs tend to move greater distances: *Scylla serrata*, for example moved an average of 461 m d$^{-1}$ (Hill 1978), and *Callinectes sapidus* averaged 40 to 50 m h$^{-1}$ (Bell et al. 2003). Unlike *P. crassipes*, ovigerous females of some species travel longer distances to release larvae. This is the case for semiterrestrial crabs that descend from the hills to release larvae along the shoreline (Wolcott & Wolcott 1982, Hicks 1985) and subtidal species, such as *C. sapidus* that can move as far as 5 km d$^{-1}$ and *Cancer magister* that travels 1.4 km over 13 d (Stone & O'Clair 2002, Carr et al. 2004).

In our study, the mean distance traveled was increased by relatively few individuals that undertook long excursions of up to 38 m. The mean distance traveled did not significantly increase with the time that crabs were free to roam between captures, which was as short as 1 d and as long as 3 mo. A similar result was obtained for *Pachygrapsus marmoratus* over a 25 to 33 d observation period (Cannicci et al. 1999). The seemingly contradictory result that crabs which were caught and released multiple times moved farther from the initial capture location with successive recaptures may be an artifact of repeatedly disturbing them. Rather than homing, *P. crassipes* scatter when they are released (Hiatt 1942, Morgan et al. pers. obs.). Thus, movement in our study was asymptotic: distance traveled increased slightly over time whereas the rate of increase declined.

Spatial and temporal movement patterns were similar between the 2 marshes and to 2 previous studies of *Pachygrapsus crassipes* in a marsh and on rocky shores (Hiatt 1942, Michaels 1988). In these studies, crabs typically did not move far, except for a few individuals that crossed open terrain or creeks. Crabs that traveled the longest distances in our study either traveled along a trampled footpath in the marsh or
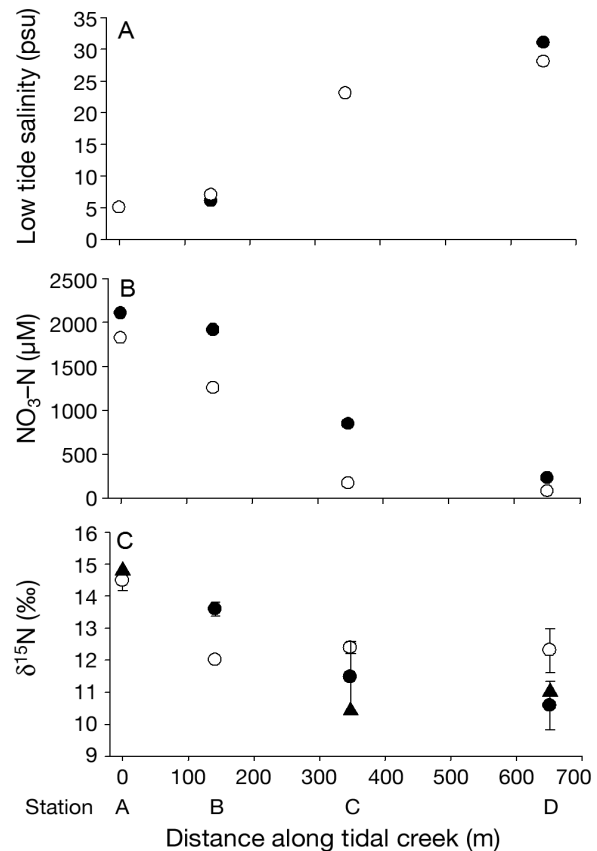


Fig. 9. *Pachygrapsus crassipes* and *Enteromorpha clathrata*. Variation in (A) low tide salinity, (B) concentration of nitrate, and (C) δ$^{15}$N values of *P. crassipes* in March (●) and September (○) 2003, and *E. clathrata* in March 2003 (▲) along a tidal creek receiving freshwater runoff from a coastal plain highly developed for agriculture. Mean values for *P. crassipes* are ±1 SD

crossed tidal creeks. In the previous studies conducted on rocky shores, a few individuals traveled longer distances across sand beaches adjacent to rocky habitat (50 to 100 m) than we observed in marshes, where burrows and vegetation provide both more cover and more obstacles to movement. Differences in water temperature, soil composition, vegetation cover and population density did not result in detectable differences in movement at our 2 study sites. Even though the 2 trap types captured crabs in different proportions at the 2 study sites, the overall distance traveled did not seem to be affected. This may, however, indicate that crabs are using habitat in different ways at the 2 marshes. Although crabs were slightly more abundant at Carpinteria than at Walker during the present study, it should be noted that similar densities of crabs were found at the 2 sites over the more extensive area sampled during our companion study (Morgan et al. unpubl. data). Furthermore, the densities of crabs at both of our study sites were simi-

lar to the average density reported for 1 creek in Goleta Slough in Southern California (4.0 ± 2.8 crabs $m^{-2}$) but were much lower than densities reported for another creek in the same slough (39.6 ± 13 crabs $m^{-2}$; Willason 1981). Thus, our estimates of movement appear to correspond to the observations made on rocky shores and may also be broadly applicable across geographic locations, except perhaps where even greater differences in environmental variables and population densities occur.

Habitat affected movement by *Pachygrapsus crassipes* generally, and not only in the case of the few individuals that traveled long distances. Crabs at Walker remained near the creek bank and very few of them moved between the creek bank and the marsh plain or remained on the marsh plain. Crabs also traveled the shortest distances along creek banks and farthest when they crossed creeks. The greater availability of burrows along the creek bank is likely responsible for the greater number of crabs and shorter distances traveled there. Burrows were most plentiful on muddy banks of tidal creeks, progressively declined 20 m away from the creek onto the marsh plain and were uncommon thereafter. Hiatt (1942) reported that crabs remained within 1.22 m of tidal creeks; however, we commonly found crabs 14 m from the nearest tidal creek.

Movement changed during the tidal amplitude cycle. *Pachygrapsus crassipes* moved away from wet areas bordering tidal creeks, where they were most abundant during spring tides, into drier areas on the marsh plain at both sites; this was especially evident for females at Walker Creek. Crabs may have migrated farther onto the marsh from creek banks either to forage during spring low tides — after more of the marsh had been inundated by the preceding high tide — or to avoid complete inundation just before spring flood tides. It is also possible that greater movement by females was due to larval release by ovigerous females during nocturnal early ebb tides, although larval release appears to occur after burrows are inundated, and asynchronously relative to the tidal amplitude cycle (S. G. Morgan unpubl. data). Regardless of this, crabs apparently returned to the creek bank during lower amplitude neap tides. *P. crassipes* may be an especially strong prospect for a marsh indicator since it moves between wet and dry areas of the marsh and likely integrates a range of vertical habitats. Assuming that the crabs feed throughout their vertical range, chemical analysis of their muscle tissues and organs would reflect an integrated view of marsh condition. We might also expect that embryos, particularly those on the outermost part of the clutch, would reflect the integration of different vertical strata. Although crabs moved farther onto the marsh during spring tides, *P.*

*crassipes* is more active during neap tides on quarter and new moons, when they are less visible to nocturnal terrestrial predators, such as birds, raccoons and weasels than during full moons (Hiatt 1942, Stenzel et al. 1976, Lindberg 1980, Michaels 1988).

Differences in movement between the sexes were also evident. More females moved inland across the marsh flat during spring tides, and more male than female crabs returned to the pitfall trap in which they had been captured initially. These behavioral differences between males and females may be explained by male crabs more strongly defending their burrows (Hiatt 1942). Even though no difference in distance traveled was observed between sexes, both patterns indicate that males were more likely to stay close to their refuges than were females. Males may therefore be better indicators of localized creek bank marsh condition than females who, in turn, may be better indicators of the condition of an integrated vertical range creek bank.

Only 7.1 and 28.6 % of recaptured *Pachgrapsus crassipes* molted before they were recaptured at Walker and Carpinteria respectively, as indicated by the presence of internal but no external tags. The Carpinteria study corresponded with the peak molting period between August and October (Hiatt 1942), just after the end of the reproductive season. The highest returns of crabs without external tags also occurred during this period at Walker.

In conclusion, *Pachygrapsus crassipes* indicated small-scale differences in exposure along a measured gradient in nutrient input and should prove to be broadly useful to future investigations of habitat condition. This species typically moves little across a broad range of habitat in marshes and on rocky shores where it occurs in high densities all along the west coast. Moreover, many semiterrestrial species of crabs around the world (Ocypodidae, Grapsidae, Gecarcinidae), with the exception of some tropical species that migrate long distances during the reproductive season to release larvae (Wolcott & Wolcott 1982, Hicks 1985, Wolcott 1988), should be excellent indicators of habitat condition because they are abundant, readily sampled and stay close to home.

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