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## Production and Population Dynamics of the Crayfish *Orconectes virilis* in Three Michigan Lakes<sup>1</sup>

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Fluctuations in mortality rather than in growth rates produced most of the year-to-year differences in biomass accumulation of three different populations of the crayfish *Orconectes virilis*. Yearly biomass changes resulted from density-dependent control of mortality and fecundity during certain portions of the life cycle. Density-dependent changes in mortality rates controlled population size for adults in all lakes and for young-of-the-year in two of the three study lakes. Growth rates were much less responsive to fluctuating densities. Disparity between the number of ovarian and attached eggs increased as density of age 1+ crayfish increased. This provided a strong density regulator on fecundity. Differences occurred in the number of recruits produced by a brood stock that survive to the end of the first growing season in the various lakes. Yet the number of females surviving to reproductive age 2 yr later was strongly regulated. Strong population regulation produced two female recruits of breeding age for every two-six parental breeding females. The high biomass and production levels of crayfish discovered in West Lost Lake in 1962-63 also occurred in the other area lakes. Higher but variable levels of recruitment resulted in larger standing crops and production in West Lost lake. This resulted from less effective density controls on the mortality rates of younger age-groups in that lake. Despite great variation in biomass of from 46 to 213 kg/ha and annual production from 60 to 142 kg/ha, the annual turnover ratio of the biomass was found to vary only between 0.94 and 1.53.

*Key words:* crayfish, *Orconectes virilis*, population dynamics, annual production, Michigan lakes

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Les différences d'une année à l'autre dans l'accumulation de biomasse de trois populations différentes d'écrevisses *Orconectes virilis* sont dues à des fluctuations de mortalité plutôt que des rythmes de croissance. Les changements annuels dans la biomasse résultent du contrôle de la mortalité et de la fécondité, dépendant de la densité, durant certaines portions du cycle biologique. Des changements dépendant de la densité dans les taux de mortalité contrôlent la taille des populations adultes dans tous les lacs et celles des jeunes de l'année dans deux des trois lacs étudiés. Les rythmes de croissance sont beaucoup moins sensibles aux fluctuations de densité. La différence entre le nombre d'œufs ovariens et d'œufs fixés augmente à mesure qu'augmente la densité des écrevisses d'âge 1+. Ceci constitue un bon agent de contrôle de la densité par la fécondité. On constate des différences dans le nombre de recrues produites par un stock reproducteur qui survit jusqu'à la fin de la première saison de croissance dans les divers lacs. Cependant, le nombre de femelles atteignant l'âge de la reproduction 2 ans plus tard est fortement contrôlé. Un contrôle rigide des populations produit deux recrues femelles sexuellement mûres pour chacune deux-six femelles reproductrices maternelles. Les niveaux élevés de biomasse et de production d'écrevisses découverts dans le lac West Lost en 1962-63 se sont produits également dans d'autres lacs. Des niveaux plus élevés mais variables de recrutement résultèrent en des biomasses et une production plus abondantes dans le lac West Lost. Ceci provint de contrôles de densité moins efficaces sur les taux de mortalité des groupes d'âge plus

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## Impact of the Introduction of Kokanee (*Oncorhynchus nerka*) and Opossum Shrimp (*Mysis relicta*) on a Subalpine Lake

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MORGAN, M. D., S. T. THRELKELD, AND C. R. GOLDMAN. 1978. Impact of the introduction of kokanee (*Oncorhynchus nerka*) and opossum shrimp (*Mysis relicta*) on a subalpine lake. *J. Fish. Res. Board Can.* 35: 1572-1579.

Introductions of opossum shrimp (*Mysis relicta*) and kokanee salmon (*Oncorhynchus nerka*) are common management tools for improvement of local sport fisheries. This paper summarizes published information from varied sources and presents supplemental data on the impact of these introductions on the Lake Tahoe zooplankton and fish communities. Concomitant with peak spawning runs of kokanee and the establishment and high densities of *Mysis* was the disappearance of the three pelagic cladoceran species in the lake. Population dynamics analysis of the cladoceran populations indicate that their elimination was due to increasing death rates (related to *Mysis* and kokanee predation) and decreasing birth rates (possibly related to cultural eutrophication). Changes have also been observed in the fish populations. Lake trout have altered their food habits to include large quantities of *Mysis*, but this has been done to the exclusion of other prey types. Thus, improvement in lake trout condition has been indicated only in years when *Mysis* is abundant. Recent evidence of a sustained decline in the mysid population suggests that unless lake trout shift back to more traditional food sources, their condition could deteriorate to below pre-mysid levels. Finally, mean weight and abundance of kokanee spawners have declined since the cladoceran disappearance, suggesting a negative impact on the whole population which fed heavily on cladocerans.

*Key words:* opossum shrimp, kokanee salmon, population dynamics, cladoceran decline, introductions, subalpine lake

MORGAN, M. D., S. T. THRELKELD, AND C. R. GOLDMAN. 1978. Impact of the introduction of kokanee (*Oncorhynchus nerka*) and opossum shrimp (*Mysis relicta*) on a subalpine lake. *J. Fish. Res. Board Can.* 35: 1572-1579.

Deux outils de gestion communément utilisés lorsqu'il s'agit d'améliorer les pêcheries sportives locales sont l'introduction de mysides (*Mysis relicta*) et de kokani (*Oncorhynchus nerka*). Nous résumons dans le présent article l'information publiée provenant de diverses sources et présentons des données supplémentaires sur les répercussions de ces peuplements sur les communautés zooplanctoniques et ichtyologiques du lac Tahoe. En même temps que les remontées reproductrices des kokani atteignent un sommet et que les *Mysis* s'établissent et deviennent très denses, on constate la disparition de trois espèces de cladocères pélagiques dans le lac. L'analyse de la dynamique des populations de cladocères indique que leur élimination est due à des taux de mortalité accrus (liés à la prédation par les *Mysis* et les kokani) et à une natalité réduite (possiblement liée à l'eutrophisation agricole). On observe également des changements dans les populations de poissons. Les touladis modifient leurs habitudes alimentaires pour inclure de grandes quantités de *Mysis*, mais cela s'est produit à l'exclusion des autres types de proies. On constate donc une amélioration dans la condition des touladis seulement dans les années où les *Mysis* sont très abondants. La preuve récente d'un déclin graduel de la population de mysides donne à croire que la condition des touladis pourrait se détériorer au point de tomber à des niveaux inférieurs à ceux d'avant-mysides, à moins que ces touladis ne retournent à des sources de nourriture plus traditionnelles. Finalement, le poids moyen et l'abondance des kokani reproducteurs ont décliné depuis la disparition des cladocères, ce qui suggère une répercussion négative sur la population entière qui se nourrissait abondamment de cladocères.

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Impact of Introduced Populations of *Mysis relicta*  
on Zooplankton in Oligotrophic Subalpine Lakes

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Running head: *Mysis*-zooplankton interactions

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## INTRODUCTION

Introductions of the opossum shrimp, *Mysis relicta*, have become a common method for improving sport fisheries, particularly in the mountain regions of the western United States and Canada and northern Europe. However, the ultimate success of these introductions, in the few cases where they have been monitored, has been compromised by unexpected and often undesirable changes in the zooplankton community structure (Northcote 1973; Rieman 1977; Morgan *et al.* 1978). Here we examine the zooplankton species composition and relative abundance in Donner and Fallen Leaf Lake, California, before and after the establishment of *Mysis relicta*. Together with detailed information already available from nearby Lake Tahoe and Emerald Bay, we hope to clarify some aspects of the *Mysis*-zooplankton interaction.

### Study Area

Donner and Fallen Leaf Lake are located near Lake Tahoe on the eastern slope of the Sierra Nevada at elevations of 1809 and 1939 m respectively (Fig. 1). Both are of glacial origin and Fallen Leaf Lake is slightly larger and deeper ( $5.6 \text{ km}^2$ ,  $z_{\text{max}}=110 \text{ m}$ ) than Donner Lake ( $3.8 \text{ km}^2$ ,  $z_{\text{max}}=67 \text{ m}$ ). The basic limnology of both lakes is similar (Dong 1975; Fuller 1975; Goldman and Rundquist 1977).

## MATERIALS AND METHODS

Zooplankton were collected on 30 August 1978 and 15 June 1979 from Donner Lake and on 17 August 1978 and 13 June 1979 from Fallen Leaf Lake. In each lake, 5 stations ranging in depth from 19-67 m in Donner Lake and 21-110 m in Fallen Leaf Lake, were sampled along a longitudinal transect (Fig. 1). At



each station, one vertical net tow was taken from the bottom to the surface with a 30 cm diameter, 80  $\mu\text{m}$  mesh plankton net. All samples were preserved in 5% formalin. The crustacean zooplankton were counted and identified at 30-40X magnification under a dissecting microscope. The entire sample was scanned for the enumeration of rare species while abundant species were counted after reduction with a Folsom plankton splitter.

Details of the methods used for the determination of primary productivity have been reported elsewhere (Goldman 1974). Briefly,  $\text{H}^{14}\text{CO}_3$  incorporation in 1 dark and 2 light bottles was measured at 8 to 13 depths throughout the euphotic zone. The amount of carbon assimilated is highly dependent on the total amount of light available on the day of the measurement. Consequently, the productivity values in Fig. 2 have been scaled to a constant light flux of 600 langley/day to facilitate comparisons among lakes over time. This value is typical of summer values for the Lake Tahoe area.

## RESULTS

The crustacean zooplankton species composition and relative abundance in Donner and Fallen Leaf Lake for all years for which records exist is presented in Table 1. All of these data except for the 1973 collections by Dong (1975) in Donner Lake are based on a single observation during the summer of the year. The 1973 data are based on 8 samples collected between May and December. Since some zooplankton species come and go over a relatively short time, the consideration of long-term changes in the zooplankton based on these data must be limited to those species which are continuously present throughout the summer. Detailed information from Lake Tahoe (Goldman *et al.* 1979) and Donner Lake (Dong 1975) indicate that *Daphnia*



*pulicaria*, *D. rosea*, *Bosmina longirostris*, *Epischura nevadensis* and *Diaptomus pallidus* (and by inference *Diaptomus* sp. from Fallen Leaf Lake) fit this criterion. There is no way to determine which, if any, of the other crustacean zooplankton also fit this criterion, so changes in their abundance over time cannot be considered at present.

The species composition and relative abundance of the Fallen Leaf Lake zooplankton in July 1913 and August 1970 was similar (Table 1). *Daphnia pulicaria* (identified as *pulex* by Kemmerer *et al.* 1923), *Bosmina longirostris* and *Diaptomus* sp. were abundant in both years. In 1970, *D. pulicaria* and *D. rosea* were not counted separately because of their morphological similarity. Data from Lake Tahoe in 1967-1968 and 1970 revealed that greater than 95% of the *Daphnia* were *D. pulicaria* (Goldman *et al.* 1979). If this were also true in Fallen Leaf Lake, the combination of rarity and superficial similarity of *D. rosea* to *D. pulicaria* might account for its absence from the 1913 record. More recent samples from August 1978 and June 1979 revealed that *Bosmina* was the only member of the zooplankton still abundant. Even though a combined volume of more than 40 m<sup>3</sup> was filtered between 1978 and 1979, no *Daphnia* and only a very small number (< 0.5/m<sup>3</sup>) of *Diaptomus* in August 1978 were collected.

The earliest sampling of the Donner Lake crustacean zooplankton occurred in 1970. *Daphnia rosea*, *Bosmina longirostris*, *Diaptomus pallidus* and *Epischura nevadensis* were present and abundant (Table 1). *Daphnia rosea* was not reported from May-December 1973 (Dong 1975) and in June 1979, although four individuals (out of a total filtered volume of 14.6 m<sup>3</sup>) were found in August 1978. Similarly, although absent in June 1979, two *Diaptomus pallidus* individuals were recorded in August 1978. Only *Bosmina longirostris* and *Epischura nevadensis* were abundant in both the August 1978 and June 1979



samples.

These data suggest that since 1970, there have been significant changes in the zooplankton of these lakes. *Daphnia pulicaria* and *D. rosea* have apparently disappeared and *Diaptomus* sp. has been reduced to a residual population in Fallen Leaf Lake as have *D. rosea* and *Diaptomus pallidus* in Donner Lake. Two factors suggest that these changes are not simply artifacts of the limited data. First, the volume of water filtered and the diversity of stations sampled in August 1978 and June 1979 should have been more than sufficient to accurately determine species composition and relative abundance. Second, only those species known to be present continuously throughout the summer were considered. Thus, it is unlikely that these changes could have resulted from chance samplings or irregular seasonal distributions.

#### DISCUSSION

Currently, no direct evidence is available to suggest a reason for the apparent decline and extinction of some of the Donner and Fallen Leaf Lake zooplankton sometime after 1970. However, indirect evidence based on extensive studies in nearby Lake Tahoe and Emerald Bay, a semi-isolated and more productive embayment of Lake Tahoe, suggests a likely explanation for at least some changes. Between 1970 and 1971, the three pelagic cladoceran species (*Daphnia pulicaria*, *D. rosea* and *Bosmina longirostris*) in Lake Tahoe disappeared from the plankton (Richards *et al.* 1975; Goldman *et al.* 1979). *Mysis relicta*, introduced into Lake Tahoe between 1963 and 1965, became firmly established in Lake Tahoe around 1970 (Morgan *et al.* 1978). *Mysis* is known to be a voracious predator on zooplankton, particularly cladocerans (Lasenby and Langford 1973; Rybock 1978; Cooper and Goldman 1980) and is considered primarily responsible for the Lake Tahoe cladoceran extinctions (Morgan *et al.*



1978; Threlkeld *et al.* 1980).

*Mysis relicta* was also introduced into Donner and Fallen Leaf Lake in 1965 (Hansen 1966). Quantitative estimates of population size in 1978 and 1979 revealed that they were established throughout each lake at relatively high densities (avg. lakewide densities 100-200/m<sup>2</sup>; Morgan 1981). Therefore, *Mysis* predation offers a reasonable explanation for the disappearance of *D. pulicaria* and *D. rosea* from Fallen Leaf Lake and the decline of *D. rosea* in Donner Lake.

A notable difference between the impact of *Mysis* on the Lake Tahoe cladocerans and their presumed impact on the Donner and Fallen Leaf Lake cladocerans is the presistence of *Bosmina longirostris* in the latter lakes. *Bosmina* also survived the establishment of *Mysis relicta* in Emerald Bay, which in addition to *Bosmina*, had supported large populations of both *D. pulicaria* and *D. rosea* (Frantz and Cordone 1963; Richardson unpublished). It has been hypothesized that two features of the Emerald Bay environment enable *Bosmina* to coexist with *Mysis* when it could not in Lake Tahoe. These are greater productivity, which results in higher birth rates to better offset predation losses and allow rapid recolonization of decimated areas, and gentler bathymetry, which in summer provides a larger proportion of warm shallow refuges which *Mysis* cannot penetrate (Goldman *et al.* 1979; Threlkeld *et al.* 1980). These factors apparently did not help either *Daphnia* species because of their greater preference for cold water (Juday 1906; Richerson 1969) and their greater susceptibility to mysid predation due to their larger size and reduced mobility (Cooper and Goldman 1980).

The response of the zooplankton in Donner and Fallen Leaf Lake provide additional support for these ideas. Figure 2 presents carbon fixation



and Secchi depth measurements for selected dates from Donner Lake, Fallen Leaf Lake, Emerald Bay and Lake Tahoe over a 10 year period from 1969 to 1978. All of the values for a given month were collected within two weeks of each other. Although it is difficult to quantitatively compare overall productivity based on so few measurements, it is clear that both in terms of carbon assimilation and Secchi depth measurements Lake Tahoe is far less productive than the other three. The ability of *Bosmina* to survive in Donner and Fallen Leaf Lake then supports the hypothesis that increased productivity increases *Bosmina*'s chances of surviving a mysid introduction.

The importance of a thermal refuge for cladoceran coexistence with *Mysis* is illustrated by data from Donner Lake. Contrary to initial expectations, the large bodied cladoceran, *Holopedium gibberum*, persisted in Donner Lake in 1973 even though *Daphnia* could not (Table 1). The rough vertical distribution data provided by Dong (1975) suggests how this may have been possible (Fig. 3). In both August and October, the only months when *Holopedium* was present in abundance, the majority of the population was found in warmer surface waters. Thus, this cladoceran, in contrast to *Daphnia rosea* (Richerson 1969), avoided potentially significant *Mysis* predation by concentrating in the epilimnion. In lakes with natural *Mysis* populations, this is probably the principal mechanism by which *Mysis* coexists with cladocerans (Threlkeld *et al.* 1980). As an example, *Mysis* is found with three *Daphnia* species in Lake Michigan, all of which are principally distributed above the thermocline (Wells 1970).

Although predation by *Mysis relicta* seems to adequately explain the cladoceran decline in Donner and Fallen Leaf Lake, whether or not *Mysis* is also responsible for the decline of *Diaptomus* in these lakes is unknown.



Similar declines in the *Diaptomus* populations of Emerald Bay and Lake Tahoe have not been observed (Goldman *et al.* 1979). Consequently, there is no basis for comparison of these effects. There may be features of the Donner and Fallen Leaf Lake environment, as yet not recognized, which have resulted in a greater impact of *Mysis* on copepods than in other lakes. Alternatively, the copepod decline may have resulted from some unknown factor operating independently of *Mysis* predation.

In any event, the decline of *Diaptomus* serves to illustrate that although we may now have a good understanding of the most obvious effects of *Mysis* introductions on oligotrophic subalpine lakes (*i.e.* their tendency to decimate resident cladoceran populations), we know little of the more subtle effects on the rest of the lake ecosystem. Consequently, until these effects are better understood, future introductions of *Mysis relicta* should be avoided.

#### SUMMARY

The crustacean zooplankton in Fallen Leaf Lake, California in July 1913 and August 1970 was dominated by *Daphnia pulicaria*, *D. rosea*, *Bosmina longirostris* and *Diaptomus* sp. Samples from August 1978 and June 1979 revealed that only *Bosmina* was still abundant. Both *Daphnia* species were no longer present and *Diaptomus* existed as a rare population. Similarly, the crustacean zooplankton of neighboring Donner Lake was dominated by *D. rosea*, *B. longirostris*, *Diaptomus pallidus* and *Epischura nevadensis* in August 1970 but by August 1978 and June 1979, only *Bosmina* and *Epischura* were still abundant. *D. rosea* and *Diaptomus* were rare.

The cladoceran fauna of nearby Lake Tahoe, California-Nevada (*D. pulicaria*, *D. rosea* and *B. longirostris*) disappeared from the plankton shortly after 1970. Detailed studies have implicated predation by *Mysis relicta* (introduced into the lake between 1963 and 1965) as the primary



cause of these extinctions. *Mysis* was also introduced into Donner and Fallen Leaf Lake in 1965 and is therefore considered the most likely reason for the decline of the cladoceran populations in these lakes. As in Donner and Fallen Leaf Lake, *Bosmina* survived *Mysis* predation in Emerald Bay, a shallower and more productive embayment of Lake Tahoe. The ability of *Bosmina* to persist in these environments when it could not in Lake Tahoe is believed related to the greater productivity and gentler bathymetry of these systems. There is insufficient comparative data to suggest a reason for the simultaneous decline of the *Diatomus* populations in Donner and Fallen Leaf Lake.

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Table 1. Historical records of crustacean zooplankton species composition and relative abundance in Donner and Fallen Leaf Lake, California. + = abundant ( $> 10/m^3$ ), \* = rare, - = absent.

| Crustacean Zooplankton           | Fallen Leaf Lake       |                        |           |           | Donner Lake            |                            |           |           |
|----------------------------------|------------------------|------------------------|-----------|-----------|------------------------|----------------------------|-----------|-----------|
|                                  | July 1913 <sup>1</sup> | Aug. 1970 <sup>2</sup> | Aug. 1978 | June 1979 | Aug. 1970 <sup>2</sup> | May-Dec. 1973 <sup>3</sup> | Aug. 1978 | June 1979 |
| <i>Daphnia pulicaria</i> (pulex) | +                      | +                      | -         | -         | -                      | -                          | -         | -         |
| <i>D. rosea</i>                  | -                      | +                      | -         | -         | +                      | -                          | *         | -         |
| <i>Bosmina longirostris</i>      | +                      | +                      | +         | +         | +                      | +                          | +         | +         |
| <i>Holopedium gibberum</i>       | -                      | +                      | -         | -         | -                      | +                          | *         | -         |
| <i>Ceriodaphnia reticulata</i>   | -                      | -                      | -         | -         | -                      | +                          | -         | -         |
| <i>Leptadora kindtii</i>         | -                      | -                      | -         | -         | *                      | -                          | -         | -         |
| <i>Diaptomus</i> sp.             | +                      | +                      | *         | -         | -                      | -                          | -         | -         |
| <i>Diaptomus pallidus</i>        | -                      | -                      | -         | -         | +                      | +                          | *         | -         |
| <i>Epischura nevadensis</i>      | -                      | -                      | -         | -         | +                      | +                          | +         | +         |
| Cyclopoid                        | +                      | +                      | -         | -         | *                      | *                          | -         | -         |

<sup>1</sup>from Kemmerer *et al.* (1923)

<sup>2</sup>Goldman,<sup>un</sup> unpublished

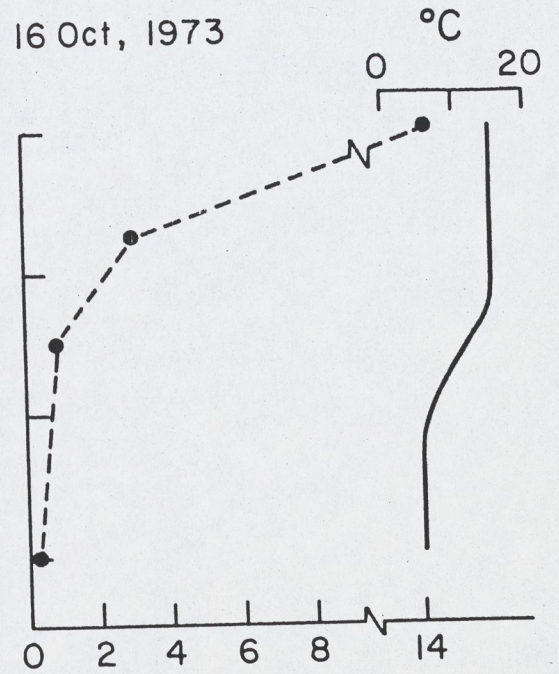
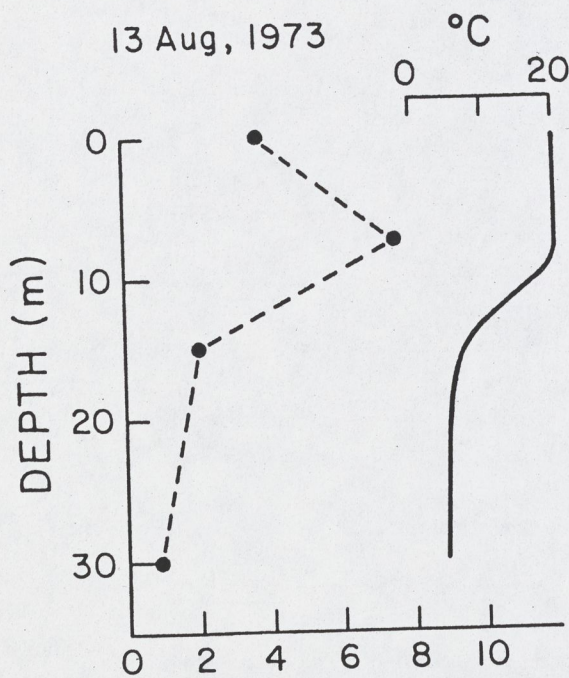
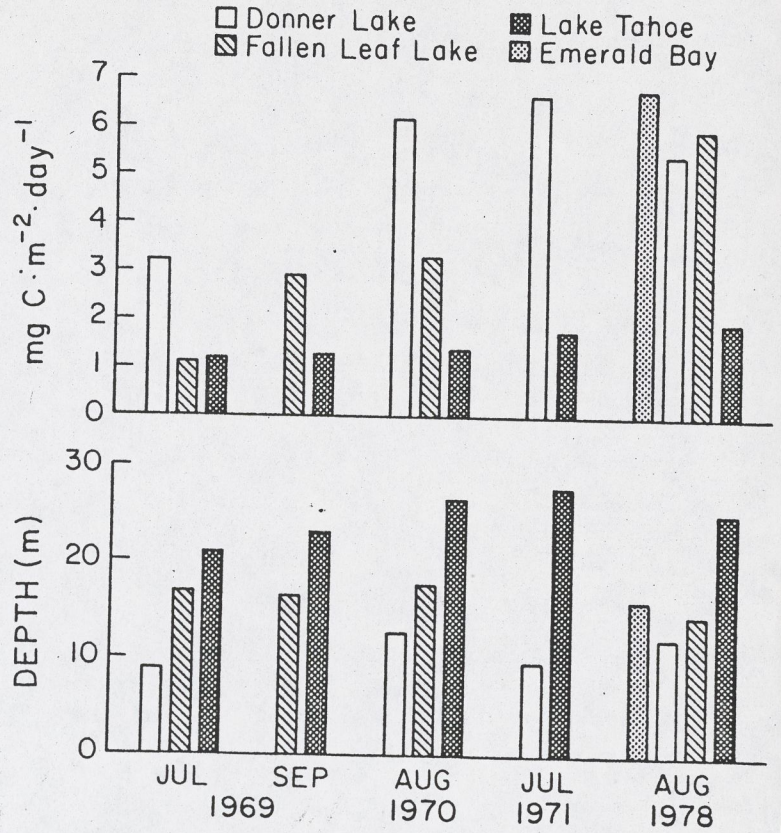
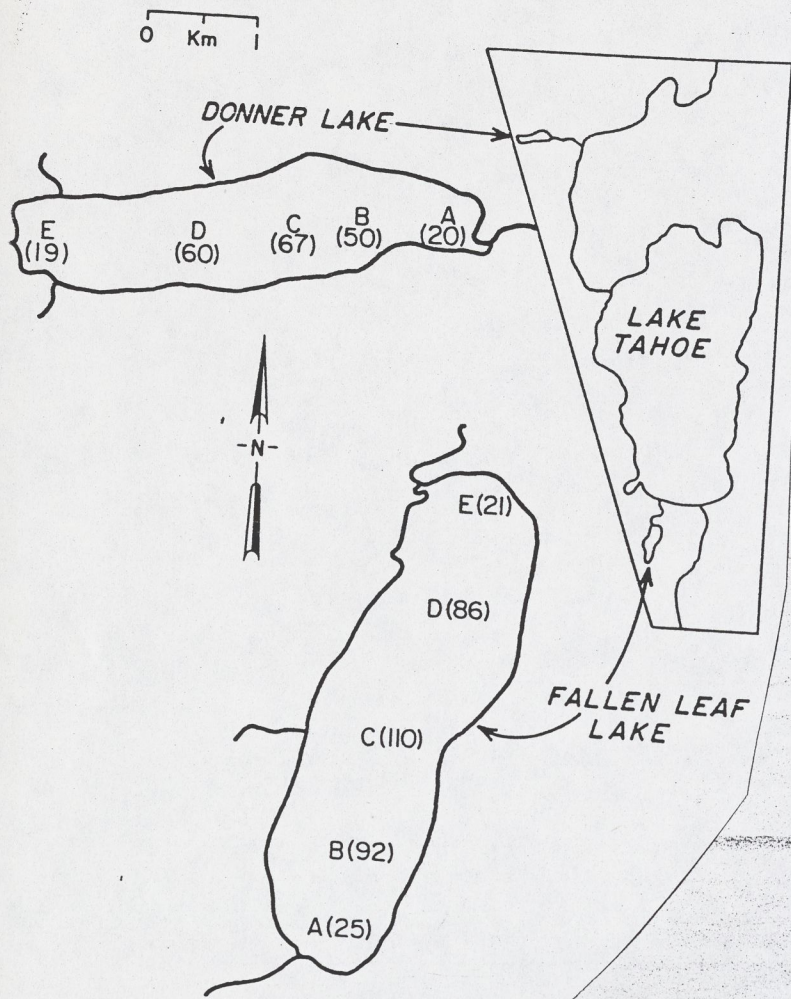
<sup>3</sup>from Dong (1975)



#### FIGURE CAPTIONS

- Figure 1. Map of Donner and Fallen Leaf Lake, California, indicating zooplankton sampling locations (A-E) and depth (m). Inset illustrates relative positions of Donner and Fallen Leaf Lake to Lake Tahoe.
- Figure 2. Overall productivity of Donner Lake, Fallen Leaf Lake, Emerald Bay and Lake Tahoe for selected dates from 1969 to 1970 based on carbon assimilation measurements (top panel) and Secchi depth (bottom panel).
- Figure 3. Vertical distribution of *Holopedium gibberum* (dashed line) and temperature profile (solid line) in Donner Lake in August and October 1973. Data are based on four stratified vertical plankton net tows taken by Dong (1975).





PERCENTAGE OF TOTAL POPULATION PER METER



## LIFE HISTORY CHARACTERISTICS OF TWO INTRODUCED POPULATIONS OF *MYTIS RELICTA*<sup>1</sup>

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**Abstract.** Introduced populations of the opossum shrimp *Mysis relicta* take 4 yr to reach reproductive age in Lake Tahoe, California-Nevada and 1-2 yr in Emerald Bay, an isolated (for *Mysis*) embayment of Lake Tahoe. Reproduction in both populations occurs in the winter and spring. The duration of embryonic stages in the Emerald Bay population based on field population statistics ranged from 50 d for the egg stage to 6 d for the last embryonic stage. The number of eggs per egg-bearing female in Emerald Bay increased significantly with the total length of the female. Over the entire brooding period, the average number of embryos per female decreased from 13.89 eggs per gravid female to 10.33 stage 5 embryos per female. This decline in brood size with age of the brood was not due to size-related mortality, but probably resulted from embryos falling out of the marsupium. A similar decline in brood size with age of the brood was not observed in Lake Tahoe. The average number of eggs per brood in Lake Tahoe was 10.73 which was significantly less than that observed in Emerald Bay. However, there was no difference in the number of stage 5 embryos per brood in both systems.

Differences in generation time and total reproductive output in the Lake Tahoe and Emerald Bay populations were most closely related to differences in the overall production and mean depth of the two systems. In addition, these traits and whether reproduction is seasonal or continuous among other mysid populations are strongly correlated with the total production of the environment. These results suggest that differences in *M. relicta* life history traits among populations may represent a phenotypic and not an evolutionary life history adaptation.

**Key words:** developmental time; evolution; Lake Tahoe; life history; *Mysis relicta*; phenotypic adaptation; productivity.

### INTRODUCTION

Information on the life history characteristics of the opossum shrimp *Mysis relicta* Lovén in a wide variety of aquatic habitats has recently become available (e.g., Brownell 1970, Lasenby and Langford 1972, Carpenter et al. 1974, Morgan and Beeton 1978). The data reveal that *M. relicta* life history patterns vary considerably among populations. Reproduction may occur throughout the year or only in the winter and spring, depending on the population, and it may take from 1 to 2 yr to reach reproductive age (Samter and Weltner 1904, Thienemann 1925, Larkin 1948).

Comparative studies of life history traits are of great importance to life history theory. However, as Stearns (1977) has pointed out, many factors may intercede to hamper their interpretation. One factor is that differences in life history characteristics may represent a phenotypic and not an evolutionary life history adaptation. Although phenotypic plasticity is undoubtedly evolutionarily derived, application of life history theory is useful only if selection of observed traits is based on characteristics of the particular environment (i.e., degree and type of environmental variability, adult vs. juvenile mortality schedules, etc.). For ex-

ample, a poorly nourished population may take longer to reproduce than a well-fed one even though they are genotypically identical and not responding to differential selective pressures. The amount of the observed variability in life history traits that may be due to phenotypic plasticity can be estimated by observing the response of introduced populations (which over the short run have limited opportunity to exhibit evolutionary changes) to different environments.

Preliminary studies suggested that the life history characteristics of introduced populations of *Mysis relicta* in Lake Tahoe, California-Nevada and Emerald Bay, a semi-isolated embayment of Lake Tahoe, differed considerably. This paper details the life history characteristics of these populations and suggests what factors may be regulating them. The mechanisms controlling variation of these traits among natural populations are also examined and compared with these results to suggest how much of this variation may be due to a simple phenotypic response.

*Mysis relicta* naturally inhabits northern cold water lakes, usually associated with areas of Pleistocene glaciation (Segerstrale 1962). *Mysis* is an important item in the diets of many sport and commercial fish, particularly lake trout (*Salvelinus namaycush*), and for this reason has been introduced into a great many lakes (Gosho 1975). Between 1963 and 1965 approximately 333,000 mysids from Waterton Lake, Alberta, Canada were introduced at various locations around

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TABLE 1. Summary of sampling dates, sites, and number of replicates per site ( $n$ ) in Lake Tahoe from 25 November 1975 to 7 April 1979, and in Emerald Bay from 9 February 1977 to 13 December 1978.

| Lake Tahoe |          |        |     | Emerald Bay |        |      |     |
|------------|----------|--------|-----|-------------|--------|------|-----|
| Year       | Date     | Site   | $n$ | Year        | Date   | Site | $n$ |
| 1975       | 25 Nov   | A-E    | 3   | 1977        | 9 Feb  | 6    | 1   |
| 1976       | 4 Oct    | 3      | 6   | 12 June     | 6      | 1    | 1   |
|            | 16 Oct   | 3      | 6   | 29 Aug      | 6      | 1    | 1   |
|            | 16 Nov   | 3      | 4   | 31 Oct      | 6      | 1    | 1   |
|            | 15 Dec   | 3      | 4   | 29 Nov      | 6      | 1    | 1   |
| 1977       | 8 Jan    | 3      | 4   | 28 Dec      | 6      | 3    | 3   |
|            | 25 Jan   | 3      | 4   | 1978        | 10 Jan | 6    | 3   |
|            | 9 Feb    | 3      | 2   | 24 Jan      | 6      | 3    | 3   |
|            | 19 March | 3      | 4   | 13 Feb      | 6      | 3    | 3   |
|            | 31 March | 3      | 4   | 1 March     | 6      | 3    | 3   |
|            | 28 April | 3, 5   | 4   | 20 March    | 6      | 3    | 3   |
|            | 10 June  | 3      | 4   | 11 April    | 6      | 3    | 3   |
|            | 23 June  | 3, 5   | 4   | 11 May      | 6      | 3    | 3   |
|            | 22 July  | 3, 5   | 4   | 11 June     | 6      | 3    | 3   |
|            | 13 Aug   | 1-3, 5 | 4   | 3 July      | 6      | 3    | 3   |
|            | 4 Oct    | 1-3, 5 | 4   | 23 July     | 6      | 3    | 3   |
|            | 25 Oct   | 1-3, 5 | 4   | 13 Aug      | 6      | 3    | 3   |
|            | 17 Nov   | 1-5    | 3   | 8 Sept      | 6      | 3    | 3   |
|            | 27 Dec   | 1-5    | 3   | 27 Sept     | 6      | 3    | 3   |
| 1978       | 10 Jan   | 1-5    | 3   | 16 Oct      | 6      | 3    | 3   |
|            | 25 Jan   | 1-5    | 3   | 6 Nov       | 6      | 3    | 3   |
|            | 14 Feb   | 1-5    | 3   | 13 Dec      | 6      | 3    | 3   |
|            | 14 March | 1-5    | 3   |             |        |      |     |
|            | 17 April | 1-5    | 3   |             |        |      |     |
|            | 9 May    | 1, 3-5 | 2   |             |        |      |     |
|            | 7 June   | 1-5    | 3   |             |        |      |     |
|            | 7 Aug    | 1-5    | 3   |             |        |      |     |
|            | 4 Oct    | 1, 3-5 | 3   |             |        |      |     |
|            | 13 Dec   | 1, 3-5 | 3   |             |        |      |     |
| 1979       | 15 Feb   | 1, 3-5 | 2   |             |        |      |     |
|            | 7 April  | 1, 3-5 | 3   |             |        |      |     |

Lake Tahoe, a cold, deep ultra-oligotrophic lake at an altitude of 1898 m, and Emerald Bay (Linn and Frantz 1965, Hansen 1966). The success of the introduction was confirmed by 1971 in Lake Tahoe and later in Emerald Bay when mysids appeared in large numbers in epibenthic sled tows and lake trout stomachs (Richards et al. 1975, Morgan et al. 1978, R. Wickwire, *personal communication*).

Emerald Bay is separated from Lake Tahoe by a sill 2-4 m deep. Many studies have shown that *Mysis* avoids the high light and temperature conditions which prevail on most occasions at the sill (Beeton 1959, 1960, Teraguchi 1969, Smith 1970, Morgan et al. 1978) and extensive sampling just inside and outside the bay mouth have failed to detect any significant exchange between these populations (S. Threlkeld and M. Morgan, *personal observation*). Therefore, for the purposes of this paper, Emerald Bay and Lake Tahoe are considered isolated bodies of water with respect to *Mysis*.

#### MATERIALS AND METHODS

*Mysis* sampling in Lake Tahoe occurred over a 3½ yr period from 27 November 1975 to 7 April 1979

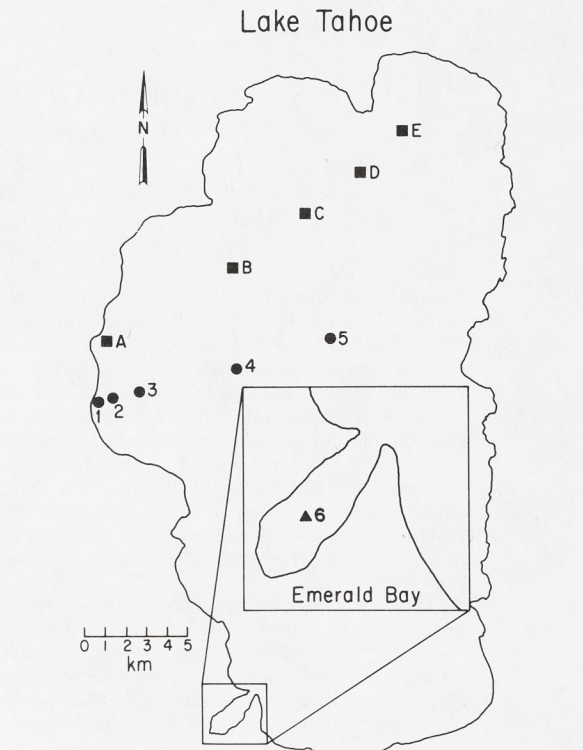


FIG. 1. Map of Lake Tahoe indicating sampling stations in the main lake and in Emerald Bay.

aboard the R/V John LeConte. Samples were collected by nighttime vertical net tows from the bottom to the surface with 0.75 m diameter bongo nets (500- $\mu$ m mesh). All specimens were preserved in 10% formalin. In most cases, three replicates were taken at each station although the number of replicates sometimes varied from two to six. No samples were taken between November 1975 and October 1976 after which intervals between samples ranged from 2 to 8 wk with the most frequent sampling occurring during the reproductive period (October-April, Table 1). Samples from October 1976 until March 1977 were collected at a station along the west shore, 175 m deep (Fig. 1, #3). In April, a 450-m station (#5) was added to this and in October 1977 stations at 50 m (#1), 100 m (#2) and 325 m (#4) were added to form a transect from mid-lake to the west shore. Station #2 was discontinued in October 1978. The November 1975 samples were collected at five stations (A-E) ranging in depth from 22-460 m along a transect from Crystal Bay to the west shore (Fig. 1). Depth had a significant impact on the size frequency distribution obtained at each station on a given date. Consequently an average lake-wide estimate of the size frequency distribution was obtained when more than one station was sampled by weighting and averaging the frequency distributions from each station (Morgan 1979).

Emerald Bay samples were collected as described



# GENETIC VARIATION AND POPULATION STRUCTURE IN A SPINY LOBSTER, *PANULIRUS MARGINATUS*, IN THE HAWAIIAN ARCHIPELAGO<sup>1</sup>

JAMES B. SHAKLEE<sup>2</sup> AND PAUL B. SAMOLLOW<sup>3</sup>

## ABSTRACT

Samples of the commercially important spiny lobster, *Panulirus marginatus*, were collected from localities throughout the Hawaiian Archipelago and subjected to starch gel electrophoretic analysis of protein variation. The amount and pattern of genetic variation exhibited by specific enzymes was determined and analyzed to see whether or not there was evidence that the species was composed of multiple stocks or subpopulations throughout its range.

The lobster exhibited polymorphisms at 7 loci (Est-3, Umb, Gpi, Mpi, Pep-1, Pep-2, and Pgm) out of the 46 enzyme-coding loci screened. However, genetic variability in the species was quite low, the average heterozygosity for all loci was 0.021. Observed genotype distributions at the variable loci agreed with Hardy-Weinberg expectations. Allele-frequency distributions for each locus were remarkably similar across localities and statistical tests failed to reveal clear patterns of genetic differentiation within the Archipelago. The results are consistent with the existence of a single panmictic stock of *Panulirus marginatus* throughout the Hawaiian Archipelago.

The rational management of any fisheries resource, whether directed at exploitation, conservation, or some other goal, requires many different types of information about the species in question, and its interaction with environmental and biological factors in its environment. Data on basic biology (taxonomy, distribution and abundance, food habits, behavior, etc.), ecological requirements, reproductive characteristics, and population dynamics are all relevant to management decisions. Although the above types of information are necessary to any meaningful management plan, they are not sufficient. Information concerning the stock or subpopulation structure of the species is also of critical importance to the formulation of any comprehensive, long-term management program (MacLean and Evans 1981).

Subpopulations or stocks are generally considered to be self-sustaining subunits of a species which are more-or-less reproductively isolated from other such groups. It is reasonable to assume that as a result of random processes and local selection pressures, these subpopulations (stocks)

will become genetically differentiated from one another. For this reason, the electrophoretic analysis of genetic characteristics provides one of the most direct, and therefore theoretically powerful, approaches to the problem of defining subpopulation structure. However, it should be emphasized that all tests of stock structure, including electrophoretic ones, are really one-sided. It is actually only possible to establish the existence of multiple differentiated stocks by falsifying the null hypothesis of a single, widespread, panmictic stock. It is not possible to prove that only a single panmictic population exists although the data (be they genetic, morphological, behavioral, or whatever) may be consistent with this hypothesis.

In the last decade, a substantial, multispecies, commercial fishery has developed in the Northwestern Hawaiian Islands (NWHI). This fishery is directed almost exclusively at demersal species and is dominated by catches of spiny lobsters (Palinuridae), snappers (Lutjanidae), and groupers (Serranidae). Because of the largely unknown and previously unexploited nature of this fishery, a coordinated, large-scale, multidisciplinary study involving personnel from the National Marine Fisheries Service Honolulu Laboratory, the U.S. Fish and Wildlife Service, the Hawaii Division of Fish and Game, and the University of Hawaii was initiated to describe, analyze, and model the major components of the NWHI ecosystem (Grigg and Pfund 1980). The genetic analysis

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of stock structure of the lobster detailed in this report was one part of this overall program (Shaklee and Samollow 1980).

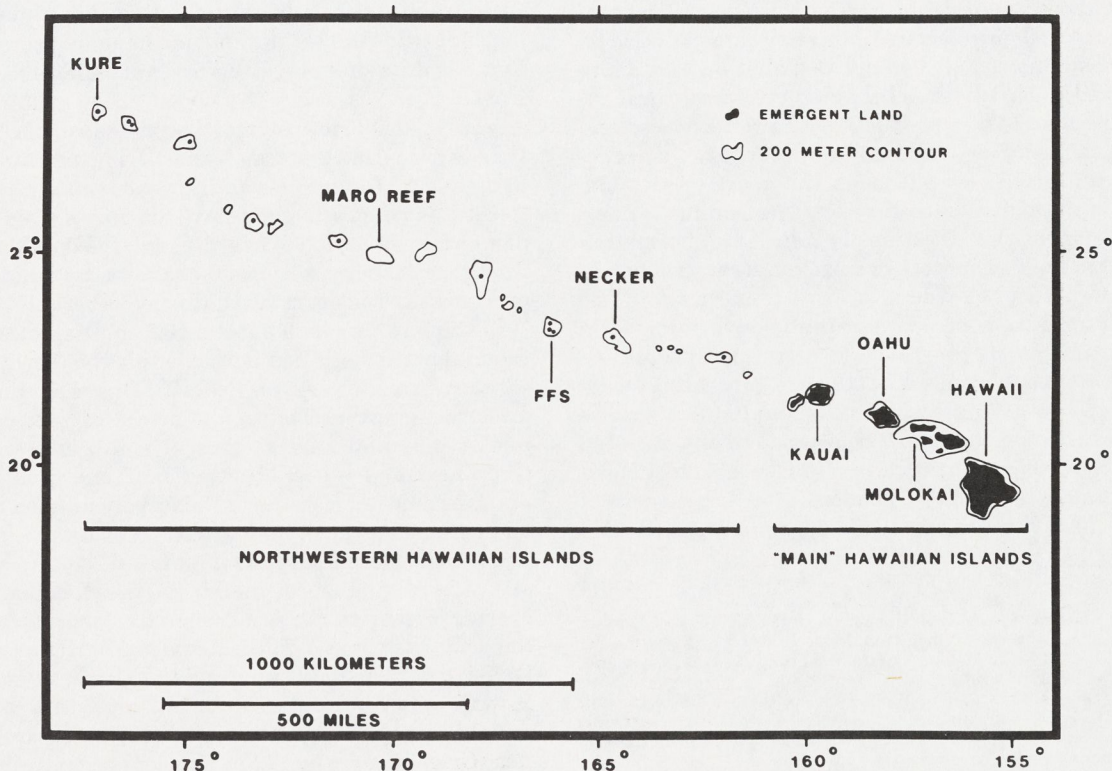
Two general questions regarding lobster sub-population structure were asked in the present study. First, was there any detectable stock heterogeneity within the entire Hawaiian Archipelago? Second, and specifically relating to the potential impact of the emerging fishery in the NWHI on the existing fishery in the main islands, was there evidence that populations in the main islands were differentiated, and thus independent, from populations in the NWHI?

The spiny lobster, *Panulirus marginatus*, is endemic to the Hawaiian Archipelago where it occurs in large numbers from Hawaii in the southeast to Kure Atoll in the northwest (Fig. 1). Highest apparent abundances are localized at Necker Island and Maro Reef (Uchida et al. 1980), the two localities where the lobster fishery is presently concentrated. *Panulirus marginatus* is generally found in waters deeper than 10 m. *Panulirus marginatus* has an annual fecundity of from 125,000 to 450,000 eggs per female (Honda 1980). After mating, females carry one or more sper-

matophores ventrally on the thorax until the eggs are extruded and fertilized. Embryonic development in this species takes about 30 d during which time the embryos remain attached to the pleopods of the female (Morris 1968). Based on studies of related species it appears that, after hatching, the larvae are planktonic for a period of 6-12 mo passing through 8-12 phyllosoma larval stages (Johnson 1956, 1968; Johnson and Knight 1966; Inoue 1978). The larvae metamorphose into puerulus postlarvae. The postlarvae settle from the plankton and assume the benthic lifestyle characteristic of the adults. Based on tag-recapture studies at Kure Atoll and French Frigate Shoals (MacDonald<sup>4</sup>) and similar studies at Oahu (Morris 1968), adults appear to be relatively sedentary, not exhibiting large-scale movements.

<sup>4</sup>C. MacDonald, Zoology Department, University of Hawaii, Honolulu, HI 96822, pers. commun. May 1982.

FIGURE 1.—Map of the Hawaiian Islands showing sampling localities. Note the 200 m depth contours.





## Mannosephosphate Isomerase in the Hawaiian Spiny Lobster *Panulirus marginatus*: a Polymorphic, Sex-Linked Locus Useful in Investigating Embryonic and Larval Sex Ratios

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### Abstract

Genetic variation at the mannosephosphate isomerase (MPI) locus was investigated in the Hawaiian spiny lobster *Panulirus marginatus*. Lobsters were collected over a 2½ yr period (October, 1978 to March, 1981) from numerous sites throughout the Hawaiian Archipelago. Electrophoretic analysis revealed that this species exhibits a 3-allele polymorphism for MPI and that the proportions of the two most common alleles are very different in the two sexes. All adult males express a "slow" MPI allele, but females generally lack it. If one assumes that sex determination in this species involves an X-Y-like chromosomal mechanism, one can hypothesize that the Y (male-determining) chromosome carries only the "slow" allele while the X chromosome is polymorphic for all three alleles. Using MPI phenotype as a criterion of sex, I examined over 2 000 embryos and found a sex ratio of 1.08 males:1 female which was significantly different from 1:1. Thus, the sex ratio in the embryos is skewed toward males. Among puerulus post-larvae and adults there was also an excess of males. The slight but significant bias of the sex ratio toward males throughout the life cycle of *P. marginatus* is not readily explained by existing theories (e.g. mate competition or structured demes).

### Introduction

Many higher invertebrates and nearly all vertebrates are dioecious. It is generally accepted that the ultimate basis for sex determination in such organisms is genetic, although sex differentiation is often directly influenced by levels of circulating hormones either early in embryonic development or later in life (Charniaux-Cotton, 1965;

Yamamoto, 1969; Mittwoch, 1973). In many situations, environmental variables and/or social factors may play an important, indirect role (Fishelson, 1970; Robertson, 1972; Fricke and Fricke, 1977; Shapiro, 1980; Conover and Kynard, 1981). Given that sex determination is usually an either-or phenomenon in dioecious organisms (functional hermaphrodites being extremely rare or unknown in most species), it is reasonable to assume that a relatively simple genetic switch mechanism effecting *either* female *or* male differentiation characterizes most species. Among many organisms, this genetic basis for sex determination is localized on the so-called sex-determining chromosomes. Such chromosomal mechanisms of sex determination are nearly universal in the higher vertebrates (tetrapods), and have been described for some species of fishes and several higher invertebrates including species of crustaceans and insects (Niiyama, 1959; White, 1973).

Despite the presence of such an apparently qualitative chromosomal switch mechanism, only a very small fraction of the known physiological and biochemical differences between females and males of a given species appear to be qualitative; moreover, such differences are almost always directly involved in reproductive processes or the gametes themselves (e.g. Goldberg, 1977; Cavener, 1980). Nevertheless, genetic studies of many species have revealed the existence of numerous sex-linked traits. In mammals, loci known to be on the X-chromosome include the genes encoding glucose-6-phosphate dehydrogenase, phosphoglycerate kinase, antihemophilic factors VIII and IX, the testicular feminization gene, and others (Ohno, 1979). However, sex-linked loci having one or more alleles restricted to one sex are almost unknown (Gordon and Ruddle, 1981).

The relative proportion of males to females in a population of a dioecious organism plays a significant role in the successful reproduction of the species and is, therefore, of considerable evolutionary importance. Fisher (1930) recognized this and proposed that organisms make an *equal investment* in the two sexes. This is generally

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interpreted as implying a 1:1 primary sex ratio. However, numerous reports (Hickey and Craig, 1966; Hamilton, 1967; Smith, 1975; Golovachev, 1978; Pristas and Trent, 1978; Smith and Stenseth, 1978; Haley, 1979; Muramatsu *et al.*, 1979; Snelson and Wetherington, 1980) indicate that, in many species, the sex ratio (primary or secondary) may deviate significantly from 1:1. Such observations, plus numerous theoretical considerations have led several authors to propose that sex ratios in many organisms need not be 1:1 (Hamilton, 1967; Werren, 1980; Wilson and Colwell, 1981; Colgan, 1982).

The present report describes the analysis of an electrophoretic polymorphism of the enzyme mannosephosphate isomerase (MPI) in the endemic Hawaiian spiny lobster *Panulirus marginatus*. The locus encoding this enzyme appears to be sex-linked, and adult males and females exhibit different MPI phenotypes. Because the enzyme is expressed in juvenile, larval, and late embryonic stages, this MPI polymorphism can be utilized to monitor the sex ratio in this species throughout the life cycle.

## Materials and Methods

*Panulirus marginatus* is a common inshore spiny lobster which is endemic to the Hawaiian Archipelago. The species is abundant and supports a commercial fishery, especially in the Northwestern Hawaiian Islands (Necker Island northwest through Kure Atoll). As adults, the two sexes are readily distinguished by external morphological characters. Females have a genital opening on the coxa of the third pereopod, an unmodified coxa on the fifth pereopod (which has a bidentate dactylus), and have biramous pleopods. Males, on the other hand, have the genital pore on the coxa of the fifth pereopod (which is distinctly spatulate), an unmodified dactylus on the fifth pereopod, and uniramous pleopods consisting of only an exopodite. Females mate with one or more males and carry a spermatophore(s) ventrally on the thorax until the eggs are extruded and fertilized externally. A single female may produce as many as 450 000 eggs per clutch (Honda, 1980). The fertilized eggs are attached to the pleopods of the female where the embryos develop for about 1 mo before they hatch and assume an independent, pelagic larval existence. As with other palinurid lobsters, there are approximately 8 to 12 phyllosoma larval stages, and pelagic life apparently lasts for 6 to 11 mo (Johnson, 1956, 1968; Johnson and Knight, 1966; Inoue, 1978). The larvae metamorphose into a puerulus post-larval stage, which settles and initiates the benthic life style characteristic of the adults.

Adult lobsters were collected from Kure Atoll, Maro Reef, Necker Island, and Oahu from October, 1978 to March, 1981. Lobsters were either taken by fishermen using commercial lobster pots made of wire mesh and baited with fish or by SCUBA divers using hand nets. After capture, the lobsters were either frozen in the field and transported frozen back to the laboratory or were

maintained alive in running seawater until brought to the laboratory. All lobsters were stored frozen at  $-20^{\circ}\text{C}$  in the laboratory until dissected and analyzed. The sex of each individual was determined (independently by two observers) by the visual inspection of external sexual characteristics as described above. A small sample of muscle from each lobster was dissected from one or more pereopods (walking legs). This sample was homogenized in a polycarbonate centrifuge tube using a motorized, stainless steel pestle in ice-cold buffer (0.1 M potassium phosphate, pH 7.0). The homogenate was centrifuged at  $5^{\circ}\text{C}$  for 20 to 40 min at  $30\,000\times g$ , and the resulting supernatant was transferred to a stoppered glass vial and stored frozen at  $-75^{\circ}\text{C}$  until it was analyzed.

Puerulus post-larvae were captured from Kure Atoll in larval collectors as described by MacDonald and Stimson (1980). The pueruli were frozen in the field, shipped frozen to the laboratory, and stored at  $-20^{\circ}\text{C}$  until dissected. Tissue samples from the pueruli consisted of all of the tissue from within the thoracic and abdominal portions of the post-larvae as well as all of the pereopods from one side of the individual. This sample was homogenized in a minimal amount of buffer as described above for adult tissues. After centrifugation, the resulting supernatants were stored frozen at  $-75^{\circ}\text{C}$  until analyzed.

Samples of embryos were obtained from captive, ovigerous females maintained in running seawater in the laboratory. Since preliminary experiments had revealed that MPI was not detectable in the developing embryos in the embryonic stages from fertilization until about 20 d thereafter, ovigerous females obtained from field collections were maintained in 50-liter aquaria until the embryos "turned brown", i.e., the eyes of the embryos were black and the body and appendages had orange pigmentation which occurred about 20 d after fertilization. At this time, large clumps of developing embryos were removed from the female's pleopods. Using a dissecting microscope and watchmakers' forceps, I removed individual embryos and placed each in a  $400\ \mu\text{l}$  plastic centrifuge tube. After addition of  $20\ \mu\text{l}$  of buffer, each embryo was hand-homogenized directly in the  $400\ \mu\text{l}$  tubes with a small glass pestle. The homogenates were then loaded directly onto polyacrylamide gels as described below and electrophoresed.

The enzyme mannosephosphate isomerase, MPI (EC 5.3.1.8), catalyzes the interconversion of mannose-6-phosphate and fructose-6-phosphate and, in so doing, plays an important role in carbohydrate metabolism. The enzyme is present in many tissues of a diversity of invertebrates and vertebrates including crustaceans, molluscs, tunicates, fish, amphibians and mammals (McMorris *et al.*, 1973; Nichols *et al.*, 1973; Shaklee *et al.*, 1974; Buroker *et al.*, 1979; Mulley and Latter, 1980; 1981a, b; Black and Johnson, 1981; R. P. Elinson, unpublished data; Shaklee, unpublished data).

Most of the adult and puerulus post-larval lobsters were analyzed by starch-gel electrophoresis. Depending upon the individual experiment, I used either Buchler-type