ECOLOGY AND PHYSIOLOGY OF THE CALIFORNIA CRAYFISH PACIFASTACUS LENIUSCUS (DANA) IN RELATION TO ITS SUITABILITY FOR INTRODUCTION INTO EUROPEAN WATERS

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There are presently eight recognized genera of crayfish in the United States and, of these, three genera comprising four species are known to California. Of the four Orconectes virilis (Hagen) is found in localized regions of north-central California and Procambarus clarki (Girard) is confined to southern California. They were probably both introduced from the eastern United States sometime in the early part of this century. The other two California species belong to the genus Pacificastacus (Bott) and they are the only native species now surviving in northern California. They are Pacificastacus nigrescens (Stimpson) (including gambeli after Miller 1960) and Pacificastacus leniusculus (Dana). The latter species is now being introduced into northern Europe to rejuvenate the crayfish industry which has been steadily declining as Astacus astacus populations are destroyed by a fungus plague. P. leniusculus (Dana), including trowbridi of Bott and klamathensis of Riegel (after Miller 1960) has prospered in many streams, lakes, and reservoirs in northern California, particularly at higher elevations. It has been intensively studied at Lake Tahoe, its tributaries, and surrounding lakes by Abrahamsson and Goldman (1970). Additional studies have focused on the metabolism of this species by a group from the University of California at Davis (Moshiri and Goldman 1969; Moshiri, Goldman, Godshalk and Mull 1970; Moshiri, Goldman, Mull, Godshalk and Coil 1971).

Of the four species occurring in California Procambarus clarki (Girard) is well known in Louisiana. In California it has been regarded mainly as a pest of the rice fields and irrigation ditches of the Central Valley rather than as a special food item. P. clarki is now farmed extensively in southern United States and is the basis of a small but growing industry. A small sport fishing bait industry in California utilizes this species since individuals are readily trapped at check dams in the rice fields. Orconectes virilis (Hagen) which has been introduced from the middle states seems to be thriving in similar habitats to those of P. clarki in northern California. It has not however, been as successful in southern California as P. clarki. Studies of a reservoir, Lake Hennessey, in the California coastal range near San Francisco indicate that Procambarus clarki is able to out-compete Pacificastacus leniusculus, as the crayfish population is shifting rapid-
ly to dominance by the former species.

*Pacifastacus nigresens* (Stimpson), blackish in color and reaching a length of only 7.6 cm, is endemic to a small area in Shasta County of northern California. It appears not to have been successful in maintaining its population as it is no longer found in its original type locality which was the vicinity of San Francisco (Riegel 1959).

*Pacifastacus leniusculus* (Dana) was apparently first shipped in 1912 from the Columbia River in Washington in large numbers to the Brookdale Hatchery of the California Fish and Game Commission in Santa Cruz County. The species has proved to be most successful in northern California. Its range on the western coast of the United States is from approximately $35^\circ30'\ N$ in California north to $45^\circ45'\ N$ in the state of Washington. How far into Canada it survives is not known to this author. Its success at high elevations (above 2000 m) attests to its adaptability to cold climates. Introductions of the Lake Tahoe crayfish to Sweden appear to be successful at least as far north as $62.5^\circ\ N$. It is apparent that the northern limit will probably be a function of water temperature suitable for egg hatching and this may vary considerably from lake to lake in northern latitudes.

**Commercial Harvest in California**

Since the early part of this century no commercial cray-fishery has existed in California. This was presumably due to a lack of market demand with only a few Californians showing interest in eating them. With the decline of *Astacus astacus* populations in Europe, an interest in commercially utilizing *P. leniusculus* developed. In 1970 the California Fish and Game Commission listed a harvest of 37,700 kg with a market value of $32,430. In 1971 the fishing season of March through October yielded a catch of 62,000 kg at a value of $51,370. Although fishing began again in March of 1972 it was abandoned in May because of a decline in market prices. Interestingly enough, none of the crayfish harvested was for the domestic market, and the entire catch was cooked and shipped frozen to Sweden. As nearly as we can determine, this recent commercial catch was taken from the Sacramento Delta area where *P. leniusculus* abounds.


Subalpine Habitat

Examination of Lake Tahoe, a particularly well suited habitat for *P. leniusculus*, is useful in describing which ecological parameters appear to be the most important. This information may prove helpful in selecting those European habitats which are most suitable for the introduction and cultivation of this species.

Lake Tahoe, situated on the California-Nevada border at an elevation of 1897 m, covering an area of 499 km² with a maximum depth of 501 m, is known for the remarkably high quality of its water. The water is very soft with pH ranging from 7.8 to 8.2. The water is sufficiently clear (secchi depth measurements run as high as 40 meters) to allow attached aquatic plants such as *Chara* to exist to over 100 m in depth. The extremely low fertility is reflected in Table 1; the lake’s productivity being limited primarily by nitrogen.

Table 1. Water chemistry in Lake Tahoe, California-Nevada, July 29, 1969 in parts per billion.

<table>
<thead>
<tr>
<th>Depth in m</th>
<th>N-NO₃</th>
<th>Total P</th>
<th>P-PO₄</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1</td>
<td>12</td>
<td>3.9</td>
</tr>
<tr>
<td>10</td>
<td>1</td>
<td>9</td>
<td>2.9</td>
</tr>
<tr>
<td>20</td>
<td>1</td>
<td>25</td>
<td>8.2</td>
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<td>21</td>
<td>6.9</td>
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<tr>
<td>50</td>
<td>1</td>
<td>8</td>
<td>2.6</td>
</tr>
<tr>
<td>105</td>
<td>1</td>
<td>22</td>
<td>7.2</td>
</tr>
</tbody>
</table>

The Tahoe Basin has steep sides, a flat bottom and a relatively narrow littoral zone. The lake does not freeze and is generally believed to be monomictic, although there is now evidence that it does not completely mix every year (Hacker and Goldman unpublished). Surface temperatures of Lake Tahoe may reach 22°C in a warm summer while winter temperatures between 4 and 5°C have been recorded. A Tahoe temperature distribution is indicated in Figure 1. The isotherms shown in this figure are for a cooler season than more recent annual temperatures.

The first introduction of *P. leniusculus* into Lake Tahoe probably took place in 1895 when 19 males and 37 females from the Klamath River were introduced into the Truckee River in the vicinity of Reno. In 1909 more crayfish were introduced "with the object of providing food for the introduced varieties of fish as well as a table delicacy for our citizens..." (La Rivers 1962). Three hundred and sixty crayfish, probably from coast streams in Oregon, were placed in the Truckee River, the Carson River,
and Washoe Lake. A third introduction into the water systems of Lake Tahoe was made in 1916. Density studies conducted in 1969 around the entire littoral zone of Tahoe gave a population estimate of 55.5 million adults weighing 1,100,000 kg. The zone of crayfish habitat is indicated in Figure 2.

Distribution

Distribution of the population within the lake is highly variable and is dependent upon the degree of local eutrophication and the nature of the substrate. A more eutrophic area of the lake at Tahoe City yielded over twice as many crayfish per trap as less productive areas. This is indicated by synoptic measures of primary productivity (Figure 3).

The maximum population density (Figure 4) in relation to depth was found to be between 10 and 20 meters. At depths below 20 m low water temperatures are a limiting factor for fecundity. At depths above 10 m high light...
intensity due to the extreme clarity of the water as well as wave action during storms are most likely limiting. Storms may occasionally displace crayfish from the shallow water by wave action and great numbers have been observed washed up on Tahoe beaches.

A number of coastal and mountain streams and lakes also provide good *P. leniusculus* habitat. There is some indication that the coastal *P. leniusculus* residents are more heat tolerant than their mountain relatives and it may prove wise to begin genetic selection for populations that show adaptation to particular types of environments. In California they now live in a rather diverse habitat ranging from the turbid waters of reservoirs, the Sacramento and San Joaquin Rivers to the clear shallow coastal streams which warm appreciably during summer.
Fig. 3. Average primary productivity of the upper 15 meters of Lake Tahoe based on three synoptic studies made in July, August and September of 1968 (Goldman, Moshiri and de Amezaga 1972).

The littoral zone of Lake Tahoe is comprised largely of sand, gravel and rocks with microphytes growing to considerable density on the abundant stone surfaces. During the last decade there has been a steady increase in growth of periphyton which is composed largely of the stalk diatom Gomphonema constrictum v. capitatum and the fungus Apostemidium guernisal (Abrahamsson and Goldman 1970). Rock substrata appear to be preferred by P. leniusculus with heaviest populations supported by medium-sized rocks since they provide more crevices for the crayfish to occupy than gravel or large boulders. Adequate cover is essential for high crayfish density since they are helpless in their soft-shelled condition
Fig. 4. Demonstration of the effect of the bottom substrate on the density and structure of the male crayfish population in an experimental area with a stony bottom off the Coast Guard Station from June 1967 through January 1968, compared to that of Crystal Bay (silt covered bottom) from June 1967 through October 1967. The diagram is based on 2,404 and 353 crayfish males respectively (Abrahamsson and Goldman 1970).

immediately after molting. In Donner Lake crayfish have been observed with SCUBA to occupy small holes dug in a clay shelf at about 10 meters.

Areas where there is an abundance of medium-sized rocks tend to provide the necessary cover for a high density of small individuals whereas the areas of sandy open bottom support fewer, but larger individuals. To escape fish predation on a relatively open bottom, large size is important whereas an abundance of cover will protect a larger population of smaller younger individuals. It is likely that large individuals may regularly migrate from the crowded shallower habitat to the more open and deeper waters which are the less populated areas of the lake. This is clearly evidenced by the size distribution with depth shown in Figure 4.
Physiological Response

Species of crayfish show a wide tolerance for oxygen concentrations in water and their physiological responses vary considerably. Some species of the southern United States are able to withstand periodic droughts by burrowing. Studies by Wiens and Armitage (1961) showed that a decrease in oxygen concentration caused a corresponding decrease in oxygen consumption for Orconectes immunis and Orconectes nais. Larimer and Gold (1961) have shown Procambarus simulans to respond to low oxygen concentrations by increasing its ventilation volume and respiratory rate. Studies by Moshiri et al. (1970) on Pacifastacus leniusculus, in contrast, indicate that this species responds to low oxygen tensions by increasing oxygen utilization efficiency under the influence of a decreased ventilatory rate. This corresponds to a decrease in the organism’s metabolism. The authors concluded that P. leniusculus has an extremely low tolerance for decreased oxygen levels, making this species best suited to lakes and streams with high oxygen concentrations and little diurnal fluctuation. Lakes ranging from extreme oligotrophy to mesotrophy appear to provide the best P. leniusculus habitat.

In Lake Tahoe and surrounding high mountain lakes where oxygen levels are high, temperature and food supply are probably the factors limiting crayfish production. Respiratory activity as measured by oxygen uptake, and utilization was shown to be lowest at 0°C and highest at 15°C (Figure 5). Temperatures above this resulted in a decrease in respiratory activity (Moshiri et al. 1970). Abrahamsson and Goldman (1970) also observed that the highest feeding activity occurred during the summer months when water temperatures reach their maximum in Tahoe. These data suggest that the cold deep water of Tahoe may limit the breeding population to depths above about 40 m. Below this depth, as was demonstrated in laboratory experiments, the cold water inhibits hatching of eggs.

Light penetration, which in the extremely clear water of Lake Tahoe is high, was thought to restrict the breeding population to the area below the 10 m depth contour. However, the problem of high light intensity will probably be important in only a few very clear lakes with extensive areas of shallow water.

Photoperiod is most likely to be of considerable importance to the establishment of P. leniusculus’ breeding regime. There is good evidence that molting and the reproductive cycle of Cambarus is regulated by the length of the photoperiod (Stephens 1952, 1955).
Pollution and Crayfish Production

Although a degree of eutrophication has occurred in Lake Tahoe near centers of high human habitation, which has increased the crayfish population, eutrophication to the point of oxygen depletion will certainly be disastrous for *P. leniusculus* populations. Lake Tahoe, despite the fact that it shows significantly richer waters in some areas from fertilization by sewage and land run-off is still sufficiently sterile that it does not show measurable oxygen depletion. Crayfish harvest from a lake such as Tahoe could serve to remove significant amounts of nitrogen and phosphorus. This might be exploited as a means of "de-eutrophicating" natural waters which have be-
come or are in the process of becoming excessively fertile.

It would be interesting to attempt to increase the productivity of _P. leniusculus_ in artificial ponds by fertilizing with the organic waste products of certain industrial food-processing plants. If this proved successful, it could provide an important means of converting our many organic wastes to usable protein throughout the world. Moshiri and Goldman (1969) determined assimilation values for plant and animal food fed to _P. leniusculus_. Assimilation rates of plant food were slightly lower than the corresponding values obtained when animal food was ingested. Considerable work remains to be done on the nutritional requirements of crayfish if they are to be cultivated in an optimal manner and if they are to be utilized in recycling some of the world's organic wastes.

The warm water resulting from the cooling of nuclear plants (thermal pollution) might also be turned to good use in the cultivation of crayfish. Experiments at Lake Tahoe indicate that water temperatures above 6.8°C are necessary for hatching the eggs of _P. leniusculus_. If this warm water were available for aquiculture at the more northern latitudes, it could be used as a thermal enhancement for early hatching or for the production of young in areas beyond the thermal restrictions which set the northern limits for natural reproduction.

Careless selection and use of pesticides is just as serious a threat to the cultivation of crayfish as it is to other aquiculture. Tests made of ten insecticides on the "rice field" or "red" crayfish, _Procambarus clarki_, by Muncy and Oliver (1963) showed that all were lethal in the normal concentrations routinely applied to control the forest tent caterpillar. Methyl parathion which has replaced DDT for many purposes was found to remain toxic in the water for over a month. It is hoped that a move towards biological control of insects and less persistent pesticides will reduce this hazard to crayfish culture.

Pollution from the atmosphere could also prove to be a serious problem for crayfish culture. In addition to wind-borne contaminants such as pesticides, there is an increasing sulfuric acid content of rain. This is largely a byproduct of the burning of coal and oil whereby sulfur dioxide and hydrogen sulfide in the presence of atmospheric water react to produce sulfuric acid (H₂SO₄). Oden and Ahl (1970) have indicated that acidity in rain has increased more than 200-fold since 1956 in some areas of Scandinavia. It is estimated that the activities of man now account for 43% of the atmospheric circulation of sulfur. Rising levels of sulfur in the air and in rain waters are already causing increasing acidity in lake waters (T.I.E. 1971). Sulfate in surface waters of Lindsley Pond, Connecticut, increased from 0.25 mg/litre in 1937 to 7.0 mg/litre in 1963. Some Canadian Shield lakes
in northern Europe have become too low in pH to support fish from the acid fallout of our industrialized society. The subject has recently been reviewed by Likens, Bormann, and Johnson (1972). Particular attention must be paid to selecting waters for crayfish culture with sufficient buffering capacity to maintain adequate pH in the face of the increasing acidity of rain. Small lakes which may already be too acid for crayfish production would probably respond to treatment with lime.

Ultimately all poisons find their way into rivers, lakes and oceans. The rising production and heavy use of mercury in the world is cause for concern by those interested in aquiculture as well as human welfare. Mining, a variety of industrial uses, fungicides in agriculture and pulp production are well known sources of environmental contamination with mercury. This is a highly lethal poison to animals, including man, particularly in its organic methylated forms. Although mercury is very expensive and secondary recovery is possible, in 1968 only 46% of the mercury used in the United States was recovered (S. C. E. P. 1970). The environmental contamination with the lost mercury has been real cause for alarm and severe mercury contamination in the waters of Japan, Sweden and the United States have been reported. Very serious loss of human life occurred recently in Iraq from mercury-coated seed grain which was eaten rather than planted.

The prospective crayfish culturist is well-advised to consider all sources of heavy metal, acid, and pesticide contamination when selecting a habitat.

Research Needs

The importance of continued research on the ecology and physiology of *P. leniusculus* cannot be over-emphasized. For example, one of the weakest links in crayfish life cycles is their frequency of molting and their susceptibility to cannibalism during the time their soft exoskeleton is hardening. Work on marine crustacean molt cycles is fairly advanced (see, for example, Sather 1966) and some of this work may be applied to crayfish research. By synchronizing crayfish molting the loss to cannibalism could be reduced. This should be possible by proper sorting for more uniform size of individuals as well as food, photoperiod and temperature control. Time of molting might also be controlled by the use of hormones.

As already noted the nutritional requirements of the various species of crayfish have received little study. They are omnivorous and will consume a variety of organic wastes. The balance of carbohydrates to protein in
crayfish diet may be of considerable importance to their growth rate and fecundity and should be the subject of carefully controlled experiments if production is to be optimized. Their ability to "clean" the littoral zone of excessively productive lakes while accumulating nutrients in growth is also of considerable ecological interest and perhaps of practical importance.

The question of acidity raised in the "Pollution and Crayfish Production" section of this report lends itself nicely to laboratory experimentation which could be coupled with studies of the basic fertility of the waters involved (Goldman 1965). As protein production becomes increasingly important, it will be essential to improve the efficiency of food conversion at all levels of the aquatic food chain. _P. leniusculus_ is an excellent experimental animal to begin the important work of recycling a part of the world's organic wastes. The First International Crayfish Symposium has been a first and important step in this direction.

**Abstract**

The ecology and physiology of the California crayfish _P. leniusculus_ is discussed in view of its potential for introduction into European waters and for aquiculture. Studies of _P. leniusculus_ at Lake Tahoe indicate that its distribution and density are highly dependent upon temperature, oxygen, and the degree of eutrophication (oligotrophic to mesotrophic waters are preferred), and type of substrata (medium-sized rocks support highest densities). Physiological studies suggest that the preference for oligo- to mesotrophic waters can be attributed to their low tolerance for decreased levels of oxygen. _P. leniusculus_ is an excellent experimental species primarily because of its high fecundity and potential as a valuable food source. This would have added benefits by providing means of converting organic wastes, such as those produced in food processing plants, to protein suitable for human consumption. Further research is needed on influence of increasing environmental contamination (e.g. mercury, pesticides, acidity of rain, fungicides) on populations of _P. leniusculus_. More information is also needed concerning specific nutritional and environmental requirements, as well as physiological and behavioral changes during various stages in their life cycle. This is particularly true of molting (ecdysis), where mortality can be very high.
Zusammenfassung


Bibliography


