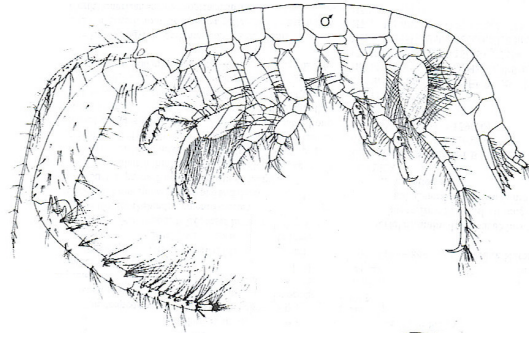


The Life History Demographics of *Corophium spinicorne* in the Carmel River Lagoon



A Capstone Project

Presented to the Faculty of Science and Environmental Policy

in the

College of Science, Media Arts, and Technology

at

California State University, Monterey Bay

in Partial Fulfillment of the Requirements for the Degree of

Bachelor of Science

By

Jessica Watson

December 11, 2007

ABSTRACT

Corophium spinicorne is the primary food source for resident juvenile steelhead trout (*Oncorhynchus mykiss*) in the Carmel Lagoon (Fields, 1984). This being the case, there is still little known about their life history dynamics. The life history dynamics of the amphipod *C. spinicorne* were analyzed from sixty samples collected from the Odello arm of the Carmel lagoon on a weekly basis from June – September 2007. *C. spinicorne* were measured and separated into three sectors; juveniles, males, and females. *C. spinicorne* portrayed no change in length or population abundance over the course of the study among the entire population or within sectors. The female sector contained two sub classes of females: those in a reproductive state and those females that were not. Fecundity or the proportion of those in a reproductive state correlated with the lunar cycle, suggesting that there may be a lunar influence. A post hoc exploratory analysis showed that there was a positive association between abundance of *C. spinicorne* and sandy bottom dominated habitats. A secondary water quality analysis found species abundance to be independent of water quality. Overall results suggest that *C. spinicorne* have a synchronous reproduction with a period much shorter than their longevity and apparently strong habitat associations. These results relate to previous results by Larson et al. (2004–6) and Perry et al. (2007) that had extreme variations in abundances throughout their studies which motivated this study. The current study suggests that these variations might in fact be due to subtle habitat variations and consequently may be more important than short-term life-cycle dynamics. These habitat variations essentially amounted to a confounding influence on our study that was designed to examine population dynamics independently of habitat variation, despite attempts to control for habitat variation by sampling a relatively homogeneous study area with four-times random spatial replication.

Acknowledgements

I would like to thank the following people for all their help and support during the course of this capstone thesis:

- Fred Watson, Advisor
 - Suzanne Worcester, Second Reader
 - Peter Martin
 - Brad Travers
 - William Perry
 - Nicholas Sherman
 - Bernice, Terry, and Josh Watson
-

Table of Contents

ABSTRACT	ii
Acknowledgements.....	iii
Table of Contents	iv
1 Introduction	6
1.1 Objectives	8
2 Methods.....	10
2.1 Overall Methodology	10
2.1.1 Statistical Analysis.....	10
2.1.2 Sampling Location.....	11
2.1.3 Field Methods	12
2.1.4 Lab Methods	14
2.1.5 AIC Analysis	15
3 Population Dynamics Results	17
3.1 Change in Population Length	17
3.2 Change in Length, by Sector of the Population.....	18
3.2.1 Change in Length, by Female Sector.....	18
3.2.2 Change in Length, by Male Sector	19
3.2.3 Change in Length, by Juvenile Sector.....	20
3.3 Change in Population Abundance	21
3.3.1 Juvenile Sector Population Abundance.....	22
3.3.2 Male Sector Population Abundance.....	23
3.3.3 Female Sector Population Abundance.....	24
3.4 Fecundity	25
4 Water Quality Analysis	27
4.1 Water Quality Results	27
5 Habitat Analysis	30
5.1 Habitat Results.....	30
6 Discussion	32
7 Conclusions	37
8 Literature Cited	38
Appendix A – <i>Specimen Identification</i>.....	42
Appendix B –<i>Abundance Calculations</i>.....	44
Appendix C –<i>Depth Gradient Figures</i>.....	45

1 Introduction

Lagoons are considered one of the most valuable components of coastal areas in terms of both the ecosystem and natural capital they support (Gonenc, 2005). Key aspects of lagoons are the highly sensitive areas that they encompass known as wetlands (Gonenc, 2005). According to the Environmental Protection Agency (EPA) half of the world's wetlands have been degraded, polluted, or completely lost (EPA 2006). This is an alarming estimate since wetlands comprise only 6 per cent of the world's surface (Williams, 1990).

To understand the basis of these diverse and drastically disappearing systems one must first understand the definition of a coastal lagoon and how it is characterized. Coastal lagoons are defined simply as shallow aquatic ecosystems that develop at the interface between coastal, terrestrial, and marine ecosystems (Gonenc, 2005). Lagoons have several physical and hydrological functions including, flood mitigation, coastal protection, recharging aquifers, sediment trapping, and global biogeochemical fluctuations (Williams, 1990).

Today many lagoons are deteriorating due to overuse of fisheries, agriculture, tourism, urbanization, industrialism, and aquaculture (Gonenc, 2005). The overuse of lagoon resources is uncontrolled which contributes to their degradation and loss through resulting hydraulic alterations, pollution, disturbance, and introduction of non-native species (EPA 2006).

The Carmel River Lagoon lies at the end of the Carmel River watershed and is separated from the ocean by a sand bar during the dry season (Casagrande, 2006). The lagoon size modestly fluctuates during the summer and fall months when the sandbar is closed. The lagoon then increases in size during winter and spring when the sandbar opens back up (Perry et al, 2007). It is during these months that the Carmel River is able to flow into the ocean (Perry et al. 2007). During the summer of 2004, the California Department of Parks and Recreation (CDPR) implemented the construction phase of the Carmel River Lagoon Enhancement Project (CRLEP) (CDPR, 2003). This project expanded the preexisting lagoon area by excavating a new channel on former Odello farmland in order to create more habitats for two Federally Threatened species: steelhead trout and California red-legged frog (Larson et al, 2005).

The Carmel River Lagoon is a sensitive area that plays an important role among the coastal zone ecosystems by providing suitable breeding areas to threatened steelhead trout (Perry et al, 2007). Central-California Coast Steelhead (*Oncorhynchus mykiss*) were listed as a threatened species on August 18, 1997 (NMFS, 2006) and have

an anadromous life cycle (Lufkin et al, 1991). This anadromous life style is categorized by having two different life stages in which they migrate in between fresh and salt waters. Steelhead are born in fresh water streams like the Carmel Lagoon, where they spend the first few years of their life (Lufkin et al, 1991). They then emigrate to the ocean where most of their growing occurs before returning to back to fresh water streams to spawn (Lufkin et al, 1991). An important aspect of this life cycle is the intermittent transitional juvenile stage in which they are in between the two. It is during this intermittent stage that the Carmel Lagoon is utilized by two discrete groups of juvenile steelhead known as smolts and summer residents (Dettman, 1984).

Steelhead trout are an important California fishery resource that has been declining on the central coast due to the degradation of local steelhead habitat (Lufkin et al, 1991). As one of the four largest watersheds on the central coast, the Carmel River has experienced declines in run sizes of ninety percent or more (NMFS, 2006). Extensive loss of steelhead populations is due to urbanization, agriculture, and water modifications of these costal estuaries (NMFS, 2006). Artificial breaching of sand-bars which is a common practice in the Carmel Lagoon has a direct effect on steelhead rearing and acclimation habitat (NMFS, 2006). These unnatural breaches sometimes impede as well as block steelhead from completing their migration in and out of the lagoon as noted by Perry (2007). Through the altering of streams and water channels adult steelhead have also been obstructed from reaching spawning grounds adding to the decline of the species.

The importance of macrobenthic and epibenthic invertebrates as food for commercial fish and invertebrate species is well documented (Covich, 1999). In August Fields (1984) found that there was ample food for juvenile steelhead residents in the Carmel Lagoon by sampling benthic macroinvertebrates and the contents of resident steelhead trout's stomachs. Overall it was found that seven species were being eaten by steelhead, six of which were benthic in origin (Fields, 1984). One of the species found in the steelhead stomachs that was considered an important food item, was the amphipod *Corophium spinicorne* (Fields, 1984). This study revealed population densities of *C. spinicorne* to be the most numerous food eaten by steelhead, exceeding 29,000 individuals per square meter (Dettman, 1984). As it was, out of 279 food items eaten 249 were *C. spinicorne* making it account for 82.5% of all that eaten (Fields, 1984). Therefore, it can be inferred that during these summer months *C. spinicorne* is a primary food source of resident steelhead trout and a contributor to their overall success.

Life history patterns, reproductive biology, and population dynamics have only been studied in a few *Corophium* species (Kevrekidis, 2005). The species focused on in these studies include *Corophium insidiosum*, *Corophium multisetosum*, and *Corophium*

orientale. However, there have been no studies conducted on the life history of *C. spinicorne*.

Larson (2004–2006) and Perry (2007) conducted multi-year abundance studies on *C. spinicorne* in the Carmel Lagoon. These studies spanned from 2004 to 2007 and looked at the abundances of macroinvertebrates in an established lagoon as well as a restoration area that was added. This study found that *C. spinicorne* abundance appeared to generally increase from 2004 to 2007, but also exhibit marked variation at shorter time scales. Even though these studies did not look at all the possible life history dynamics they still give an overall picture on how abundances change over time in established and newly colonized lagoons. Studies such as these provide a frame work to establish more specialized life history dynamic studies.

Due to the minimal amount of peer reviewed literature on *C. spinicorne* life history dynamics, questions arise regarding life span, fecundity, abundance, and physical growth rates. These are basic questions that are needed in order to understand population dynamics. It is vital when studying a species to have baseline data on spatial and temporal population dynamics in a given system. Once the basic population dynamics such as these are established for *C. spinicorne* biotic and abiotic factors that influence population dynamics can be studied.

There are several approaches when conducting studies on population dynamics. Experiments conducted in both the field and the lab can tease out some important life history patterns such as life span, abundance, recruitment, and fecundity. In the literature concerning population dynamics of *Corophium sp.*, data were usually collected during a one year field study period. This study period length allows enough time to pass to observe seasonal trends. However, another influencing factor is the frequency of how often samples are collected whether it be days, weeks, or months. These small temporal scale studies look at the fluctuations in populations that lead to the larger scale patterns providing useful information.

1.1 Objectives

The objective of this study was to describe the life history dynamics over a four month period in terms of the simplest and best models fit to data by using a model comparison approach. Although there is a great deal of questions that could be addressed in this study I asked these specific questions:

- ❖ Did the mean length of *C. spinicorne* in Carmel Lagoon change over the 4-month sampling period? This question was addressed at the population level, and also separately for males, females, and juveniles.
-

- ❖ Did the mean abundance of *C. spinicorne* in Carmel Lagoon change over the 4-month sampling period? This question was addressed both at the population level, and also separately for males, females, and juveniles.

- ❖ What was the mean amount of fecundity within the population of *C. spinicorne* over a 4-month sampling period?

It is helpful to consider the possible answers to the above questions, and how they would be interpreted. Firstly, if abundance was found to increase over time, then this would indicate that the overall population was growing during the study. Alternatively, there are multiple factors that could cause abundance to decrease over time. Due to the multiple possibility of explanations for the dynamics that might be observed a model comparison approach is needed.

2 Methods

2.1 Overall Methodology

Population dynamics were examined by random sampling invertebrates from the Carmel Lagoon weekly with replication. From these samples the following was quantified: abundance, length, sex, and reproductive state of each individual *C. spinicorne*. Hypotheses were then compared in order to describe the dynamics of these variables over time.

2.1.1 Statistical Analysis

The following terminology is used to describe the dynamics of *C. spinicorne* abundance and individual size:

- L_t : Mean length (mm) of individuals at time, t .
- $g_t = dL_t/dt = (L_{t+\Delta t/2} - L_{t-\Delta t/2}) / \Delta t$: The mean rate of change in length over time (mm).
- $\Delta t = t_i - t_{i-1}$: Two consecutive sampling dates.
- P_t : Mean population abundance (/m²) at time, t .
- $P_{j,t}$: The population density of juveniles at time, t .
- $P_{F,t}$: The population density of females at time, t .
- $P_{M,t}$: The population density of males at time, t .
- $dP_t/dt = (dP_{t+\Delta t/2} - dP_{t-\Delta t/2}) / \Delta t$: The mean population growth rate.
- r = Intrinsic growth rate parameter.
- K = Carrying capacity parameter.
- $(K-P)/K$: A density dependent control on growth rate.
- t = Time in days where zero is the starting date of the study (in this study June 15, 2007).
- θ = A phase date parameter for a periodic population.
- $f_t = P_{Fet} / P_{F,t}$: The population fecundity at time, t .
- $P_{Fet} / P_{F,t}$: The population of females observed in reproductive state at time, t divided by the number of females in the overall population at time, t .
- w : A parameter representing the period of an oscillation.

Hypotheses were compared using a model comparison approach in order to find the best fit model of *C. spinicorne* life history dynamics (Burnham and Anderson, 2002).

2.1.1.1 Hypotheses Relating to the Change in Mean Length.

$$H_{L,1}: g = 0$$

$$H_{L,2}: g = k$$

$$H_{L,3}: g = k * L_t$$

2.1.1.2 Hypotheses Relating to the Change in Mean Abundance.

$$H_{P,1}: dP/dt = 0$$

$$H_{P,2}: dP/dt = r$$

$$H_{P,3}: dP/dt = r * P_t$$

$$H_{P,4}: dP/dt = r * P_t * (K-P)/K$$

$$H_{J,0}: P_{J,t} = 0$$

$$H_{J,1}: P_{J,t} = k$$

$$H_{J,2}: P_{J,t} = k * f_{t-\tau}$$

$$H_{M,0}: P_{M,t} = 0$$

$$H_{M,1}: P_{M,t} = k$$

$$H_{M,2}: P_{M,t} = k * P_{M,t}$$

$$H_{M,3}: P_{M,t} = k * P_{M,t}(1-P)/K$$

$$H_{F,0}: P_{F,t} = 0$$

$$H_{F,1}: P_{F,t} = k$$

$$H_{F,2}: P_{F,t} = k * P_{F,t}$$

$$H_{F,3}: P_{F,t} = k * P_{F,t}(1-P)/K$$

2.1.1.3 Hypotheses Relating to the Fecundity.

$$H_{B,0}: f_{t-\tau} = 0$$

$$H_{B,1}: f_{t-\tau} = k$$

$$H_{B,2}: f_{t-\tau} = k * t$$

$$H_{B,3}: f_{t-\tau} = k * \sin(t - \theta)/w$$

At the outset, it was noted that it might not be possible to address all of the above hypotheses with available resources. However, they were all listed during the proposal phase, so that their *a priori* status could be recorded.

2.1.2 Sampling Location

The Carmel River Lagoon and marsh, located south of Carmel, California, encompasses the Carmel River State Beach and includes about 15 acres of aquatic habitat and another 33 acres of marshland (Dettman, 1984). The site location at which samples were taken consisted of one homogeneous 60 meter section of the Odello arm (O1) (Figure 1).



Figure 1: The chosen sampling site at O1 in the Odello Arm of the Carmel River Lagoon (modified from Larson et al., 2005).

2.1.3 Field Methods

On the sixty meter sample area flags were numbered and set at one meter intervals from each other (Figure 2). Once a week, for 15 weeks (June to September), four samples were taken without replacement; at locations in the lagoon directly adjacent to four randomly chosen flags on the shore (Figure 2). For each invertebrate sampling date water quality data such as temperature, salinity, dissolved oxygen, and PH were measured with an YSI Environmental 556 MPS Multiprobe System at .25m depth intervals.

The sampling method used is a replicate of that used in Larson et al.(2004–6) and Perry et al. (2007). To sample *C. spinicorne* which is an benthic macroinvertebrate a D-net (mesh size 500 μm) on a 1.5 m pole was extended away from the sampler's body perpendicular to the shore. Samples were taken by wading a short distance into the

water as far as depth would allow (approx. 0.5 NGVD). The pole and net were lightly and quickly dragged against the lagoon floor once. Figure 3 illustrates this sampling method and the equation that was used to determine the area of water that was sampled. The area of water per sample is calculated to be 0.486 m² (Larson et al., 2005) (Appendix A). When possible the contents of the grab were immediately washed in a 0.5mm sieve and if not possible the contents of the net were emptied into a 250 mL glass jar. The jar was then marked with the date, time and flag number from which it was collected.



Figure 2: Study Site Layout (photo courtesy William Perry 2007).

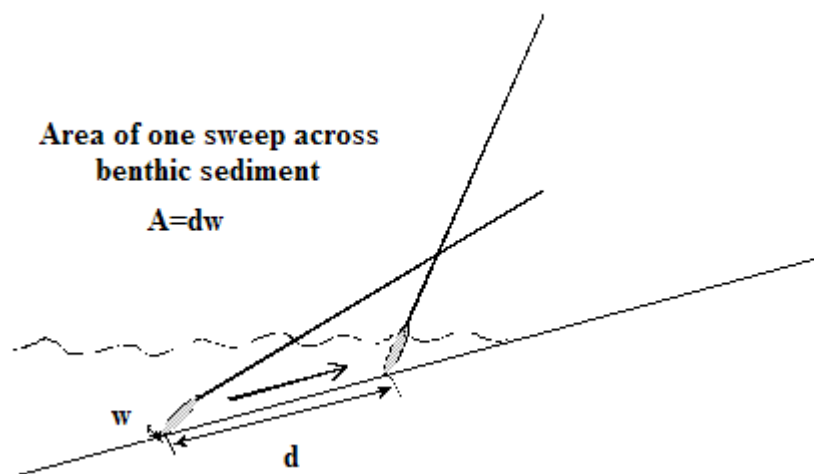


Figure 3: Epibenthic surface area calculation (adapted from Larson et al. 2005)

2.1.4 Lab Methods

In lab each sample was preserved in glass sample jars using 90% Ethanol. To separate the *C. spinicorne* from other present macroinvertebrate and the entrained sediment, the sample was mixed in a 2 gallon bucket filled approximately a quarter full with water. It was then swirled vigorously and immediately decanted into a series of five sieves ranging in size from #10 to #35 (100mm–.50mm). This was performed 3–4 times to remove all unwanted invertebrates and suspended debris from the sediment. The sediment was carefully inspected for *C. spinicorne* before being returned to the sample jar. Next each sieve was sorted using a combination of manual removal and decanting in a 30 cm by 22cm grid sorting tray.

Using the methods of Kevrekidis (2005) the sorted *C. spinicorne* were then classified in to sectors of juveniles, females, and males. This sorting was conducted by using a microscope to look for key characteristics of the species morphology that was referenced from Bousfield (1997) (Fig 3&4). A variation in this approach was taken with regards to morphological categorization (see Appendix B). Females were separated into 2 groups; 1) females without embryos 2) mature females with embryos. The number of embryos were noted but not used in this study. Sexual dimorphism is only evident in adult animals therefore specimens equal to or below a body length of 2mm were difficult to separate the sexes and thus classified as immature juveniles. Sorted sectors and sub sectors were then stored in smaller BMI vials and preserved with 30/70, glycerin and ethanol solution. The number of individuals in each sample, date collected, location collection, sorting date, and identification date were then recorded in a Microsoft Access database.

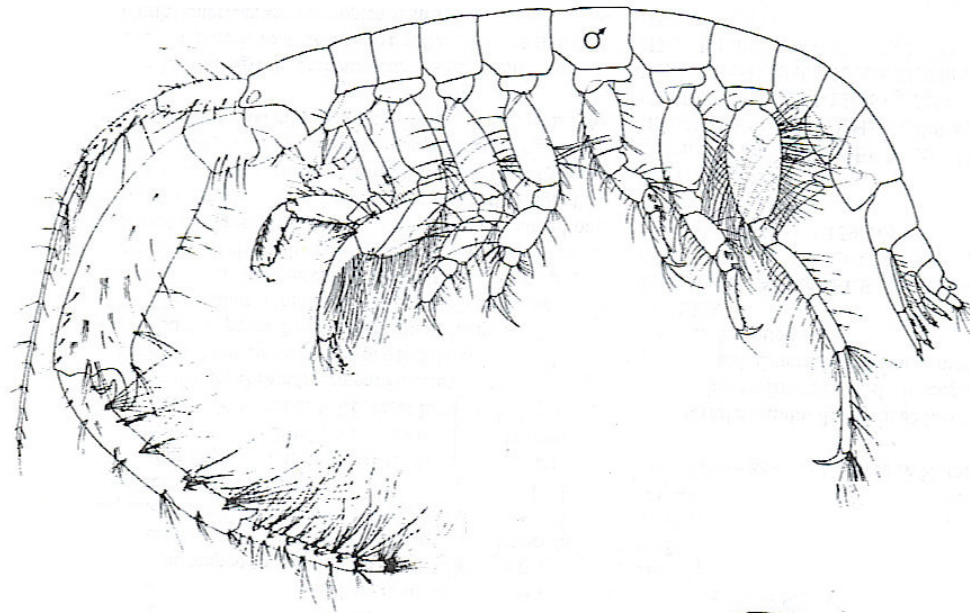


Figure 4: Overall *C. spinicorne* body morphology of a male specimen (drawing taken from Bousfield, 1997).

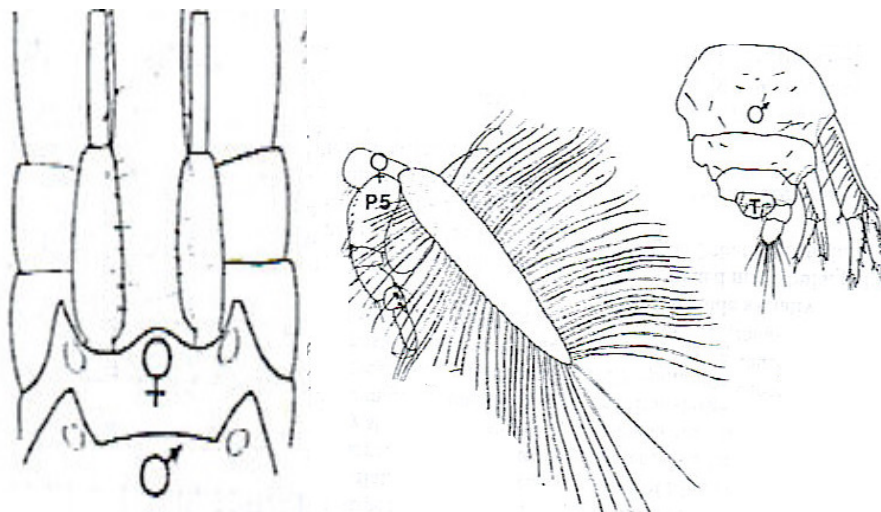


Figure 5: The head plate morphologies and underside appendages which were the main identifying characteristics used to separate females from males (drawing taken from Bousfield, 1997).

2.1.5 AIC Analysis

For each response variable, the stated *a priori* hypotheses were compared using AIC (Akaike, 1974, Anderson and Burnham, 1994). Thus, the best model of those compared

was chosen as that under which the sampling data were most likely, after penalizing models by their number of parameters. This allowed otherwise unknown life history patterns such as change in population length, change in population abundance, change in sector population abundance, and fecundity to be better understood in the Carmel Lagoon during the summer months. Likelihood of the data is measured under each hypothesized model, and penalized by the number of parameters used in the model in order to find the AIC value.

$$AIC = N \cdot \ln(WSS) + 2 \cdot M$$

- N: The number of data points, excluding any data with zero weight.
- M: The number of adjustable parameters.
- WSS: The weighted sum of squared residuals.

Therefore the lowest AIC value on the number line from plus to minus infinity is then considered the best model of those compared (Akaike, 1974). AIC weights (AICw) were computed, and used as measures of relative support for each hypothesis compared to the others. The sum of all AICw for a given response variable is by definition, 1 (Akaike, 1974).

3 Population Dynamics Results

The primary population dynamics analysis was conducted in order to answer the objective questions outlined in section 1.1.

3.1 Change in Population Length

As stated in section 2.1 the *a priori* hypothesized models for describing the change in the populations mean length over the given study period were:

$$H_{L,1}: g = 0$$

$$H_{L,2}: g = k$$

$$H_{L,3}: g = k * L_t$$

The best supported model was $H_{P,1}$ ($AICw = 0.75$). Subsequently $H_{P,2}$ was the next best supported model ($AICw = 0.20$)(Fig 13). Therefore, I inferred that the change in mean length within the population over time is more likely to be zero. Thus there was no strong evidence for change in length during the study.

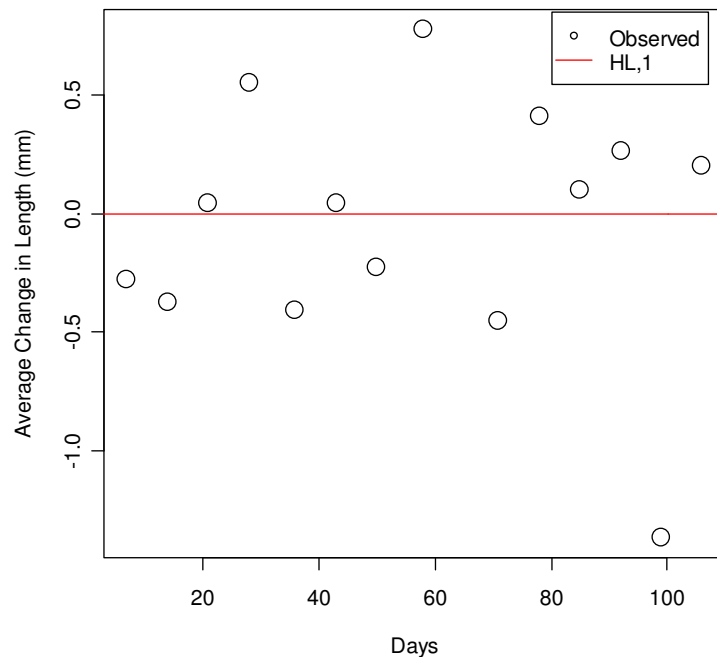


Figure 6: Models for the Populations Average Change in Length

3.2 Change in Length, by Sector of the Population

After conducting the previous analysis an exploratory post hoc investigation was preformed among the three different sectors within the population: females, males, and juveniles. The reason behind this analysis was to see if there was any variation that was not seen in the overall population but was present within sectors. These models follow the same definitions as the *a priori* hypothesized models for describing the mean change in the populations length over the given study period for each specific sector.

3.2.1 Change in Length, by Female Sector

As stated in section 2.1, the following are based on the same definitions as the *a priori* hypothesized models for describing the populations mean change in length over the given study period.

$$H_{Lf,1}: g = 0$$

$$H_{Lf,2}: g = k$$

$$H_{Lf,3}: g = k * L_{ft}$$

The best supported model was $H_{Lf,1}$ (AICw = 0.77). Subsequently $H_{Lf,2}$ was the next best supported model (AICw = 0.19)(Fig 14). Therefore, I inferred that the mean change in length within the female population over time is more likely to be zero. Thus there was no strong evidence for change in length during the study.

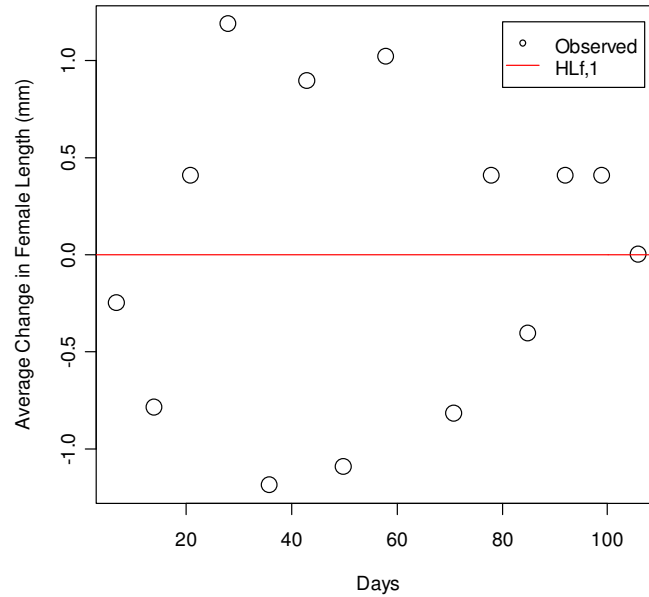


Figure 7: Female Population Length Models

3.2.2 Change in Length, by Male Sector

As stated in section 1.1, the following are based on the same definitions as the *a priori* hypothesized models for describing the populations mean change in length over the given study period.

$$H_{Lm,1}: g = 0$$

$$H_{Lm,2}: g = k$$

$$H_{Lm,3}: g = k * L_{mt}$$

The best supported model was $H_{Lm,1}$ ($AIC_w = 0.77$). Subsequently $H_{Lm,2}$ was the next best supported model ($AIC_w = 0.19$) (Fig 16). Therefore, I inferred that the mean change in length within the male population over time is more likely to be zero. Thus there was no strong evidence for change in length during the study.

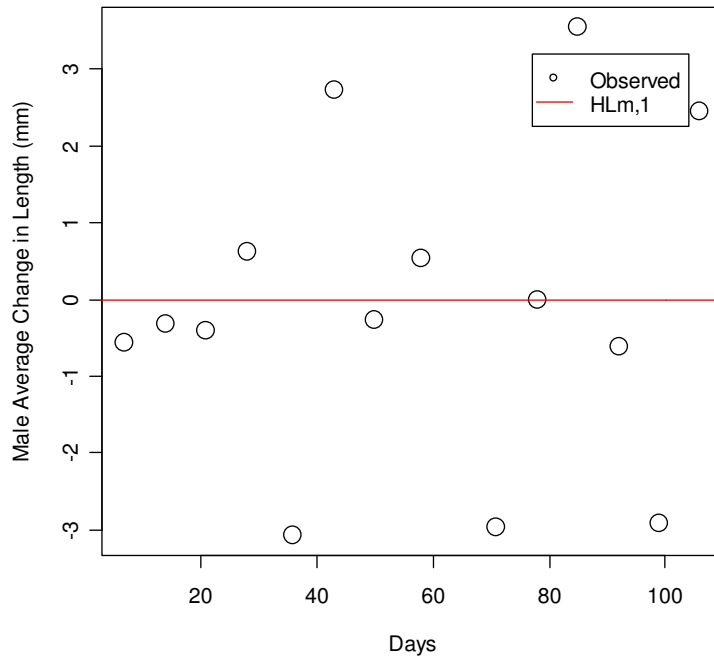


Figure 8: Male Population Length Models

3.2.3 Change in Length, by Juvenile Sector

As stated in section 1.1, the following are based on the same definitions as the *a priori* hypothesized models for describing the populations mean change in length over the given study period

$$H_{Lj,1}: g = 0$$

$$H_{Lj,2}: g = k$$

$$H_{Lj,3}: g = k * L_{jt}$$

The best supported model was $H_{Lj,1}$ (AICw = 0.77). Subsequently $H_{Lj,2}$ was the next best supported model (AICw = 0.20) (Fig 16). Therefore, I inferred that the mean change in length within the juvenile population over time is more likely to be zero. Thus there was no strong evidence for change in length during the study.

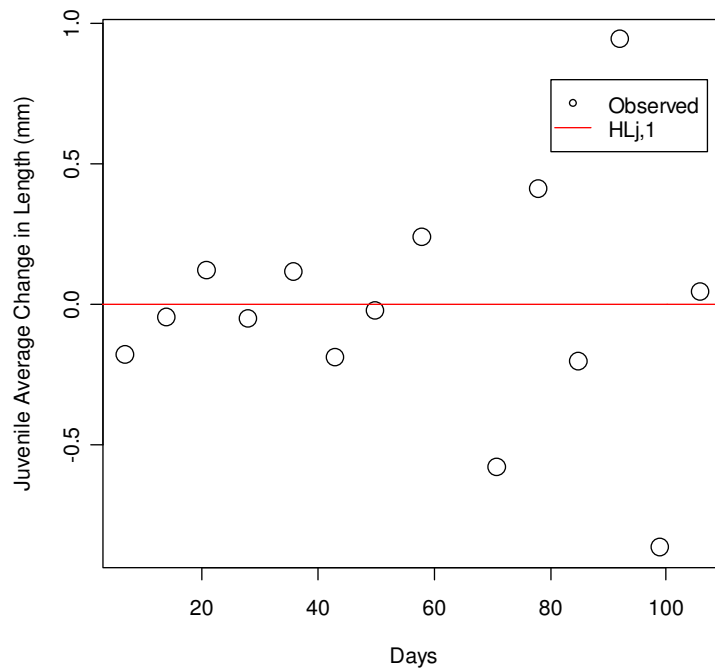


Figure 9: Juvenile Population Length Models

3.3 Change in Population Abundance

As stated in section 1.1 the *a priori* hypothesized models for describing the average change in the populations abundance over the given study period were:

$$H_{P,1}: dP/dt = 0$$

$$H_{P,2}: dP/dt = r$$

$$H_{P,3}: dP/dt = r * P_t$$

$$H_{P,4}: dP/dt = r * P_t * (K-P)/K$$

The best supported model was $H_{P,1}$ (AICw = 0.77). Subsequently $H_{P,2}$ was the next best supported model (AICw = 0.20) (Fig 17). Therefore, I infer that the average change in the population abundance over time is more likely to be zero. Thus there was no strong evidence for change in abundance during the study.

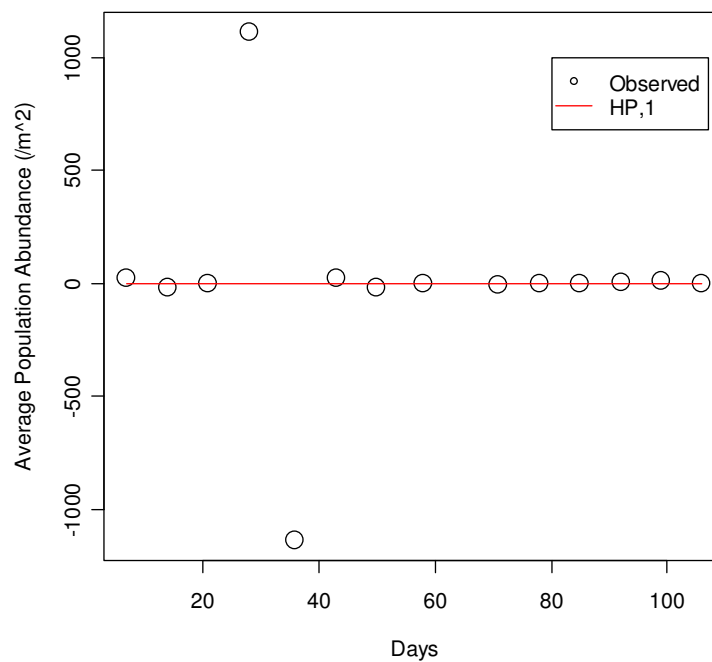


Figure 10: Population Abundance Models

3.3.1 Juvenile Sector Population Abundance

As stated in section 1.1 the *a priori* hypothesized models for describing the change in the juvenile population abundance over the given study period were:

$$H_{J,0} : P_{J,t} = 0$$

$$H_{J,1} : P_{J,t} = k$$

$$H_{J,2} : P_{J,t} = k * f_{t-\tau}$$

The best supported model was $H_{J,0}$ (AICw = 0.77). Subsequently $H_{J,1}$ was the next best supported model (AICw = 0.20) (Fig 18). Therefore, I infer that the average change in the juvenile population's abundance over time is more likely to be zero. Thus there was no strong evidence for change in abundance during the study.

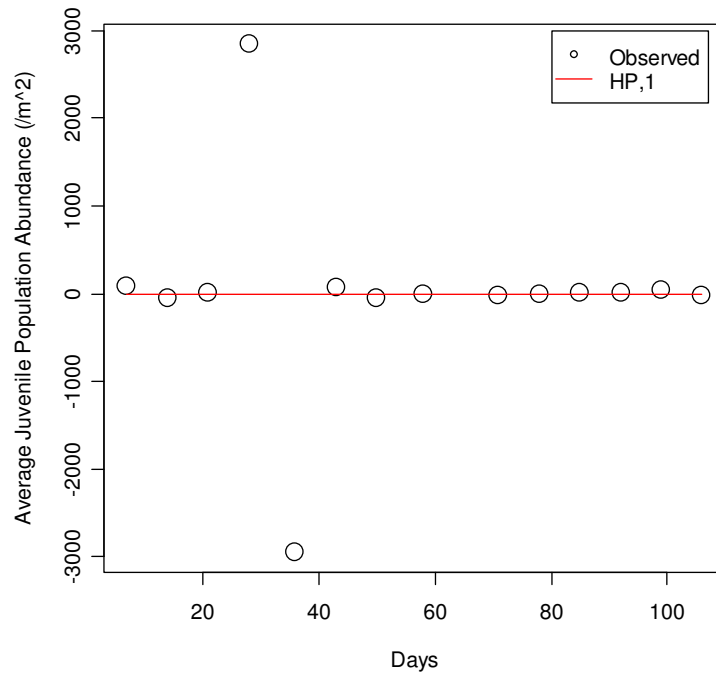


Figure 11: Juvenile Population Abundance Models

3.3.2 Male Sector Population Abundance

As stated in section 1.1 the *a priori* hypothesized models for describing the change in the male population abundance over the given study period were:

$$H_{M,0} : P_{M,t} = 0$$

$$H_{M,1} : P_{M,t} = k$$

$$H_{M,2} : P_{M,t} = k * P_{M,t}$$

$$H_{M,3} : P_{M,t} = k * P_{M,t}(1-P)/K$$

The best supported model was $H_{M,0}$ (AICw = 0.74). Subsequently $H_{M,1}$ was the next best supported model (AICw = 0.19) (Fig 19). Therefore, I infer that the average change in length within the male population over time is more likely to be zero. Thus there was no strong evidence for change in length during the study.

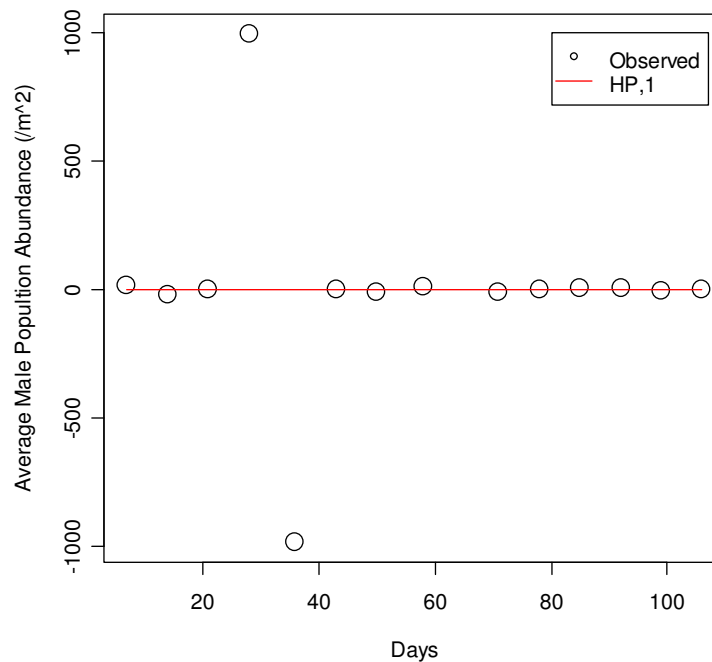


Figure 12: Male Population Abundance Models

3.3.3 Female Sector Population Abundance

As stated in section 1.1 the *a priori* hypothesized models for describing the change in the female population abundance over the given study period were:

$$H_{F,0} : P_{F,t} = 0$$

$$H_{F,1} : P_{F,t} = k$$

$$H_{F,2} : P_{F,t} = k * P_{F,t}$$

$$H_{F,3} : P_{F,t} = k * P_{F,t} (1-P)/K$$

The best supported model was $H_{F,0}$ (AICw = 0.74). Subsequently $H_{F,1}$ was the next best supported model (AICw = 0.19) (Fig 20). Therefore, I infer that the average change in length within the female population over time is more likely to be zero. Thus there was no strong evidence for change in length during the study.

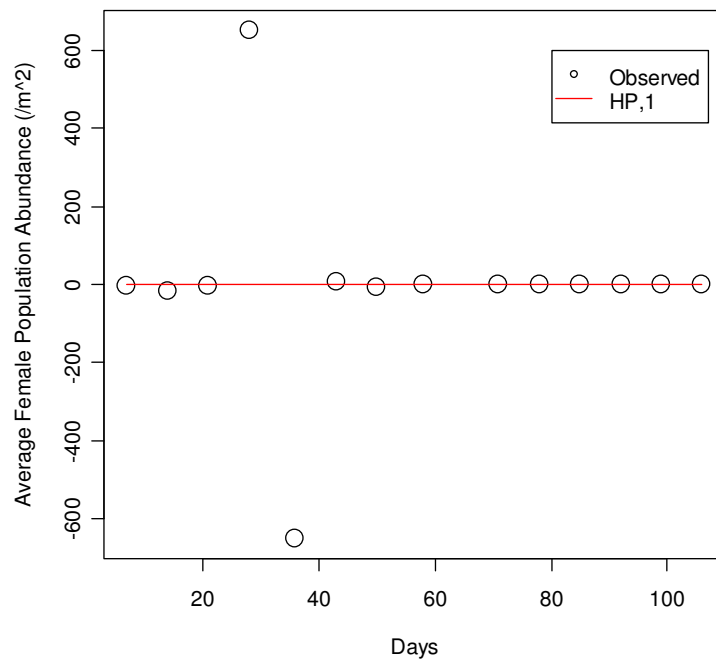


Figure 13: Female Population Abundance Models

3.4 Fecundity

As stated in section 1.1 the *a priori* hypothesized models for describing the average fecundity over the given study period were:

$$H_{B,0} : f_{t-\tau} = 0$$

$$H_{B,1} : f_{t-\tau} = k$$

$$H_{B,2} : f_{t-\tau} = k * t$$

$$H_{B,3} : f_{t-\tau} = k * \sin(t - \theta)/w$$

The best supported model was $H_{B,3}$ ($AIC_w = 0.41$). A near-monthly periodic pattern was noticed ($w=28$), so an exploratory hypothesis based on a lunar cycle ($w=29.5$) was added to the stated models as model $H_{B,3E}$: $f_{t-\tau} = k * \sin(t - \theta)/29.5$. The evidence to implicate a lunar cycle might have been influencing the fecundity rates of the population is the inference that moonlight might affect predation rates. Thus it can be inferred that times of low amounts of light at night would be conducive to releasing young. This new model became the best supported model ($AIC_w = 0.57$) (Fig 21). Thus I inferred that the female population's reproductive cycle corresponds with the lunar phases during the month.

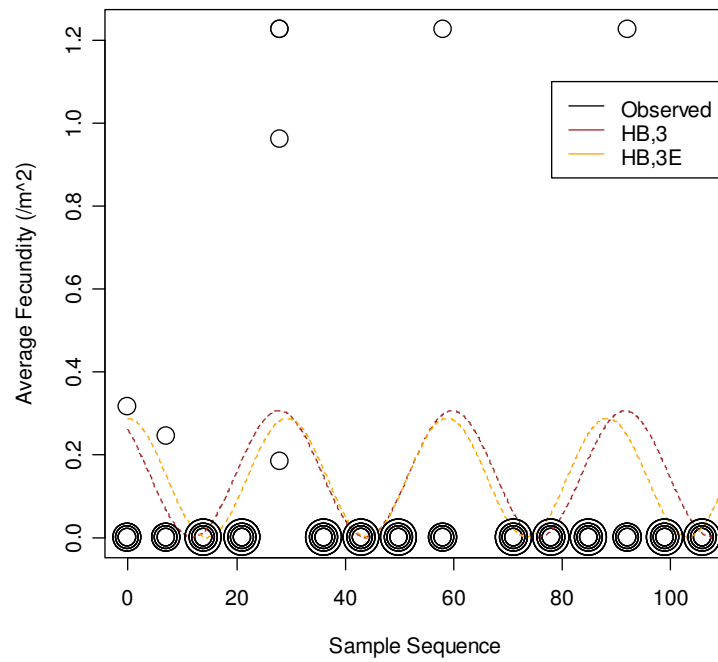


Figure 14: Average Fecundity Models

4 Water Quality Analysis

Water quality data was collected in conjunction with demographic data. As an adjunct to the primary analysis of population dynamics the focus of the study and was used as a secondary explorative analysis to look for possible contributing factors to the life history patterns that were observed.

4.1 Water Quality Results

The Carmel lagoon water elevation declined steadily over the study period (Fig 15A). There were three events in the study period when the water elevation of the study site increased slightly. Comparisons between water quality factors and water elevation were analyzed at 0.5 m (NGVD) since samples for the most part were collected at this elevation.

Over the entire course of the study there was no apparent correlation between water elevation and the pH (Figure 15A). pH declined slightly across water elevation depth gradients (Appendix C).

There was no clear association noted during the course of this study between salinity and the water elevation (Figure 15B). The lagoon actually got slightly fresher over time which is somewhat counter intuitive since the elevation was decreasing. Salinity stayed consistent over elevation gradients until 0 m (NGVD), when it then had a rapid increase (Appendix C).

The temperature had no clear association with the water elevation over the course of the study (Figure 15C). Temperature only decreased slightly over decreasing depth elevation gradients (Appendix C). August 6, 2007 was the only sampling event where there was a deviation from this pattern.

Dissolved oxygen concentrations showed no apparent pattern with the water elevation over the course of the study (Figure 15D). There was a observed drop in dissolved oxygen with increasing water depth (Appendix C). Generally anoxic conditions were reached at the bottom water elevations.

There was no substantial relationship observed between the number of specimens collected and the water quality data collected over the course of this study (Fig 16 A–H). The only trend that was seen was a slight negative correlation between temperature and *C. spinicorne*. It can thus be concluded that abiotic factors had no apparent influence on the population of *C. spinicorne* in the Carmel Lagoon.

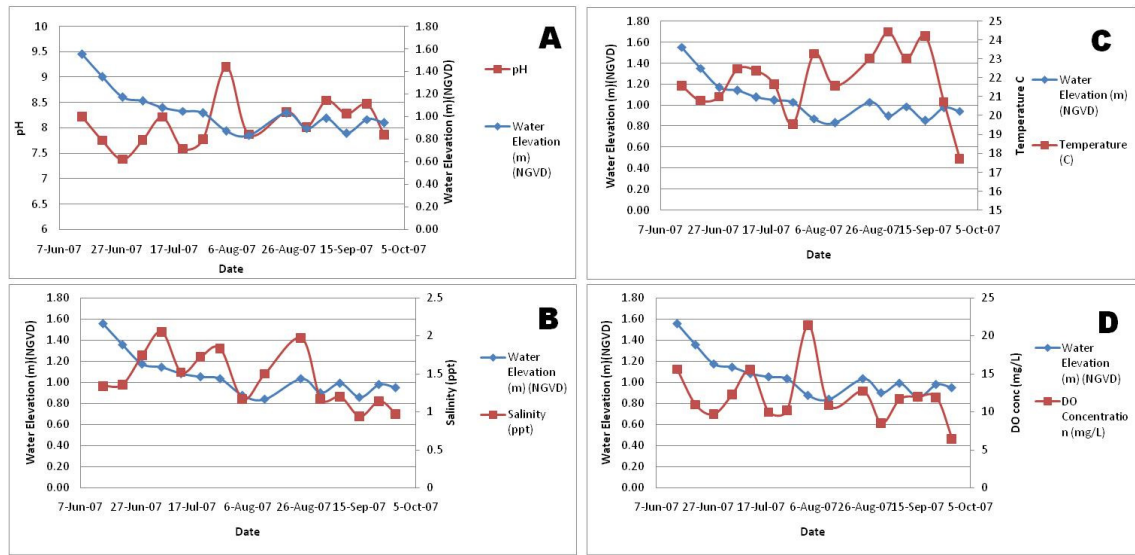


Figure 15: Variation in environmental water quality variables (potential influences on population dynamics) over the course of the study: (A) pH; (B) salinity; (C) water temperature; (D) dissolved oxygen.

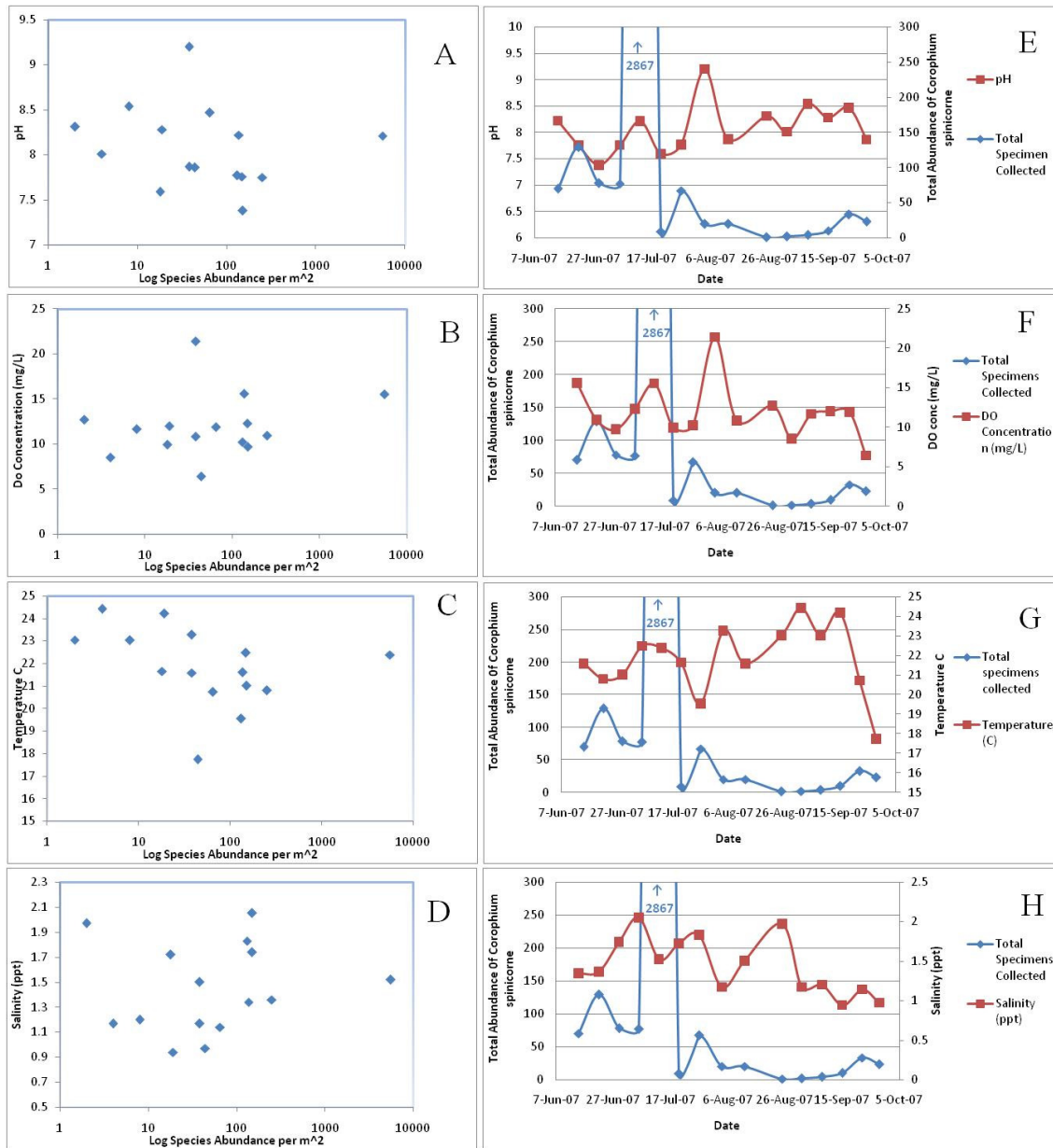


Figure 16: Variation in environmental water quality variables (potential influences on abundances) over the course of the study: (A) pH; (B) salinity; (C) water temperature; (D) dissolved oxygen.

5 Habitat Analysis

Dominant habitat substrate was qualitatively observed in the field in order to provide context for the primary variables of interest. These notes were then quantified in a post hoc exploratory analysis in order to look for possible associations between abundances and dominant habitat types.

5.1 Habitat Results

C. spinicorne abundance was orders of magnitude higher in two samples than in the other 58 samples. Post hoc, I noticed that the habitat from which these samples were taken also happened to have the highest sand cover. Therefore, in a post hoc exploratory analysis, I briefly examined the amount of dominant substrate type of each sample. These data were qualitatively recorded in the field, and then converted to a 3-class categorical measure post-hoc where 0= none (0 – 5%), 1= some (5 – 50%), 2= a lot (>50%). Data were then averaged and plotted against the abundance of *C. spinicorne* on the given sampling dates. The highest abundance of *C. spinicorne* corresponded to the greatest prevalence of sandy habitat. While this was a very clear correspondence, the sample size was limited (only two sandy samples), and the analysis was post-hoc, so I consider this result to be indicative, rather than conclusive (Figure 17).

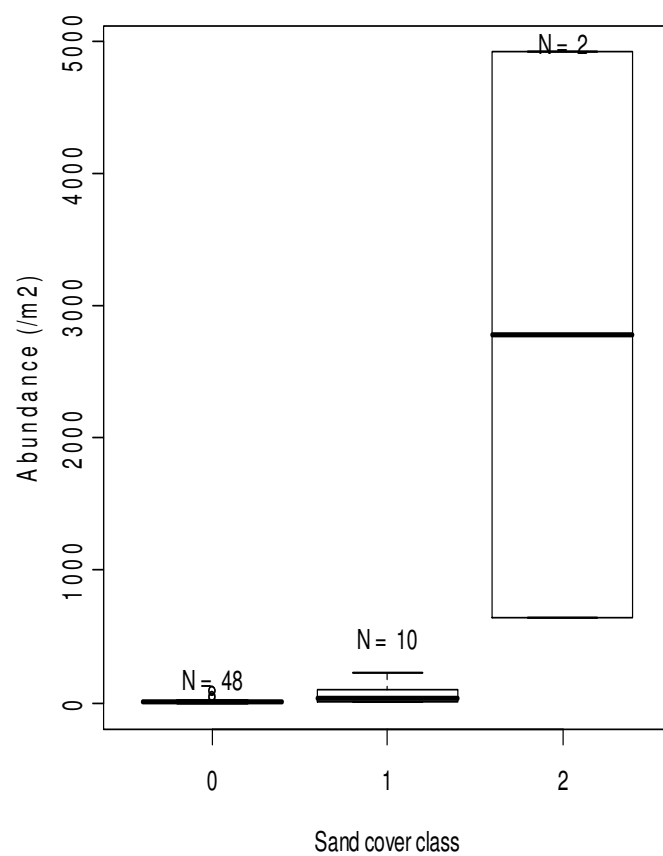


Figure 17: Average *C. spinicorne* Abundance (m²) with Regards to Sand as a Dominant Habitat Type

6 Discussion

The mean length of *C. spinicorne* did not change during the course of this study. This same pattern was mirrored in all three sectors of the populations (males, females, juveniles). The interpretation of these results depends on additional population characteristics, such as whether or not reproduction is synchronous or asynchronous.

Synchronous reproduction is when a lot of reproduction happens at the same time, followed by an intervening period of no reproduction. If this population had synchronous reproduction and a longevity of individual organisms that was short relative to the frequency of reproduction, one would expect the results to have shown a change in mean length due to there being distinguishable generations within the population. However, the results do not support this inference. So either reproduction is asynchronous, or the longevity is long relative to the frequency of reproduction.

Asynchronous reproduction is when reproduction is happening all the time, with individual organisms reproducing at independent times that are not related to the timing of reproduction of other individuals. For example, if the change in length is occurring at a rapid rate due to the constant influx of new generations, then there might be no apparent change in mean length. Thus, the results of this study are consistent with either the inference that this population is comprised of overlapping sectors that blur any possible observation of the change in mean length of any specific sector, or with a synchronous reproduction with a period much shorter than the longevity.

The results for the juvenile population change in length however are confounded by the fact that their sector was determined by length. A constant population length as opposed to actual net growth of juveniles could be explained by an influx of new juveniles into the system at the same rate as those exceeding the upper limit of the length classification. Since this pattern was observed in all three sectors than it is most probable that this is not the case and that one of the previous explanations is more appropriate.

The overall population exhibited no evidence of a change in abundance of *C. spinicorne* over the course of this study. This same pattern was mirrored in all three sectors of the populations (males, females, juveniles). There are multiple interpretations of these results that depend on additional population characteristics.

One possible explanation for these population results could be that *C. spinicorne* longevity is long relative to the frequency of reproduction. Therefore, they live for long periods of time and grow very slowly, so that during a 4 month sampling period, no

changes in abundance would be apparent. If this population had a synchronous reproduction and a longevity of individual organisms shorter relative to the frequency of reproduction, one would expect the results to have shown a change in abundances due to there being distinguishable generations within the population. If their life span was synchronous to their life cycle one would expect with the monthly reproduction there would also be a monthly drop in abundance due to mortality. However, the results do not support this inference.

Another possibility is *C. spinicorne* populations had synchronous reproduction and longevity of individual organisms short relative to the frequency of reproduction. For example if the population of *C. spinicorne* had longevity of 2 months influx of new generations would cause small increases or decreases within the results. However, due to the constant influx of new generations longevity of 4–6 months would show no apparent change in abundance. Thus, the results of this study are consistent with either the inference that this population is comprised of overlapping sectors that blur any possible observation of the change in abundance of any specific sector, or with a synchronous reproduction with a period much longer than the longevity.

Perry et al. (2007) and Larson et al. (2004–6) found that the abundance of *C. spinicorne* in the pre-existing lagoon and Odello arm steadily grew over the course of their studies (Fig 18). The abundance of *C. spinicorne* population observed in this study did not follow the same patterns observed in either previous abundance studies. In the present study, I observed mostly very low abundances, and one very large one. By comparison, previous authors observed values that were mostly between my two extremes. Due to the different time scales being compared in these studies one would expect a difference in trends. However, had this study continued on for a comparable amount of time such as a year patterns might have been unable to be distinguished. Another possible explanation is that the Perry et al. (2007) and Larson et al. (2004–6) studies abundances generally increased over time in the Odello section due to the gradual establishment of a stable, productive substrate following excavation. It is possible that during the current study trends were less apparent than the previous study due to the now established community.

Fecundity results support a reproduction cycle is more likely to be on a lunar cycle than any of the other dynamics considered (i.e. constant fecundity, zero fecundity, or a linear trend in fecundity). Asynchronous reproduction would have been consistent with a constant amount of fecundity that had no defined cycle. Therefore, these results are not consistent with an asynchronous reproduction and instead support synchronous reproduction.

Other *Corophium sp.* population fecundity studies found incubating females all year round with recruitment occurring in spring, ceasing during summer, peaking in autumn, and decreasing during winter (Cunha et al, 2000, Prato and Biantolino, 2006). Thus, the unfavorable summer conditions constrain breeding and synchronize the timing of reproduction (Cunha et al, 2000). However, in late autumn and during winter as temperature decreases brooding time is increased and synchrony is progressively lost (Cunha et al, 2000). Therefore in order to more definitively infer that *C. spinicorne* do not have synchronous reproduction further studies that continue into late autumn and winter should be conducted to establish if there is a seasonal trend.

Overall the results of the population dynamics study of *C. spinicorne* are consistent with synchronous reproduction with a period much longer than the longevity. Since lunar periodicity in reproduction was observed, than it could be hypothesized that longevity was more than a few months, possibly much longer. From a conservational view these are important findings. This allows managers who are considering steelhead habitat restoration projects similar to the Carmel River Lagoon Enhancement Project to plan for an establishment phase of newly developed lagoons. This establishment phase would have to be monitored for food source abundances over long temporal scales in order to identify when *C. spinicorne* populations were established enough to sustain resident juvenile steelhead.

Water quality results indicate that the Carmel Lagoon is not a static body. It is clear from these results that the water quality of this system varies temporally as well as seasonally. Despite this constantly changing system, in all water quality cases excluding temperature, there was no evidence of an association between abundance of *C. spinicorne* and water quality. Evidence supported a possible weak negative association between temperature and *C. spinicorne* abundances. This very weak relationship showed that when temperature decreased abundance in the lagoon increased. Since this was such a weak association it could in fact just be an artifact of variability in both abundances and temperature. However, since Cunha et al. (2000) did find a relationship between fecundity of *C. multisetosum* and temperature this pattern could be consistent and become stronger over the varying seasons.

Dissolved oxygen concentrations and the abundance of *C. spinicorne* collected were apparently independent of each other. This does not rule out the possible effect that stratification of the water column has on abundance. Due to the fact that *C. spinicorne* spend a part of their life living on the benthos it seems intuitive that the anoxic conditions observed at the lowest levels of the water elevation would have a negative effect on abundance. However, samples were taken at 0.5 NGVD thus guarding against any artifacts in that data that could be associated with anoxic conditions.

In a post hoc analysis, an apparent correlation was observed between dominant habitat substrate and *C. spinicorne* abundance. The evidence supports that in this study habitat dominated by a sandy substrate facilitates *C. spinicorne* benthic communities. This may be due to the fact that it provides better substrate for tube building while mud and pond weed do not.

Therefore overall evidence supports that abundance is independent of water quality and possibly positively influenced by dominant substrate, at least within the relatively narrow range observed during my four-month mid-year sampling period. This supports the idea that during the summer months, optimal juvenile steelhead habitat is in sandy areas containing little pond weed where *C. spinicorne* abundances are at their highest.

It is important when designing a restoration project such as the Carmel Lagoon Enhancement Project to take into consideration the effects that dominant habitat substrate has on the organisms. For example, a suggestion can be made that steelhead trout not only need cover which is provided from downed logs and grasses, but also sandy areas interspersed in this habitat. Though the sand may not be optimal in providing protective cover for steelhead it is suggested that it increases abundances of food sources like *C. spinicorne*.

Since the Odello Arm was a human creation it does not experience the same natural diversity of substrate types like the original Lagoon. Future restoration planners would be advised to consider implementing pondweed management and deliberately depositing sand in patches through the restoration area. By setting up a patchwork of sand free areas void of pond weed my study indicates that food sources for steelhead would be optimized by increasing the dominant prey's habitat.

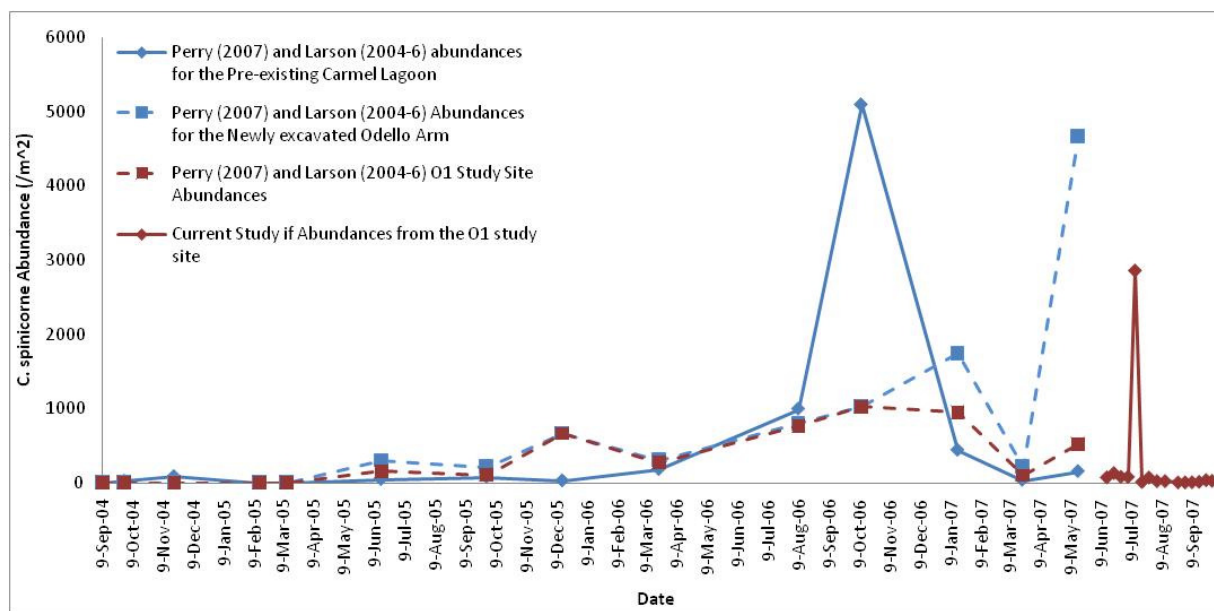


Figure 18: Comparison of abundances of Perry et al. (2007) and Larson et al. (2004–6) study to this study.

7 Conclusions

This study contributed to the understanding of life history dynamics of *C. spinicorne* by reporting that the evidence supports that *C. spinicorne* had synchronous reproduction with a period much shorter than the longevity. Since *C. spinicorne* is a dominant food source of resident steelhead this study acts as a baseline study for future projects to use when considering how to increase food availability for these threatened species.

This study also found that *C. spinicorne* abundances varied with dominant habitat substrate throughout the study period. Thus, it is important for the managers of Lagoons to examine these variations more in depth in order to assess the food availability for resident steelhead trout. This monitoring should be conducted in the same location for a time period of no less than a year in order to observe seasonal variations on a biweekly scale.

Lastly, this study also contributes to methodological development of *C. spinicorne* life history dynamic studies. It was observed that even with 4x replication it was still very hard to control for variation. Therefore, more replicates should be conducted in order to account for all the confounding factors that could possibly be present at a study site.

8 Literature Cited

- Akaike, H. 1987. *Factor Analysis and AIC*. Psychometrika. Vol. 52. NO. 3. pp317–332
- Anderson, D., K. Burnham, and G. White. 1994. AIC model selection in overdispersed capture–recapture data. *Ecology* 75:1780–1793.
- Barnhart, R. A. 1986. *Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest)–steelhead*. U.S. Fish Wild. Serv. Biol. Rep. 82(11.60), 21 p.
- Bousfield, 1997. The amphipod super family Corophioidea on the Pacific coast of North America. *Amphipacifica*. Vol. II. NO. 3. pp67–139.
- California Department of Parks and Recreation (CDPR). 2003. Revegetation Mitigation and Monitoring Plan: Carmel River Lagoon Enhancement Project, Carmel River State Beach. CDPR, Central Service Center and Monterey District. Revised September, 2003.
- Casagrande, J. (2006) *Wetland Habitat Types of the Carmel River Lagoon*. The Watershed Institute, California State University Monterey Bay, Publication No. WI-2006-05, ~19pp.
- Covich, A., Palmer, M., Crowl, P.. 1999. The role of benthic invertebrate species in freshwater ecosystems: zoobenthic speices influence energy flows and nutrient cycling. *BioScience*. V49. 2(119).
- Covich, A.P., and Thorp, J.H.. 2001. Introduction to the subphyllum Crustacea. Pp.773–805 IN: J.H. Thorp and A.P. Covich (eds.) *Ecology and Classification of North American Freshwater Invertebrates* . Academic Press, San Diego, California.
- Cunha M., Moreira M., Sorbe J. 2000. Predicting amphipods brood size variation in brackish environments : an empirical model for *Corophium multisetosum* Stock, 1952 (Corophiidae) in Ria de Aveiro (NW Portugal), *Journal of Experimental Marine Biology and Ecology*, 248, 207–223.
- Dettman, D.H. 1984. The Carmel Lagoon and its use by Steelhead, D.W. Kelley and Associates, Prepared for the Monterey Peninsula Water Management District.
-

-
- (EPA) Environmental Protection Agency. 2006. *Threats to Wetlands*. Available at: <http://www.epa.gov/owow/wetlands/facts/threats.pdf>
Accessed 2007 Feb 8.
- Fields, W. Jr., 1984. The Invertebrate fauna of the Carmel River system and food habits of fish in the Carmel River System. Monterey Peninsula Water Management District, Monterey, California. USA.
- Gonenc, I., Wolfin, J. 2005. Coastal Lagoons Ecosystem Processes and Modeling for Sustainable Use and Development.
- Gooderham, J. and Tsyrlin, E.. 2002. The Waterbug Book: A Guide to the Freshwater Macro-invertebrates of Temperate Australia . CSIRO Publishing, Collingwood Australia.
- Harrington, J. and Born, M.. 2000. Measuring the Health of California Streams and Rivers, A Methods Manual for: Water Resource Professionals, Citizen Monitors, and Natural Resource Students . 2nd edition. California: Sustainable Land Stewardship International Institute.
- Janssen, H., M. Scheepmaker, M. Van Couwelaar and S. Pinkster. 1979. *Biology and Distribution of Gammarus aequidauda and G. insensibilis (Crustacea: Amphipoda) in the lagoon system of Bages-Sigean (France)*. Bijdragen tot de Dierkunde 49: 42–70.
- Kevrekidis, T. 2005. *Life history, aspects of reproductive biology and production of Corophium orientale (Crustacea: Amphipoda) in Monolimni lagoon (Evros Delta, North Aegean Sea)*. Hydrobiologia. Vol 537: 53–70pp.
- Larson, J., Watson, F., Casagrande, J., & Pierce, B. et al..2006. Carmel River Lagoon Enhancement Project: Water Quality and Aquatic Wildlife Monitoring, 2005–6 Report to California Department of Parks and Recreation. The Watershed Institute, California State University Monterey Bay, Publication No. WI-2006-06, 102 pp.
- Larson, J., Watson, F., Masek, J., Watts, M., & Casagrande, J..2005. Carmel River Lagoon Enhancement Project: Water Quality and Aquatic Wildlife Monitoring. Report to California Department of Parks and Recreation. The Watershed Institute, California State University Monterey Bay, Publication No. WI-2005-12, 130 pp.
-

Lufkin A. editor, 1991, *California's Salmon and Steelhead*. 1st Edition. Oxford: University of California Press.

Merriam-Webster Online Dictionary. 2006. Available at: <http://www.m-w.com/>

Perry, W., Watson, F., Casagrande, J., & Hanley, C..2007. Carmel River Lagoon Enhancement Project: Water Quality and Aquatic Wildlife Monitoring, 2006-7. Report to California Department of Parks and Recreation. The Watershed Institute, California State Monterey Bay, Publication No. WI-2007-02, 100 pp.

Prato, E. and Biantolino, F..2006. Life history of the amphipod *Corophium insidiosum* (Crustacea: Amphipoda) from Mar Piccolo (Ionian Sea, Italy). *Sci. Mar. (Barc.)* 70(3): 353-362

(NMFS) National Marine Fishery Services. 2006. *California Central Valley Steelhead DPS*. Available at: http://swr.nmfs.noaa.gov/recovery/Steelhead_SCCS.htm

Smith, D.G. 2001. Pennak's Freshwater Invertebrates of the United States. Porifera to Crustacea. USA: John Wiley & Sons, Inc. 617p.

Watson, F., Casagrande J., 2004. Potential effects of groundwater extractions on Carmel Lagoon. Central Coast Watershed Studies. Watershed Int. Cal State U. Monterey Bay. http://science.csumb.edu/%7Eccows/pubs/reports/CCoWS_CalAmLagoonGW_040908_fw.pdf Accessed 2007 March 30.

Williams, M. editor, 1990. *Wetlands: A Threatened Landscape*. 1st Edition. Oxford: Blackwell Publishers.

Appendix A – Specimen Identification

The observed differences in the head morphologies were not as distinct as depicted in the drawings by Bousfield (Figure 12). The males head plate had smoother curvatures and not as pronounced dips near the eyes. The females head plate had a more irregular dome located in its center (Figure 12). This morphology though like the males was not as distinct as depicted in the Bousfield study of 1997.

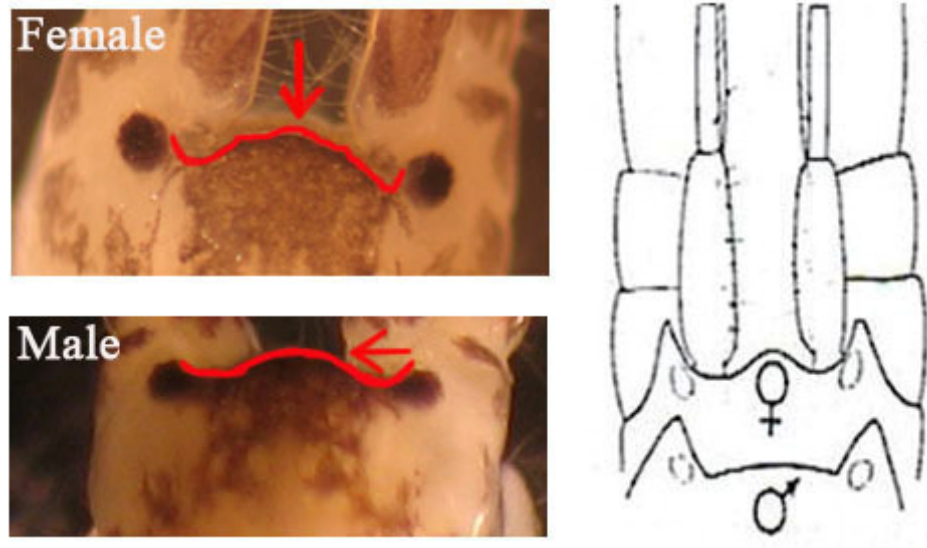


Figure 18: Examples of the head morphologies of both males and females observed during the study (photos by author, drawing taken from Bousfield, 1997).

The observed differences in the underside appendages of *Corophium spinicorne* were very distinct and resembled those depicted in the drawings by Bousfield (Figure 7). The males underside appendages had no hairs and were broader than that of the female (Figure 13). It was also noted that adult males had more pronounced and distinctively larger front antennae. The female's underside appendages were covered with hairs in order to form brood pouches (Figure 13). Females were identified in three different reproductive stages which included: non-reproductive empty brood pouch, reproductive with brood pouch containing eggs, and reproductive with brood pouch containing developing young (Figure 13).

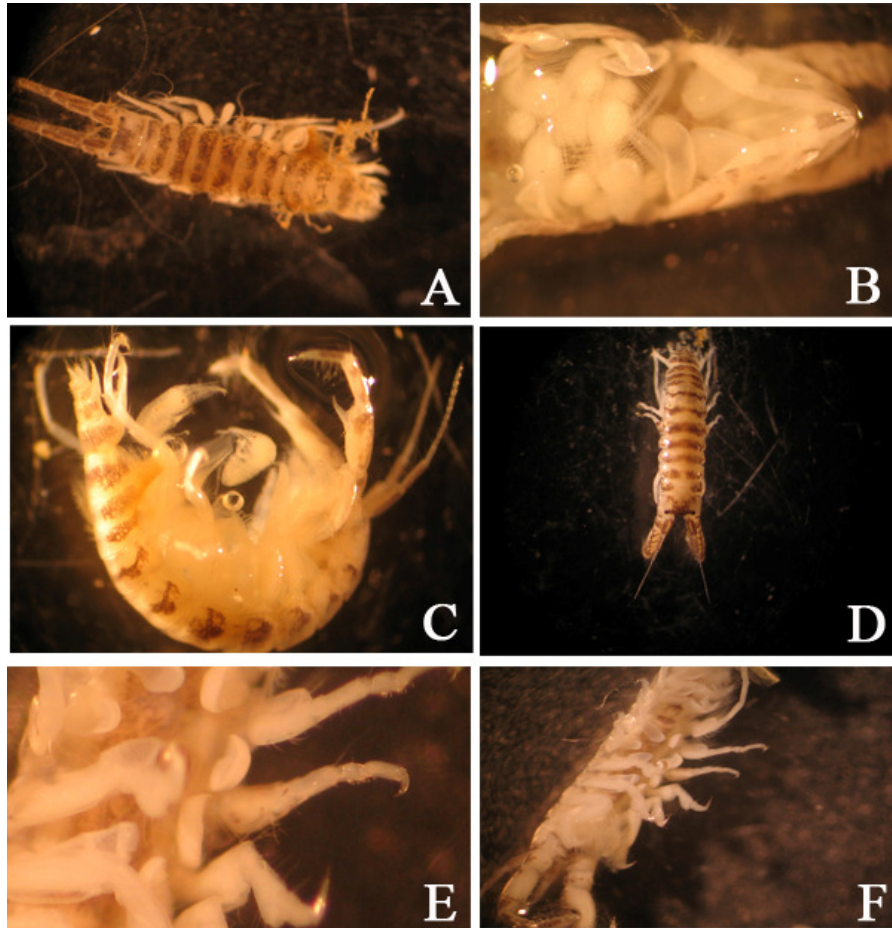


Figure 19: (A) Female morphology, (B) Female brood pouch filled with eggs, (C) Female with brood pouch filled with developed offspring, (D) Male morphology, (E) Close up of male underside appendages, (F) Male underside with absence of brood pouch.

A great amount of difficulty exists in using head plate morphology to distinguish between the two sexes of *Corophium spinicorne*. The underside appendages are relatively more distinct thus providing a more efficient and precise route of sexual dimorphism identification. The absences and presences of hairs on the underside appendages are recommended as the primary mode of identification for future *Corophium spinicorne* studies.

The different stages of female reproduction are easily identified within a sample. This study did not analyze the different stages of reproduction. All reproductive stages were lumped together in order to acquire fecundity data. Future studies should look at the different proportions of reproductive states as well as the temporal scales at which each occurs.

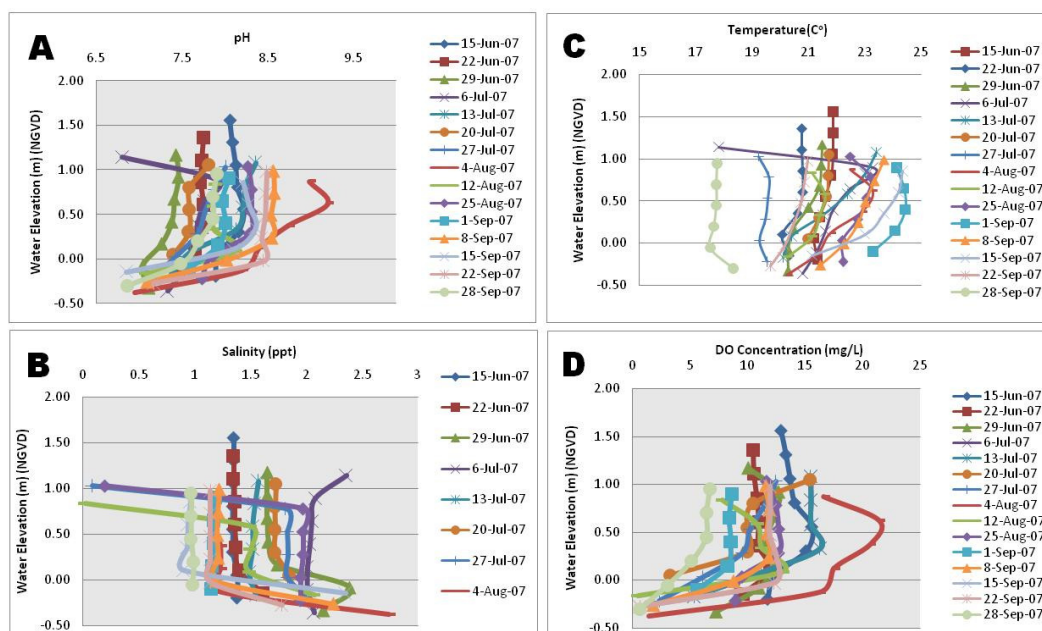
Appendix B –Abundance Calculations

Each sampling day four separate samples were collected. The number of individual *C. spinicorne* were then counted in each one of these samples and recorded. In order to obtain abundances (/m²) each count was divided by the area sampled which was 0.486 m². An average was then taken of the four samples to obtain the average abundance for each sampling day.

Table 1: Population Average Abundance Calculations

Date	Counts				Abundance #/m2				Average Abundance	stdev
6/15/2007	2	1	30	104	4	2	62	214	70	100
6/22/2007	13	10	226	2	27	21	465	4	129	224
6/29/2007	5	80	13	53	10	165	27	109	78	72
7/6/2007	7	52	11	79	14	107	23	163	77	71
7/13/2007	15	4914	639	5	31	10111	1315	10	2867	4868
7/21/2007	3	0	10	5	6	0	21	10	9	9
7/28/2007	4	6	8	113	8	12	16	233	67	110
8/4/2007	16	11	1	10	33	23	2	21	20	13
8/12/2007	1	1	1	35	2	2	2	72	20	35
8/25/2007	1	1	0	0	2	2	0	0	1	1
9/1/2007	2	2	0	0	4	4	0	0	2	2
9/8/2007	1	3	1	3	2	6	2	6	4	2
9/15/2007	14	0	0	5	29	0	0	10	10	14
9/22/2007	31	18	6	10	64	37	12	21	33	23
9/29/2007	29	9	6	0	60	19	12	0	23	26

Appendix C – Depth Gradient Figures



\
