

Copyright Warning & Restrictions

The copyright law of the United States (Title 17, United States Code) governs the making of photocopies or other reproductions of copyrighted material.

Under certain conditions specified in the law, libraries and archives are authorized to furnish a photocopy or other reproduction. One of these specified conditions is that the photocopy or reproduction is not to be “used for any purpose other than private study, scholarship, or research.” If a user makes a request for, or later uses, a photocopy or reproduction for purposes in excess of “fair use” that user may be liable for copyright infringement,

This institution reserves the right to refuse to accept a copying order if, in its judgment, fulfillment of the order would involve violation of copyright law.

Please Note: The author retains the copyright while the New Jersey Institute of Technology reserves the right to distribute this thesis or dissertation

Printing note: If you do not wish to print this page, then select “Pages from: first page # to: last page #” on the print dialog screen

The Van Houten library has removed some of the personal information and all signatures from the approval page and biographical sketches of theses and dissertations in order to protect the identity of NJIT graduates and faculty.

ABSTRACT

SIZE-FREQUENCY DISTRIBUTION OF *PALAEMONETES PUGIO* IN TWO NEW JERSEY ESTUARIES AND PREDATOR-PREY INTERACTIONS WITH *FUNDULUS HETEROCLITUS*

by
Celine Santiago

Predation by *Fundulus heteroclitus* is known to be an important factor regulating the abundance and size distribution of *Palaemonetes pugio* in the salt marsh habitat.

A preliminary study showed that *P. pugio* from a polluted estuary, Piles Creek, were relatively larger than those found in a more pristine estuary, Little Sheepshead Creek. Possible causes could be differences in competition, inherent environmental components, reproductive effort, or predation. To investigate the differences in size frequency, data on relative abundances of both species and size frequency distribution of *P. pugio* were collected for comparison from the two estuaries.

It was determined that *P. pugio* were preyed upon more frequently in LSC than in PC due to there being nearly three times as many *F. heteroclitus* in LSC than in PC. It was concluded that size selective predation is limiting the number of adult shrimp from ultimately reaching their maximum length.

**SIZE-FREQUENCY DISTRIBUTION OF
PALAEMONETES PUGIO IN TWO NEW JERSEY ESTUARIES
AND
PREDATOR-PREY INTERACTIONS WITH
*FUNDULUS HETEROCLITUS***

by
Celine Santiago

**A Thesis
Submitted to the Faculty of
New Jersey Institute of Technology
in Partial Fulfillment of the Requirements for the Degree of
Master of Science in Environmental Science**

**Department of Chemical Engineering,
Chemistry, and Environmental Science**

January 1997

APPROVAL PAGE

SIZE-FREQUENCY DISTRIBUTION OF
PALAEEMONETES PUGIO IN TWO NEW JERSEY ESTUARIES
AND
PREDATOR-PREY INTERACTIONS WITH
FUNDULUS HETEROCLITUS

Celine Santiago

Dr. Judith S. Weis, Thesis Advisor Date
Professor, Department of Biological Sciences, Rutgers University

Dr. Peddrick Weis, Committee Member Date
Professor, Department of Anatomy, Cell Biology, and Injury Science,
University of Medicine and Dentistry of New Jersey

Dr. Richard Trattner, Committee Member Date
Associate Chairperson for Environmental Science and
Professor of Chemical Engineering, Chemistry, and Environmental Science,
New Jersey Institute of Technology

BIOGRAPHICAL SKETCH

Author: Celine Santiago
Degree: Master of Science
Date: January 1997

Undergraduate and Graduate Education:

- Master of Science in Environmental Science
New Jersey Institute of Technology, Newark, New Jersey, 1997
- Bachelor of Science in Environmental Science
Rutgers University, Cook College, New Brunswick, New Jersey, 1995

Major: Environmental Science

The following work is dedicated to my family
for their unwavering faith in me and constant moral support.

ACKNOWLEDGMENT

I want to extend my appreciation to my thesis advisor, Dr. Judith Weis, not only for the use of her laboratory and equipment, but most importantly for her guidance, and timely advice.

Special thanks to Dr. Richard Trattner and Dr. Peddrick Weis for serving as committee members, and to my friends and colleagues in the Dean of Student Services Office at the New Jersey Institute of Technology for their encouragement.

I would also like to thank those brave souls who laughed in the face of mosquitoes and biting flies, who volunteered their time and sacrificed their clean clothes in the process, all for the sake of science: David Capitaz, Catherine Cappello, and Steven Crumpton. They were a tremendous help to me in the field.

This research was funded in part by grants provided by the Rutgers University Marine Research Station, Tuckerton, New Jersey and also by Project SUPER (Stepping Up in the Physical Sciences, Engineering, and Research), offered through the Douglass Project, sponsored by Douglass College, Rutgers University.

TABLE OF CONTENTS

Chapter		Page
1	INTRODUCTION.....	1
1.1	Salt Marsh.....	1
1.1.1	Ecology of a Salt Marsh.....	1
1.1.2	Tidal Cycle.....	1
1.1.3	Detritus and Nutrient Cycling.....	2
1.2	<i>Palaemonetes pugio</i>	3
1.2.1	Distribution and Density.....	3
1.2.2	Ecological Importance.....	4
1.2.3	Life History.....	4
1.2.4	Growth.....	6
1.2.5	Environmental Requirements.....	6
1.2.6	Diet.....	7
1.2.7	Behavior.....	8
1.3	<i>Fundulus heteroclitus</i>	8
1.3.1	Distribution and Density.....	8
1.3.2	Ecological Importance.....	10
1.3.3	Diet.....	11
1.3.4	Behavior.....	11
1.4	Predator-prey Interactions Between <i>F. heteroclitus</i> and <i>P. pugio</i>	12
1.4.1	Prey Selectivity.....	12

TABLE OF CONTENTS
(Continued)

Chapter		Page
	1.4.1 Predation and Community Structure.....	13
	1.4.2 Effects of Pollution.....	15
	1.5 Objective.....	17
2	MATERIALS AND EXPERIMENTAL METHODS.....	19
	2.1 Study Sites.....	19
	2.1.1 Piles Creek.....	19
	2.1.2 Little Sheepshead Creek.....	19
	2.2 Temperature and Salinity.....	19
	2.3 Sampling Procedures.....	22
	2.3.1 <i>Fundulus heteroclitus</i>	22
	2.3.2 <i>Palaemonetes pugio</i>	22
	2.4 Statistical Procedures.....	23
3	RESULTS.....	25
	3.1 Temperature and Salinity.....	25
	3.2 <i>Fundulus heteroclitus</i>	25
	3.3 <i>Palaemonetes pugio</i>	30
	3.3.1 Total Collected.....	30
	3.3.2 Percent Ovigerous in Population.....	33
	3.3.3 Size Frequency Distribution.....	33
	3.3.4 Percent Young-of-the-Year in Population.....	35

TABLE OF CONTENTS
(Continued)

Chapter	Page
4	DISCUSSION..... 53
4.1	Environmental Conditions..... 53
4.1.1	Temperature and Salinity..... 53
4.1.2	Inherent Environmental Components..... 54
4.2	Reproductive Effort and Timing..... 55
4.3	Role of Competition..... 56
4.4	Role of Predation..... 57
5	CONCLUSION..... 59
	BIBLIOGRAPHY..... 61

LIST OF TABLES

Table	Page
1. Sampling Dates for Piles Creek and Little Sheepshead Creek.....	23
2. Weekly Temperature Measurements (°C).....	26
3. Weekly Salinity Measurements (‰).....	27
4. Total <i>F. heteroclitus</i> Collected Weekly from Piles Creek.....	28
5. Total <i>F. heteroclitus</i> Collected Weekly from Little Sheepshead Creek.....	29
6. Total <i>P. pugio</i> Collected Weekly from Piles Creek.....	31
7. Total <i>P. pugio</i> Collected Weekly from Little Sheepshead Creek.....	32
8. Percent Ovigerous Females in Population.....	33
9. <i>P. pugio</i> Mean Size Comparisons for Adults.....	37
10. <i>P. pugio</i> Mean Size Comparisons for Young-of-the-Year.....	38
11. Percent Young-of-the-Year in Population.....	39

LIST OF FIGURES

Figure	Page
1. Adult <i>Palaemonetes pugio</i> (Grass Shrimp).....	3
2. Adult <i>Fundulus heteroclitus</i> (Common Mummichog).....	10
3. Piles Creek (PC), Linden, New Jersey.....	20
4. Little Sheepshead Creek (LSC), Tuckerton, New Jersey.....	21
5. Weekly Temperature Measurements.....	26
6. Weekly Salinity Measurements.....	27
7. Week 1 Shrimp Lengths (May 28 th , 29 th).....	40
8. Week 2 Shrimp Lengths (June 5 th , 6 th).....	41
9. Week 3 Shrimp Lengths (June 10 th , 11 th).....	42
10. Week 4 Shrimp Lengths (June 18 th , 19 th).....	43
11. Week 5 Shrimp Lengths (June 24 th , 26 th).....	44
12. Week 6 Shrimp Lengths (July 8 th , 9 th).....	45
13. Week 7 Shrimp Lengths (July 15 th , 16 th).....	46
14. Week 8 Shrimp Lengths (July 23 rd , 24 th).....	47
15. Week 9 Shrimp Lengths (July 29 th , 30 th).....	48
16. Week 10 Shrimp Lengths (August 6 th , 7 th).....	49
17. Week 11 Shrimp Lengths (August 12 th , 13 th).....	50
18. Week 12 Shrimp Lengths (August 19 th , 20 th).....	51
19. September Shrimp Lengths (September 29 th , 30 th).....	52

CHAPTER 1

INTRODUCTION

1.1 Salt Marshes

1.1.1 Ecology of a Salt Marsh

Salt marshes are well known as highly variable environments where conditions such as salinity, temperature, turbidity, and oxygen concentration of the water can fluctuate rapidly, both temporally and spatially (Fernandez-Delgado 1989). They are also among the most productive estuarine environments in mid- to high- latitudes worldwide and, like other estuarine habitats, they function as nurseries for a variety of nektonic species (Boesch and Turner 1984).

Much of the intertidal marsh surface remains a very wet habitat even at low tide, when puddles and surface films of residual tidal water can serve as low-tide aquatic refuge for organisms small enough to use them (Kneib 1984, 1987b). At high tide; when marshes are inundated with water, the submerged vegetation provides a significant amount of cover and refuge for its inhabitants from predators and, consequently, enhances their survival (Heck and Thoman 1981, Vince et al. 1976).

1.1.2 Tidal Cycle

There are three essential components involved in salt marsh exchanges: water, vegetation, and soil (Troccaz et al. 1994). The tides coming in and out represent a nutrient supply, but may also export the diverse productions of the marsh. Boesch and Turner (1984) termed this “outwelling,” which means the flux of organic matter and nutrients into and out of salt marshes. In addition to the variation in nutrient and organic

matter cycling, it has been shown that the temperature of tidal water varies as well both seasonally and with the direction of the tidal flow (Valiela et al. 1977).

The densities of some organisms can change significantly during the spring tide¹ portion of the tidal cycle. Kneib (1984) noted that inundation time and frequency in the high intertidal zone are related to the lunar tidal cycle, with some areas being inundated longer and more frequently on spring than on neap tides.

1.1.3 Detritus and Nutrient Cycling

Salt marshes have long been recognized as highly productive areas with a negligible utilization of the living grasses, which die off and provide the energetic base for the detrital food chains dominating their associated creeks and embayments (Welsh 1975). Smooth cordgrass, *Spartina alterniflora*, is the predominant emergent vegetation commonly found in New Jersey salt marshes, including our study sites.

Detritus production and nutrient processing by salt marshes may contribute to the enrichment and regulation of estuarine food chains (Boesch and Turner 1984). Organic detritus in estuarine waters and sediments is composed primarily of small amorphous aggregates, much of which is not of obvious vascular origin (Welsh 1975, Boesch and Turner 1984). Direct utilization of estuarine vascular plants by herbivorous invertebrates seems to be rare (Teal 1962). Macroconsumers (i.e., mummichogs) gain nutrition predominantly from microbes and microfauna associated with the detritus rather than the plant material itself, which is found lacking in nutritional value (Prinslow et al. 1974). Odum and Heald (1975) reported that detritus was an important food resource for many young fishes, both directly and indirectly by sustaining prey species, but emphasized the

role of intermediate detritus consumers, such as small crustaceans (i.e., *Palaemonetes pugio*), in linking detritus and fish production (Welsh 1975).

1.2 *Palaemonetes pugio*

1.2.1 Distribution and Density

Palaemonetes pugio (Figure 1), commonly known as grass shrimp, are among the most widely distributed, abundant, and conspicuous of the brackish shallow, and intertidal benthic macroinvertebrates in the estuaries of the Atlantic and Gulf coasts (Wood 1967, Welsh 1975). They are found along the Atlantic and Gulf coasts of the United States from Massachusetts to southern Texas (Wood 1967, Welsh 1975). Nixon and Oviatt (1973) estimated adult low-tide densities of up to 212 shrimp/m² from a New England salt-marsh embayment (assuming shrimp were evenly distributed throughout the marsh at low tide). Other reports show that actual densities in certain areas may be considerably higher (i.e., shrimp can be as high as 800 shrimp/m² in local patches within seagrass beds as reported by Nelson 1981).

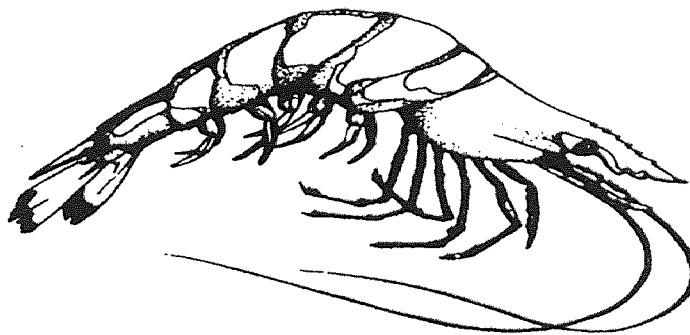


Figure 1 Adult *Palaemonetes pugio* (Grass Shrimp).

¹ Tides occurring near the time of the new and full moon, when the range of the tide is greatest

1.2.2 Ecological Importance

Ecologically speaking, *P. pugio* is a vital part of the estuarine community due to its role as an opportunistic omnivore in estuarine food webs (Welsh 1975, Morgan 1980, Kneib 1985, Posey and Hines 1991) and as prey of fishes (Kneib 1987a). Grass shrimp play a pivotal role in facilitating the transport of energy and nutrients between various estuarine trophic levels including primary producers, decomposers, carnivores, and detritivores (Welsh 1975, Morgan 1980). For instance, shrimp repackage their waste materials into protein-rich products that can be utilized by themselves or many other trophic levels. In laboratory experiments, Welsh (1975) showed that after 12 days, shrimp caused suspended particulate carbon to increase tenfold compared with tanks containing solely detritus or marsh water, and caused particulate nitrogen to increase even more so. They add stability to the energetic fluxes in the community as a whole and a greater efficiency to the food web (Welsh 1975).

1.2.3 Life History

The general spawning season of grass shrimp (*Palaemonetes* spp.) extends from March through October but varies with species and geographical location. For example, in Narragansett Bay, Rhode Island, spawning does not start until May and only lasts through mid-September (Welsh 1975) whereas in Galveston Bay, Texas, the breeding season continues from March through October (Alon and Stancyk 1984, Wood 1967).

Copulation occurs within 7 hours after molting. Ovigerous (pregnant) females of *Palaemonetes* spp. can carry as many as 486 eggs in one brood (Welsh 1975) and the eggs hatch anywhere between 12 to 60 days after fertilization which is also dependent on

species and geographical location. The female molts again within a few days after spawning and may produce an additional brood depending on the species or time of spawning as seen by Wood (1967) but not by Welsh (1975). In the case of a second spawning peak, the ovigerous female yields a smaller clutch than that exhibited earlier in the season (Wood 1967).

At hatching, grass shrimp are approximately 2.6 mm. in length (Broad 1957). Larvae are planktonic predators and feed upon zooplankton in addition to algae and detritus. Larval development may range from 11 days to several months, with the larvae experiencing anywhere between 7 to 12 molts, depending on environmental conditions. The final larval stage undergoes metamorphosis at about 6.3 mm. (Broad 1957), to become postlarvae, which closely resembles the adult.

Juvenile *P. pugio* mature when they are 1.5 to 2 months old (about 15 to 18 mm. in length). Welsh (1975) noted that when first retained in mid-July, juveniles comprised 20% of the total sample caught. By August, juveniles constituted over 99% of the total sample, indicating a rapid transition to a new year class. During late summer and fall, this density peak of *P. pugio* (especially juveniles) has been noted from Rhode Island to Texas (Nixon and Oviatt 1973, Welsh 1975, Wood 1967, Knowlton et al. 1994).

Most young-of-the-year spawn late in the year as adults. Postlarvae that survive the fall and winter, spawn in the following spring. Older, overwintering shrimp usually spawn early in the following year and die by next winter (Anderson 1985). *P. pugio*'s overall lifespan ranges anywhere from 6 to 13 months (Alon and Stancyk 1982).

1.2.4 Growth

In all populations studied, growth to adult size is most rapid during warmer months and considerably slower during colder periods (Wood 1967, Alon and Stancyk 1982, Nixon and Oviatt 1973, Welsh 1975). Estimated mean growth rates of young shrimp (9 to 15 mm.) were calculated to be as high as 0.268 ± 0.026 mm. d^{-1} during most of the year but slowed down significantly to 0.070 ± 0.032 mm. d^{-1} in the winter months in a Georgia intertidal marsh (Kneib 1987b). This rapid summer-time growth allows shrimp to reach reproductive size by July and August.

Overall mean size is smallest in the fall when bigger individuals have presumably died, peaks in spring, and decreases again in the summer when the smaller recruits join the population (Alon and Stancyk 1982). In addition to the difference in magnitude between the young and the adults, Welsh (1975) noted a significant distinction between the sexes of *P. pugio*. Females on average were 14% larger than males in the winter and up to 30% larger in the summer. Adult grass shrimp may reach a maximum size of up to 50 mm (Alon and Stancyk 1982).

1.2.5 Environmental Requirements

Variable salinity and temperature are probably the most important physical factors affecting grass shrimp (Morgan 1980, Wood 1967). *P. pugio*'s broad distribution is most likely due to its ability to tolerate wide fluctuations in salinity, temperature, and oxygen (Wood 1967, Welsh 1975). *P. pugio* larvae are metabolically active over a wide range of water temperatures, and display physiological adaptations in response to seasonal temperature fluctuations. Larvae survive best, mature earlier, and often pass through

fewer larval stages when salinities are near the optimum of 20 to 25 ppt. (Broad 1957). Because grass shrimp are eurythermal, *P. pugio* thrives at temperatures of 5 to 38°C (Wood 1967) in coastal waters, but survival is greater between 18 to 25°C. Growth is fastest when water temperatures are above 30°C but drops rapidly when water temperature falls below 14°C (Wood 1967).

Since grass shrimp are demersal, characteristics of the substrate may also be an important factor. *P. pugio* are commonly found on muddy substrates and are abundant where turbidity is relatively high. Knowlton et. al. (1994) reasoned that substrate selection is also influenced by salinity.

1.2.6 Diet

Based on the gut content analysis of *P. pugio*, it has been determined that they are opportunistic omnivores (Odum and Heald 1972). Evidence made available by Morgan (1980), indicates that *P. pugio*'s diet varies considerably depending on the particular type of aquatic food available. They may be detritivores (i.e., microflora), or secondary consumers (i.e., polychaetes). Kneib (1987a) found that adult grass shrimp, which are an important prey item in the diet of large killifish, *Fundulus heteroclitus* (Nixon and Oviatt 1973), can consume, and thus reduce the abundance of killifish larvae and potentially contribute to the control of one of their principal predators.

In a *Spartina* tidal marsh, *P. pugio* was found to feed primarily on *Spartina* detritus. In fact, feeding by *P. pugio* was the major pathway by which the detritus was made available to other consumers (Welsh 1975), however, alternative food experiments

imply that predation is preferred to grazing (Morgan 1980, Broad 1957). Moreover, the larval stages of *Palaemonetes* spp. are found to be obligate predators (Broad 1957).

1.2.7 Behavior

Adult grass shrimp living in tidal creeks migrate seaward (downstream) or drift with the current during ebb tides and migrate upstream into tidal creeks during incoming tides. *P. pugio* frequently inhabit areas near underwater structures and are prone to gravitate toward dense stands of underwater macrophytes, as demonstrated by Heck and Thoman (1981).

Tide height is an especially important factor in the number of large juvenile and subadult shrimp found in the intertidal marsh, with distributions expanding and contracting with changes in tidal amplitude (Kneib 1987b). There is a distinct difference in the use of the salt marsh habitat by young shrimp (< 20 mm.) and larger adults (> 25 mm.) at low tide. At low tide, the young are found in shallow aquatic microhabitats on the surface of the intertidal marsh, separated from the adults, which reside in adjacent subtidal creeks (Kneib 1987a). In the absence of submerged aquatic vegetation, adults remain in shallow depth zones (< 35 cm.) along the shoreline (Ruiz et al. 1993).

The intertidal zone appears to be the principal nursery environment for salt marsh populations of the grass shrimp (Kneib 1987b).

1.3 *Fundulus heteroclitus*

1.3.1 Distribution and Density

Fundulus heteroclitus (Figure 2); commonly known as the killifish and/or the mummichog, occurs in sheltered coastal waters along the Atlantic coast of North

America from Newfoundland to northern Florida and is especially characteristic of tidal marsh systems (Kneib 1986). Although occasionally occurring in freshwater (Samaritan and Schmidt 1982, Denoncourt et al. 1978), the species is best known from the tidal salt marsh, a relatively extreme physical environment for which mummichogs are well adapted (Bigelow and Schroeder 1953).

Many of the important predators in soft-substrate communities; such as the *Fundulus* spp., are highly mobile and their densities are difficult to assess. This is especially true in the intertidal zone where the area available to natant organisms fluctuates with the lunar and daily tidal cycles (Kneib 1984). However, it is the general consensus that populations of salt marsh killifish are very dense relative to most other fish within this habitat (Valiela et al. 1977). Nixon and Oviatt (1973) attempted to estimate adult *F. heteroclitus* low-tide densities using the assumption that organisms were evenly distributed and reported findings of 11 fish/m² in a New England salt-marsh embayment. Kneib and Wagner (1994) ascertained that the prospect of a uniform distribution was highly unlikely. Furthermore, Ruiz et al. (1993) found that mummichogs as well as grass shrimp had their peak densities in the shallowest zones, which deviates significantly from uniform distributions.

Many population studies have been performed using *F. heteroclitus*. Investigators agree that the species does not survive beyond a fourth growing season. In a study conducted by Samaritan and Schmidt (1982), young of the year accounted for 55% of the specimens collected in an August sample. Killifish in their second growing season constituted 27% of their sample, and those in their third growing season encompassed 18%. By October, the collections consisted entirely of juveniles. Their findings match

those of Valiela et al. (1977) who similarly noted not only the three yearly age classes; with the one year old class contributing to most of the biomass, but also concur with the disappearance of the older fish by October.

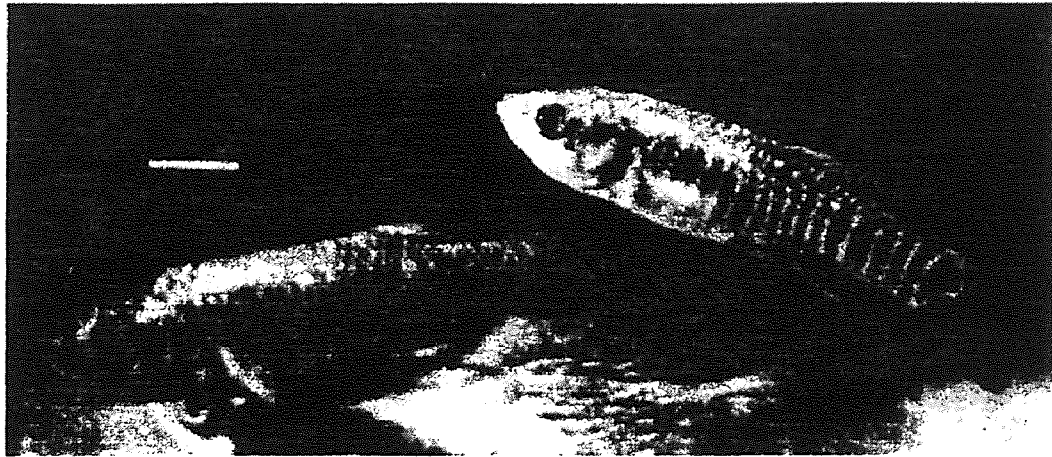


Figure 2 Adult *Fundulus heteroclitus* (Common Mummichog). The male is dark with light stripes; the female is light with dark stripes. (Bar = 1 cm.). (Weis and Weis 1989).

1.3.2 Ecological Importance

F. heteroclitus occupies an intermediate level trophic position within the structure of salt marsh communities on the east coast of the United States. *Fundulus* spp. also act as important prey items for organisms such as the blue crab, *Callinectes sapidus* (Kneib 1986), various birds, etc. The high annual production and mortality of mummichogs (Valiela et al. 1977) implies that they are important in the trophic dynamics of salt marshes.

Killifish are an important link in energy transfers between the marsh surface and the subtidal systems. They function as both predator and prey in the trophic structure of east coast tidal marshes (Nixon and Oviatt 1973, Kneib 1986). Additionally, their

movements on and off the marsh surface are thought to be an important aspect in the export of organic materials from the marsh surface (Valiela et al. 1977).

Lastly, killifish are economically significant due to their extensive use as bait by the recreational fishing industry as a result of their seemingly inexhaustible numbers.

1.3.3 Diet

Fundulus heteroclitus feed mainly on the marsh surface (Valiela et al. 1977) and primarily during daytime high tide. Daylight is an important component in their feeding schedule due to their being visual feeders (Weisberg et al. 1981).

The diet of adult *F. heteroclitus* is comprised primarily of small crustaceans (i.e., *Palaemonetes pugio*) and annelids (Kneib and Stiven 1978, Samaritan and Schmidt 1982) which account for 40% of their diets from May to June (Wiltse et al. 1984). Detritus and live plant material such as algae also constitute a major portion of the gut contents of fish leaving ditches as the tide ebbs. According to a number of authors, the ingestion of such material occurs incidentally in the course of foraging for small crustaceans and other fauna and is of little nutritional value to the fish (Prinslow et al. 1974, Kneib et al 1980, Kneib 1986, Allen et al. 1994). Weisberg (1981) indicated that subtidal food sources alone were insufficient to support the growth of *F. heteroclitus* at normal densities and that access to food in the vegetated intertidal marsh was essential to maintain the natural mummichog population.

1.3.4 Behavior

Unlike the adults, which can utilize the intertidal zone only when it is flooded, the young remain on the marsh even at low tide for 6 to 8 weeks, inhabiting shallow puddles of

residual tidal water that form between clumps of vegetation and around fiddler crab (*Uca* spp.) burrows (Kneib 1986).

Larger individuals of most species are among the first to reach high marsh sites on incoming tides and are often the first to leave on ebbing tides (Kneib and Wagner 1994). Adult killifish greater than 40 mm. in length follow flooding tides into tidal creeks of the salt marsh and, if the tide is high enough, move onto the marsh surface to feed (Valiela et al. 1977, Vince et al. 1976) but remain primarily within 25 m. of the creek's open water (Kneib and Wagner 1994). Fishes and crustaceans that move into the intertidal marsh early and leave late in the tidal cycle maximize their foraging time in this productive environment but face increased risk of being stranded the further they venture from permanent aquatic refuge (Gibson 1988). Larger individuals, because of their greater swimming abilities, penetrate farther into the vegetated marsh and may have a proportionately greater impact on high marsh prey species. Wright (1993) and Wiltse et al. (1984) concluded that feeding by *Fundulus* spp. probably has its greatest effect on marsh surface prey when the specific growth rate of the killifish is greatest and its population density is high.

1.4 Predator-Prey Interactions Between *F. heteroclitus* and *P. pugio*

1.4.1 Prey Selectivity

Experimental data provided by Vince et al (1976) has demonstrated that prey-selection behavior, mediated by the physical characteristics of salt marsh habitats, determines the abundance and spatial distribution of salt marsh invertebrates. Prey size preference changes with the size of the predator and is further complicated by habitat complexity.

Body size is clearly one of the most important characteristics of an organism from an ecological and evolutionary point of view. Size has a great influence on an animal's energetic requirements, its potential for resource exploitation, and its susceptibility to natural enemies (Werner and Gilliam 1984). The upper limit of the size of prey consumed increases with the increasing size of *F. heteroclitus*, and is most likely a function of the killifish's morphology. *Fundulus* spp. swallow their prey intact, so mouth gape is an important factor when feeding (Vince et al. 1976). Small fish feed mainly on the smallest size classes of grass shrimp, whereas medium fish feed equally upon small and medium shrimp. The largest fish, especially those >60 mm. (Kneib 1987a), feed on all three size classes of shrimp, but to a greater degree on those considered medium and large (Vince et al. 1976). One of the most important predators of *F. heteroclitus* in salt marshes may be the blue crab (*Callinectes sapidus*). Size selective predation by blue crabs on killifish can indirectly affect the structure of salt marsh benthic invertebrate assemblages such as *P. pugio* (Kneib and Stiven 1982).

1.4.2 Predation and Community Structure

There has been some controversy and disagreement over whether bottom-up forces (i.e., nutrient availability) or top-down forces (i.e., predators) predominate in populations and communities (Hunter and Price 1992). The relative importance of these two types of mechanisms varies among environments, and depends on external factors (i.e., nutrient supply rates, recruitment of specific consumers), as well as internal conditions (i.e., chemistry of producers, prey selectivity of predators) [Foreman et al. 1995].

Predation by fish can play a major role in structuring aquatic communities (Kerfoot and Sih 1987) by directly affecting mortality and size structure of the prey populations (Werner and Gilliam 1984). At the community and population levels, prey selection by predators can alter habitat selection behaviors of prey species as well as their abundance, size distributions and life histories, and consequently effect their prey indirectly as well. At the whole system scale, predator-prey interactions and their avoidance alters the community structure by either amplifying or dampening nutrient cycling rates and accelerating the exchange of nutrients among habitats (Paine 1980, Kitchell et al. 1994).

The predator-prey relationship is one of the strongest selection factors which contributes to the evolution of behavior (Csanyi and Doka 1993). Behavioral responses to predation involve changes in consumer diet and/or habitat use. Therefore it is possible that these changes can also be transmitted through the food web, as are changes in consumer numbers as demonstrated by the cascading effect described by Paine (1980). As predators grow and begin to feed upon macroinvertebrates, population sizes should drop dramatically, resulting in cycles of large amplitude (Heck and Orth 1980).

As a response to predation pressure, prey may avoid predators by shifting habitat use, reducing feeding rates, decreasing foraging distances, reducing movement, or changing their diel activity patterns (Turner and Mittlebach 1990). In experimental populations, Kneib (1987a) reported that small size classes react to the presence of predators by foraging in “safe” habitats, which were sometimes energetically less beneficial than those occupied by the predator.

Fundulus spp. and *Palaemonetes* spp. are often found in water less than one meter in depth, and are both known to utilize intertidal habitats with emergent vegetation (Kneib 1984, Boesch and Turner 1984) which provides refuge just as submerged aquatic vegetation does (Heck and Thoman 1981). Werner and Gilliam (1984) have shown that in freshwater fish, the young of many species are confined to macrovegetation or similar cover due to predation risk, but move into more open habitats and diverge in niche as they grow larger.

In the absence of submerged aquatic vegetation, grass shrimp prefer shallow water in the presence of fish predators, supporting the common belief that shallow water also provides refuge from predation for mobile epibenthic fauna. This was confirmed by Posey and Hines (1991) in both laboratory and field experiments in which shrimp occurred in all depth zones in the absence of predators; however, when killifish were introduced, shrimp quickly shifted to the shallowest zones. A study done by Ruiz et al. (1993) reported that both *F. heteroclitus* and *P. pugio* are found most frequently in the shallow zone (15 to 20 cm.) and significantly less in the mid and deep zones (60 to 80 cm.). For fish and shrimp, mortality in the deepest zone was much greater (80%) compared to that found in the shallowest zone (20 to 45%).

1.4.3 Effects of Pollution

Behavioral effects of toxic contaminants may have profound effects on an organism's ability to obtain live food, avoid predation, and reproduce successfully in its natural environment. Environmental stress often results in low predation pressure because predators are either rare or very inefficient (Kerfoot and Sih 1987) in these areas.

Some heavy metals are among the most harmful of the elemental pollutants with mercury being one of the most toxic metals to aquatic organisms. Bacteria living in aquatic sediments have the ability to biotransform inorganic mercury into methylmercury (Jenson and Jernelov 1969) which is known to accumulate in fishes' brains (Backstrom 1969).

Toppin et al. (1987) have shown that killifish from a polluted or "stressed" waterway; Piles Creek (PC), in Linden, New Jersey, showed reduced rates of growth, fin regeneration, and longevity compared to killifish from uncontaminated reference sites, rarely living beyond 3 years of age. Weis and Weis (1989) supported this observation when they reported that female PC fish were significantly smaller than those found in an unpolluted reference site of the same year class. Furthermore, Weis and Khan (1990) established that exposure to mercury significantly reduced prey capture ability of the PC mummichogs, and later reported that PC fish were not as effective at catching prey than killifish studied from a cleaner environment (Weis and Khan 1991).

In studies by Smith and Weis (in press), it was noted that PC mummichogs were generally much less energetic in their pursuit of prey, namely grass shrimp. Their experiment revealed that it was irrelevant whether the shrimp used were from PC or taken from a more pristine reference site, Sheepshead Creek (SC), in Tuckerton, New Jersey. According to gut content analysis, PC fish had a less varied and less nutritious diet than did SC fish, with detritus constituting 85% of their diet (versus 41% in SC). *P. pugio* accounted for only 12% of the gut contents weight in PC fish versus 25% in SC fish. As a consequence of their reduced motor skills, PC mummichogs were also more vulnerable to predation (Smith and Weis in press).

Additionally, during the course of their research, Smith and Weis (in press) noted that in general, *P. pugio* located in PC were larger than those seen at SC.

1.5 Objective

The obvious inconsistencies described by Smith and Weis (in press) in the predator-prey relationships between the two populations of *F. heteroclitus* and *P. pugio* at PC and SC need to be addressed. The repercussions caused by a shift in the predator-prey relationship may affect the trophic structure and, ultimately, the entire community. The observation of larger shrimp at PC has prompted the hypothesis that they have grown larger due to reduced predation as a result of the impaired behavior exhibited by their main predator, the killifish.

There are several other feasible explanations for the observed difference in length of grass shrimp between SC and PC. SC shrimp may be smaller as a response to factors such as overcrowding and/or increased competition. Size-selective predation could limit the number of adult shrimp from ultimately reaching their maximum length; and SC shrimp may be preyed upon more frequently due to a greater number of predators present. Another possibility is that there are inherent components lacking in SC, yet pronounced within PC's environment such as excess nutrients, optimum temperature and/or salinity, etc., that may stimulate growth. Lastly, there may be a significant difference in reproductive effort between the two sites with PC starting earlier than SC, which would give PC a "jump start" and allow a prolonged period of growth.

My primary objectives are to: 1) try to determine whether *P. pugio* is in fact larger at PC than at SC, and 2) look at the relative numbers of the two species and try to

determine whether it is due to reduced predation pressure on *P. pugio* by *F. heteroclitus* as a consequence of impaired predatory ability. In order to accomplish said objectives, it is necessary to ascertain the relative numbers of *F. heteroclitus* and *P. pugio* at the two sites. Therefore, I took representative samples of each species from the two populations (PC and SC) for quantitative comparison over a period of 4 months - once a week for 12 weeks and a single visit again 4 weeks later as a follow-up to monitor the young-of-the-year (YOY) shrimp population's progress.

CHAPTER 2

MATERIALS AND EXPERIMENTAL METHODS

2.1 Study Sites

2.1.1 Piles Creek

The polluted study site, Piles Creek (PC), is a polluted tributary of the Arthur Kill located in Linden, New Jersey (Figure 3). PC is surrounded by industrial sites, a sewage treatment plant, a power plant, and a major highway, the New Jersey Turnpike. There is limited freshwater flow into the area and, as a result, both the sediments and the organisms living within the creek have high concentrations of heavy metals and other pollutants. Analyses have revealed mercury (10 to 20 $\mu\text{g g}^{-1}$), cadmium (5.8 $\mu\text{g g}^{-1}$), copper (623 $\mu\text{g g}^{-1}$), and other contaminants in PC sediments (Khan et al. 1989). PC also contains organic contaminants from oil spills in the Arthur Kill and other sources.

2.1.2 Little Sheepshead Creek

Little Sheepshead Creek (LSC) was used as the unpolluted reference site, located in non-industrialized Tuckerton, New Jersey (Figure 4). Khan et al. (1989) reported low sediment levels of contaminants such as mercury (0.054 $\mu\text{g g}^{-1}$), cadmium (0.13 $\mu\text{g g}^{-1}$), and copper (12.9 $\mu\text{g g}^{-1}$).

2.2 Temperature and Salinity

Water temperature readings were taken from each of the creeks and were recorded weekly at both sites using a digital temperature probe. Additionally, specific gravity measurements were taken, using a hydrometer, and converted to salinity (‰).

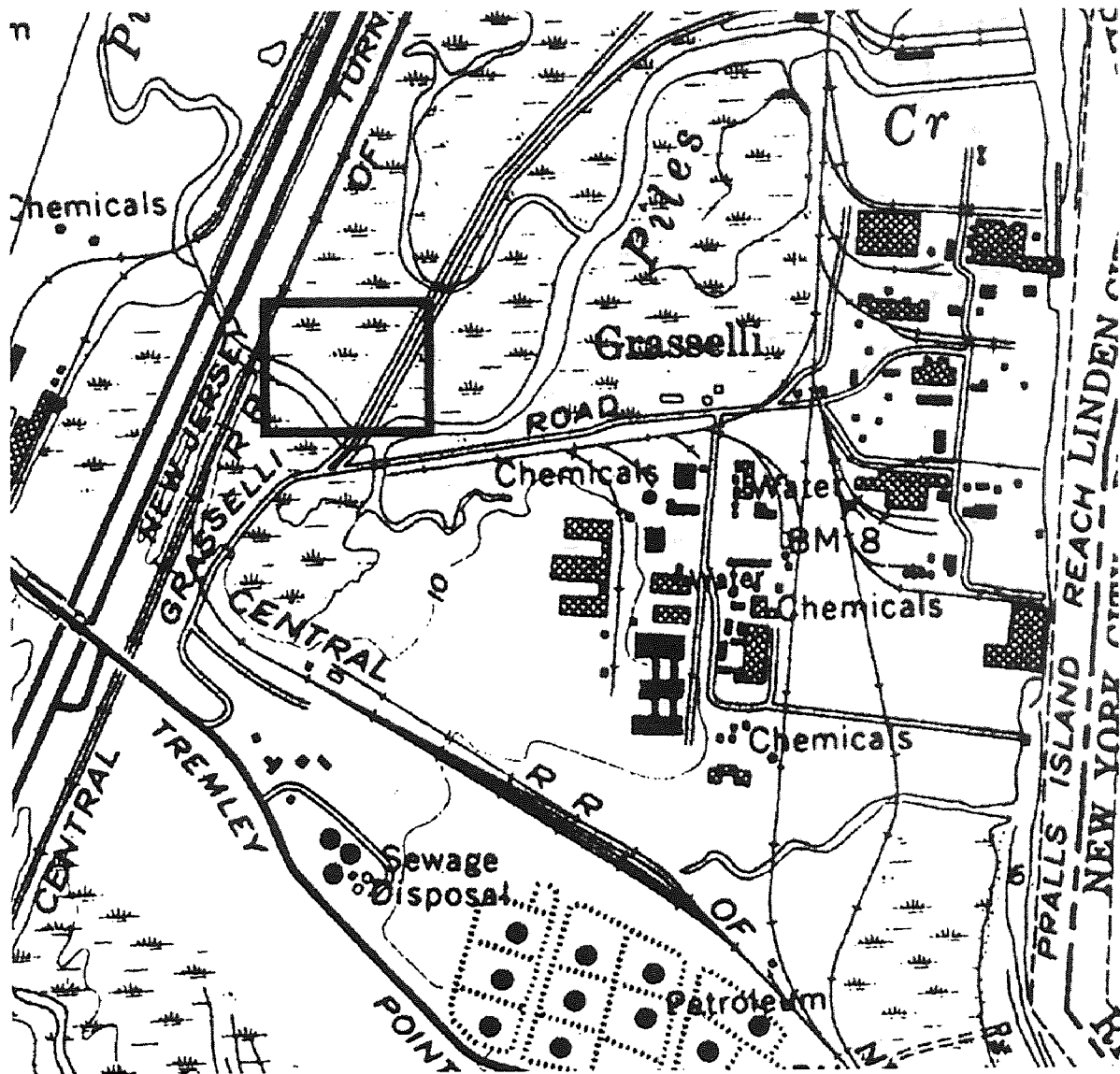


Figure 3 Piles Creek (PC), Linden, New Jersey. The sampling area (enclosed by the rectangle) is located adjacent to the New Jersey Turnpike and feeds into the Arthur Kill estuary. PC is highly industrialized and is laden with heavy metals, organics and other pollutants.

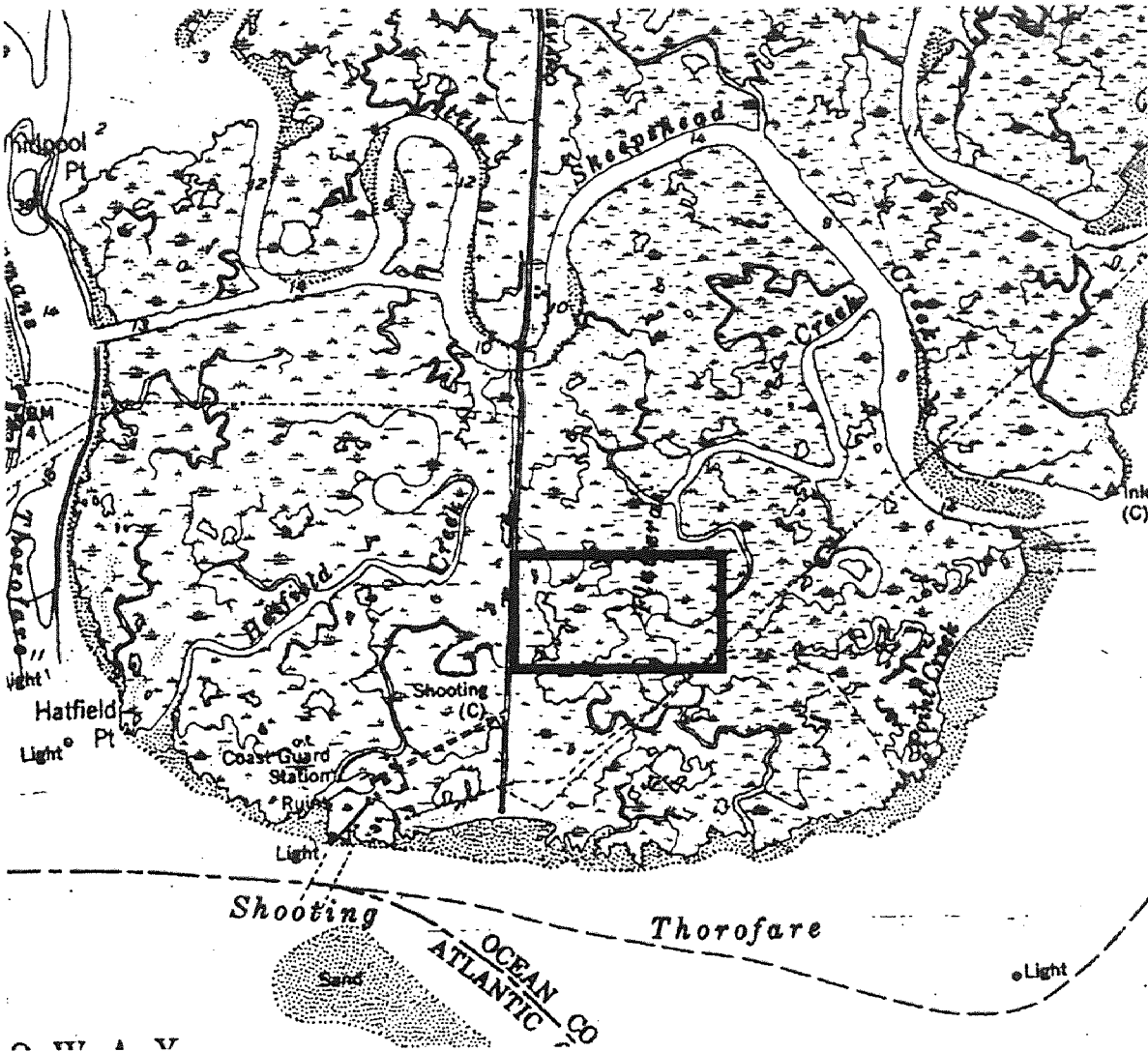


Figure 4 Little Sheepshead Creek (LSC), Tuckerton, New Jersey. The sampling area (enclosed by the rectangle), is located at the northern entrance to Great Bay. It is the site of a large tract of pristine marsh and a major estuary that retains most of its natural characteristics.

2.3 Sampling Procedures

Both PC and LSC were visited once weekly for data collection purposes as detailed in Table 1. A follow-up visit was made 4 weeks later in September to monitor the YOY shrimp population. At that time, no samples were taken of killifish, nor were temperature and salinity readings recorded.

2.3.1 *Fundulus heteroclitus*

Five standard, wire mesh (stainless steel) minnow traps were placed for a one-hour period each week for twelve weeks to obtain catch-per-unit-effort data. Data was collected during daylight, three to four hours before high tide. Approximately one-half cup of dried cat food was placed inside the traps and used as bait. The opening to the trap was placed into the flow of the current alongside the creek bank. The same locations (numbered 1 through 5) were used consistently throughout the study for each site. Mummichogs were then placed into water-filled buckets, counted and returned to their respective populations.

2.3.2 *Palaemonetes pugio*

Five umbrella nets were used to collect the grass shrimp weekly for a twelve week period in order to obtain catch-per-unit-effort data. Data was collected during daylight, three hours before high tide. The square nets (side = 106.68 cm.), had a 5.0 mm. mesh. They were placed on the shallow edge of the unvegetated creek bed and were left undisturbed for fifteen minutes.

Captured shrimp were placed into water-filled buckets and were measured to the closest 2.5 mm. from the anterior end of the rostrum to the posterior edge of the telson.

Table 1 Sampling Dates² for Piles Creek and Little Sheepshead Creek

	Piles Creek	Little Sheepshead Creek
Week 1	May 29	May 28
Week 2	June 5	June 6
Week 3	June 10	June 11
Week 4	June 19	June 18
Week 5	June 24	June 26
Week 6	July 8	July 9
Week 7	July 15	July 16
Week 8	July 23	July 24
Week 9	July 29	July 30
Week 10	August 7	August 6
Week 11	August 13	August 12
Week 12	August 19	August 20
September	September 29	September 30

In addition to recording individual measurements, the number of ovigerous females caught were also noted (by presence of egg mass) and recorded. All shrimp were returned to their natural population after measurement.

2.4 Statistical Procedures

The two sample t-test (t) and the non-parametric Mann-Whitney (rank sum) test (U) were executed employing the Statistix[®] 3.5 software program on an IBM compatible personal

² All sampling was done in 1996

computer. It was necessary to employ both tests by virtue of the fact that data could not be assumed to have a normal distribution.

CHAPTER 3

RESULTS

3.1 Temperature and Salinity

Water temperature (Table 2) for PC ranged from a low of 19 to a high of 27° C, with a mean of $\approx 24^{\circ}\text{C}$ ($\pm 0.701\text{ SE}^1$). LSC ranged from 13 to 29° C, with a mean of $\approx 22^{\circ}\text{C}$ ($\pm 1.416\text{ SE}$). Salinity (Table 3) ranged from 9 to 21 ‰ in PC (mean $\approx 15\text{ ‰}$, $\pm 1.048\text{ SE}$) and from 12 to 38 ‰ in LSC (mean $\approx 28\text{ ‰}$, $\pm 2.240\text{ SE}$).

Using the two sample t-test, it was determined that there is no significant difference between the temperatures reported for each site ($t = 0.79$, $P = 0.437$). However, it was determined that there was a significant difference found between the two sites with regard to salinity ($t = <5.19>^2$, $P = 0.000$).

3.2 *Fundulus heteroclitus*

Over the course of the twelve week sampling period (12 data points), a total of 3,048 killifish were caught in PC [mean = $254\text{ wk.}^{-1} \pm 40.6\text{ SE}$] (Table 4) in addition to 8,963 that were caught at LSC [mean = $747\text{ wk.}^{-1} \pm 49.1\text{ SE}$] (Table 5). This represents nearly a three-fold difference between the two sites and is deemed highly significant using the two sample t-test ($t = <7.74>$, $P = 0.000$), as well as the Mann-Whitney test ($U = 1.000$ [PC], $U = 143.0$ [LSC], $P = 0.000$). Additionally, the two sample t-test and the Mann-Whitney test were used to evaluate the number caught in each trap (60 data points), or catch per unit effort, at PC (mean = $51 \pm 5.9\text{ SE}$) and LSC ($149 \pm 82.8\text{ SE}$). The results

¹ *SE = standard error*

² *< > represents a negative value*

Table 2 Weekly Temperature Measurements (°C)

	Wk 1	Wk 2	Wk 3	Wk 4	Wk 5	Wk 6	Wk 7	Wk 8	Wk 9	Wk 10	Wk 11	Wk 12	Avg
PC	25	19	25	23	23	27	24	22	20	26	23	26	24
LSC	13	18	18	19	26	27	25	21	24	29	20	28	22

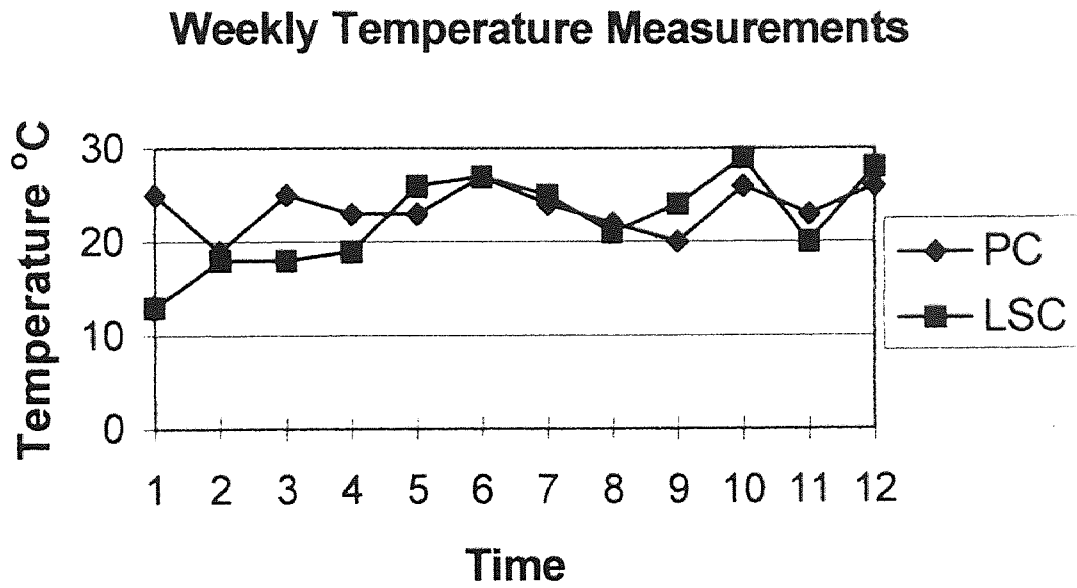
**Figure 5** Weekly Temperature Measurements

Table 3 Weekly Salinity Measurements (‰)

	Wk 1	Wk 2	Wk 3	Wk 4	Wk 5	Wk 6	Wk 7	Wk 8	Wk 9	Wk 10	Wk 11	Wk 12	Avg
PC	19	15	9	17	15	21	10	18	15	14	19	13	15
LSC	38	31	31	23	34	30	34	29	31	31	12	15	28

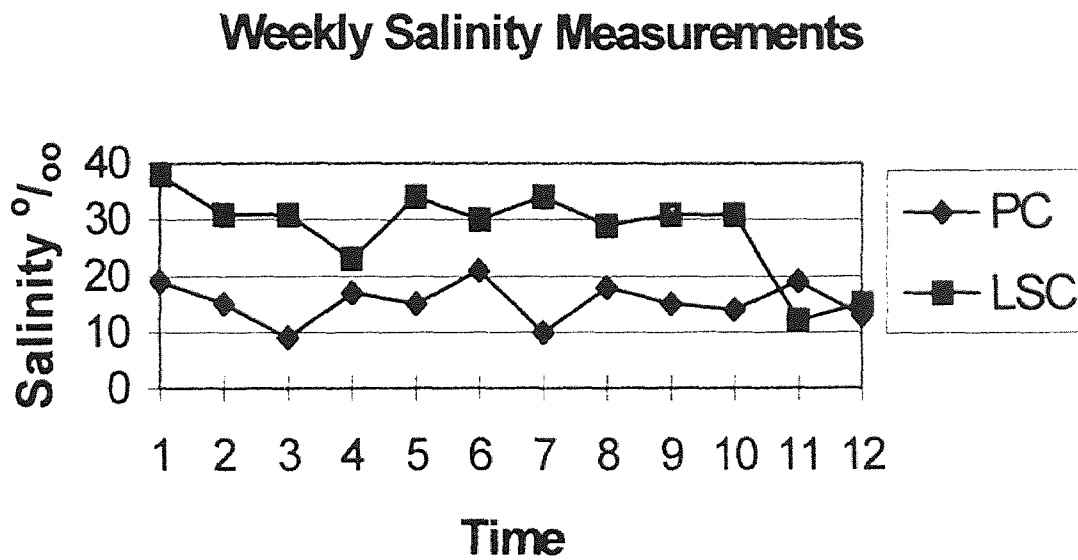
**Figure 6** Weekly Salinity Measurements

Table 4 Total *F. heteroclitus* Collected Weekly From Piles Creek

	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12	Total
1	61	26	17	61	91	14	19	93	1	166	70	135	754
2	0	95	13	59	3	2	44	3	61	7	29	154	470
3	45	68	66	49	97	40	34	91	11	190	82	40	813
4	0	4	16	2	50	33	20	39	41	42	36	104	387
5	35	17	98	64	158	15	2	38	2	134	44	17	624
Total	141	210	210	235	399	104	119	264	116	539	261	450	3048

Table 5 Total *F. heteroclitus* Collected Weekly From Little Sheephead Creek

	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12	Total
1	79	122	120	21	225	14	92	136	222	133	4	113	1281
2	283	187	0	264	133	129	185	238	12	290	405	210	2336
3	49	162	186	183	157	109	139	185	174	218	63	140	1765
4	206	334	183	151	202	111	54	112	158	186	85	102	1884
5	123	230	181	236	83	196	19	30	160	230	126	83	1697
Total	740	1035	670	855	800	559	489	701	726	1057	683	648	8963

were similar ($t = 8.04$, $U = 555.0$ [PC], $3.045E+3$ [LSC], $P = 0.000$) to that found per week (12 data points).

3.3 *Palaemonetes pugio*

3.3.1 Total Collected

A total of 2,628 [mean = $202 \text{ wk.}^{-1} \pm 38.8 \text{ SE}$] grass shrimp were taken in PC (Table 6) and merely 968 in LSC [mean = $74 \text{ wk.}^{-1} \pm 15.2 \text{ SE}$] (Table 7). A two sample t-test ($t = 3.07$, $P = 0.001$) as well as the Mann-Whitney test ($U = 131.5$ [PC], $U = 37.50$ [LSC], $P = 0.017$) were used to calculate the significance between each individual week and the September sample (13 data points). The resulting data represented a significant difference between the PC site and that of LSC. Additionally, these two tests were used to evaluate the number caught in each trap (65 data points), or catch per unit effort, at PC (mean = $40 \pm 6.6 \text{ SE}$) and LSC (mean = $15 \pm 2.7 \text{ SE}$). The results for both the t-test ($t = 3.60$, $P = 0.001$) and the Mann-Whitney ($U = 2.759E+3$ [PC], $U = 1.466E+3$ [LSC], $P = 0.003$) were comparable to those calculated per week. As with *F. heteroclitus*, there was a difference of approximately 3:1 between the two populations, however, the larger number of *P. pugio* were collected in PC whereas the larger number of *F. heteroclitus* were taken in LSC.

The total weekly number of shrimp that were caught was highly variable throughout the sampling period for LSC ranging from a low of 9 (week 3) to a high of 177 (week 4). PC showed less variation in the weekly number of shrimp caught after reaching a peak in week 5 (total = 473).

Table 6 Total *P. pugio* Collected Weekly From Piles Creek

Net #	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12	Sept	Total
1	3	3	7	0	9	112	62	83	5	156	157	45	16	658
2	7	15	12	31	140	93	83	73	0	38	86	139	114	831
3	1	7	25	51	85	37	17	42	156	17	15	85	7	545
4	2	0	1	0	234	0	3	33	40	14	3	147	48	525
5	1	3	10	6	5	5	6	1	3	13	3	13	0	69
Total	14	28	55	88	473	247	171	232	204	238	264	429	185	2628

Table 7 Total *P. pugio* Collected Weekly From Little Sheepshead Creek

Net #	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12	Sept	Total
1	0	0	6	106	0	4	2	11	4	0	6	77	4	220
2	27	0	0	0	8	4	5	4	12	0	0	48	12	120
3	6	3	0	0	0	24	6	31	48	20	32	49	3	222
4	0	12	3	0	56	10	49	5	8	3	16	2	16	180
5	0	0	0	71	28	11	27	6	48	11	4	0	20	226
Total	33	15	9	177	92	53	89	57	120	34	58	176	55	968

3.3.2 Percent Ovigerous in Population

Ovigerous grass shrimp were observed at both sites at the same time in the sampling period (week 3). 165 (18%) ovigerous females were recorded in LSC and 495 (20%) in PC during weeks 3 through 12 (Table 8). The follow-up in September yielded no ovigerous females from either site. Data on ovigerous females for weeks 1 and 2 are not included as observations were not instituted until week 3.

Table 8 Percent Ovigerous Females in Population

	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
PC	29	13	35	19	2	14	44	13	27	4
LSC	11	47	25	46	17	4	10	0	0	1

3.3.3 Size Frequency Distribution

Weeks 1 through 6 were dominated by the previous year's overwintering shrimp, ranging in length from 20 to 50 mm. at both locations as seen in Table 9 and Figures 7 through 12. During the first 6 weeks, overall shrimp length means were between 32 mm. (± 0.849 SE) and 41 mm. (± 0.077 SE) whereas in LSC, the overall shrimp length means fell between 27 mm. (± 2.093 SE) and 38 mm. (± 0.705 SE). Significant differences in mean length ($P < 0.050$) were calculated individually for weeks 1 through 3, and weeks 5 and 6. In week 6, the greater mean was in LSC (mean = 38 ± 0.706 SE) rather than PC (35 ± 0.355 SE). Week 4 had no calculated difference in mean shrimp length and in total, PC means were larger than LSC for weeks 1, 2, 3, and 5.

It wasn't until week 7 that the YOY recruited into the population (Table 10 and Figures 13 through 19) with means of 12 mm. (± 1.453 SE) and 17 mm. (± 0.344 SE) in PC and LSC respectively. The two sample t-test and the Mann-Whitney test also calculated significant differences in mean shrimp lengths ($P = 0.000$) for week 7 with respect to both YOY ($t = <4.06>$, $U = 4.000$ [PC], $u = 56.00$ [LSC]) and adults ($t = <4.95>$, $U = 4.223E+3$ [PC], $u = 7.577E+3$ [LSC]), however, the greater mean was in LSC (17 ± 0.344 SE), not PC (12 ± 1.453 SE). Thereafter, in weeks 8 through 12 together with the September sample, PC grass shrimp remained larger than LSC with significant differences ($P < 0.050$) in adult lengths.

Results for YOY differed slightly. As the young-of-the-year continued to grow, it became increasingly more difficult to make the distinction between new recruits and last year's population. Often times, there was no distinct cut-off in size distribution discernible between cohorts introduced into the population this year and the older shrimp from the previous year for the majority of the sampling period in both PC and LSC. The problem of distinguishing between young and old cohorts was circumvented through the use of growth rate data provided by G. Smith, who determined the growth rate of YOY *P. pugio* ($\cong 17$ to 23 mm.) to be 0.163 mm. d^{-1} in PC and 0.153 mm. d^{-1} in LSC in a preliminary study.

In order to determine the cut-off point between the YOY and the previous year's shrimp, I started with week 7 when the first YOY were detected. I then used the results from G. Smith's preliminary study and calculated the growth rate based on a 20 mm. shrimp. I used 20 mm. as a reference point for both sites because that was the largest sized YOY that initially recruited into the population. Week 8's upper limit was

calculated to be 21 mm., with week 9 increasing to 22 mm. Week 10's cut-off point was figured to be 23 mm. The growth rates for weeks 11 and 12 were 25 mm. in PC, and 24 and 25 mm. in LSC for the same two weeks.

The two sample t-test was ineffective in weeks 8 and 9 due to a very small sample size in PC (N = 1). However, using the Mann-Whitney test, there was no calculated significant difference in mean lengths between PC (U = 3.000) and LSC (U = 24.00) for week 8 (P = 0.216). There was also no significant difference (P = 0.762) found for week 9 (U = 15.50 [PC], U = 23.50 [LSC]). Although there was a significant difference (P < 0.050) found in week 7 between the YOY mean lengths, it should be deemed inconclusive by virtue of the fact that the PC population of YOY were not accurately represented (N = 3) in comparison to that of LSC (N = 20). Week 10, week 12, and the September sample showed no significant differences (P > 0.050) in YOY shrimp lengths. Week 11 was the only sample that reported significant differences (P = 0.004 {t}, P = 0.010 {u}) in YOY mean shrimp lengths between PC (21 ± 0.866 SE) and LSC (19 ± 0.462 SE) using both the two sample t-test (t = 3.07) and the Mann-Whitney test (U = 436.5 [PC], U = 1.546E+4 [LSC]).

3.3.4 Percent Young-of-the-Year in Population

The percentage of YOY shrimp in the total population were calculated for both sites in Table 11. LSC consistently had an overwhelming percentage of YOY from the time they recruited into the population in week 7 through week 12. The number of YOY in LSC ranged from a low of 22% in week 7, to a high of 91% in week 12. PC had considerably

fewer (< 1% to 48%) YOY grass shrimp relative to the total population for the same period. PC had the largest percentage (78% vs. 60%) in the September sample.

Table 9 *P. pugio* Mean Size Comparisons for Adults

WEEK	SITE	N	MEAN	S.E.	T-VALUE	U-VALUE	P VALUE ⁵
1	PC	14	36	0.975	2.06	330.0	0.045 (t)
	<i>LSC</i>	33	32	<i>1.215</i>		<i>132.0</i>	0.022 (u)
2	PC	28	41	0.708	8.28	406.0	0.000 (t)
	<i>LSC</i>	15	30	<i>1.046</i>		<i>14.00</i>	0.000 (u)
3	PC	55	32	0.850	2.09	345.5	0.040 (t)
	<i>LSC</i>	9	27	<i>2.093</i>		<i>149.5</i>	0.059 (u)
4	PC	88	33	0.454	<1.60>	6.333E+3	0.112 (t)
	<i>LSC</i>	177	34	<i>0.453</i>		<i>6.244E+3</i>	0.013 (u)
5	PC	473	35	0.251	4.96	2.846E+4	0.000 (t)
	<i>LSC</i>	92	32	<i>0.477</i>		<i>1.505E+4</i>	0.000 (u)
6	PC	247	35	0.355	<4.23>	4.081E+3	0.000 (t)
	<i>LSC</i>	53	38	<i>0.706</i>		<i>9.011E+3</i>	0.000 (u)
7	PC	171	32	0.301	<4.95>	4.223E+3	0.000 (t)
	<i>LSC</i>	69	36	<i>0.073</i>		<i>7.577E+3</i>	0.001 (u)
8	PC	232	34	0.291	3.26	4.532E+3	0.001 (t)
	<i>LSC</i>	30	32	<i>0.987</i>		<i>2.428E+3</i>	0.007 (u)
9	PC	203	37	0.437	5.00	1.116E+4	0.000 (t)
	<i>LSC</i>	81	33	<i>0.755</i>		<i>5.283E+3</i>	0.000 (u)
10	PC	146	35	0.479	5.33	1.564E+3	0.000 (t)
	<i>LSC</i>	11	26	<i>0.472</i>		<i>42.00</i>	0.000 (u)
11	PC	245	36	0.367	2.72	4.120E+3	0.007 (t)
	<i>LSC</i>	26	32	<i>1.397</i>		<i>2.250E+3</i>	0.014 (u)
12	PC	222	33	0.300	2.01	2.299E+3	0.046 (t)
	<i>LSC</i>	15	31	<i>.213</i>		<i>1.032E+3</i>	0.014 (u)
[SEPT]	PC	28	38	0.612	3.33	476.5	0.002 (t)
	<i>LSC</i>	22	36	<i>0.393</i>		<i>139.5</i>	0.001 (u)

⁵ (t)=P-value for t-test, (u)=P-value for Mann-Whitney test

Table 10 *P. pugio* Mean Size Comparisons for Young-of-the-Year

WEEK	SITE	N	MEAN	S.E.	T-VALUE	U-VALUE	P VALUE
7	PC	3	12	1.453	<4.06>	4.000	0.000 (t)
	LSC	20	17	0.344		56.00	0.020 (u)
8	PC	1	15	+++ ⁶	+++	3.000	+++ (t)
	LSC	27	18	0.444		24.00	0.216 (u)
9	PC	1	20	+++	+++	15.50	+++ (t)
	LSC	39	20	0.218		23.50	0.762 (u)
10	PC	92	21	0.133	1.39	1.089E+3	0.164 (t)
	LSC	23	20	0.487		1.027E+3	0.831 (u)
11	PC	19	21	0.866	3.07	436.5	0.003 (t)
	LSC	32	19	0.462		171.5	0.010 (u)
12	PC	207	22	0.165	1.30	1.787E+4	0.196 (t)
	LSC	161	22	0.208		1.546E+4	0.234 (u)
SEPT	PC	145	29	0.307	0.56	2.340E+3	0.577 (t)
	LSC	33	28	0.838		2.445E+3	0.846 (u)

⁶ +++ Data not available due to small sample size

Table 11 Percent Young-of-the-Year in Population

WEEK	SITE	# YOY	N	%
7	PC	3	171	2
	<i>LSC</i>	<i>20</i>	<i>89</i>	<i>22</i>
8	PC	1	232	< 1
	<i>LSC</i>	<i>27</i>	<i>57</i>	<i>47</i>
9	PC	1	204	< 1
	<i>LSC</i>	<i>39</i>	<i>120</i>	<i>33</i>
10	PC	92	238	39
	<i>LSC</i>	<i>23</i>	<i>34</i>	<i>68</i>
11	PC	19	264	7
	<i>LSC</i>	<i>32</i>	<i>58</i>	<i>55</i>
12	PC	207	429	48
	<i>LSC</i>	<i>161</i>	<i>176</i>	<i>91</i>
SEPT	PC	145	173	84
	<i>LSC</i>	<i>33</i>	<i>55</i>	<i>60</i>

Week 1 Shrimp Lengths

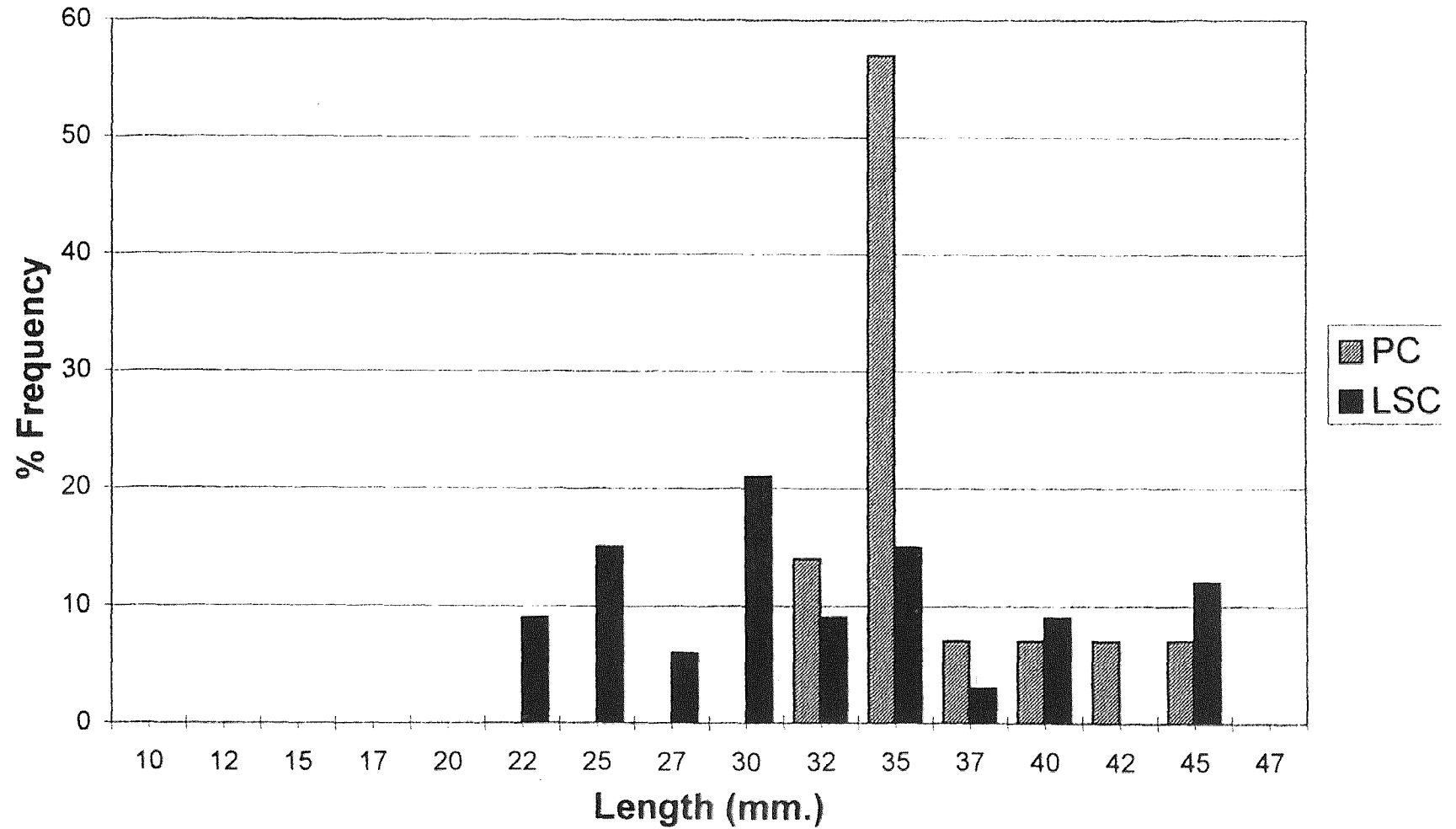


Figure 7 Week 1 Shrimp Lengths (May 28th, 29th)

Week 2 Shrimp Lengths

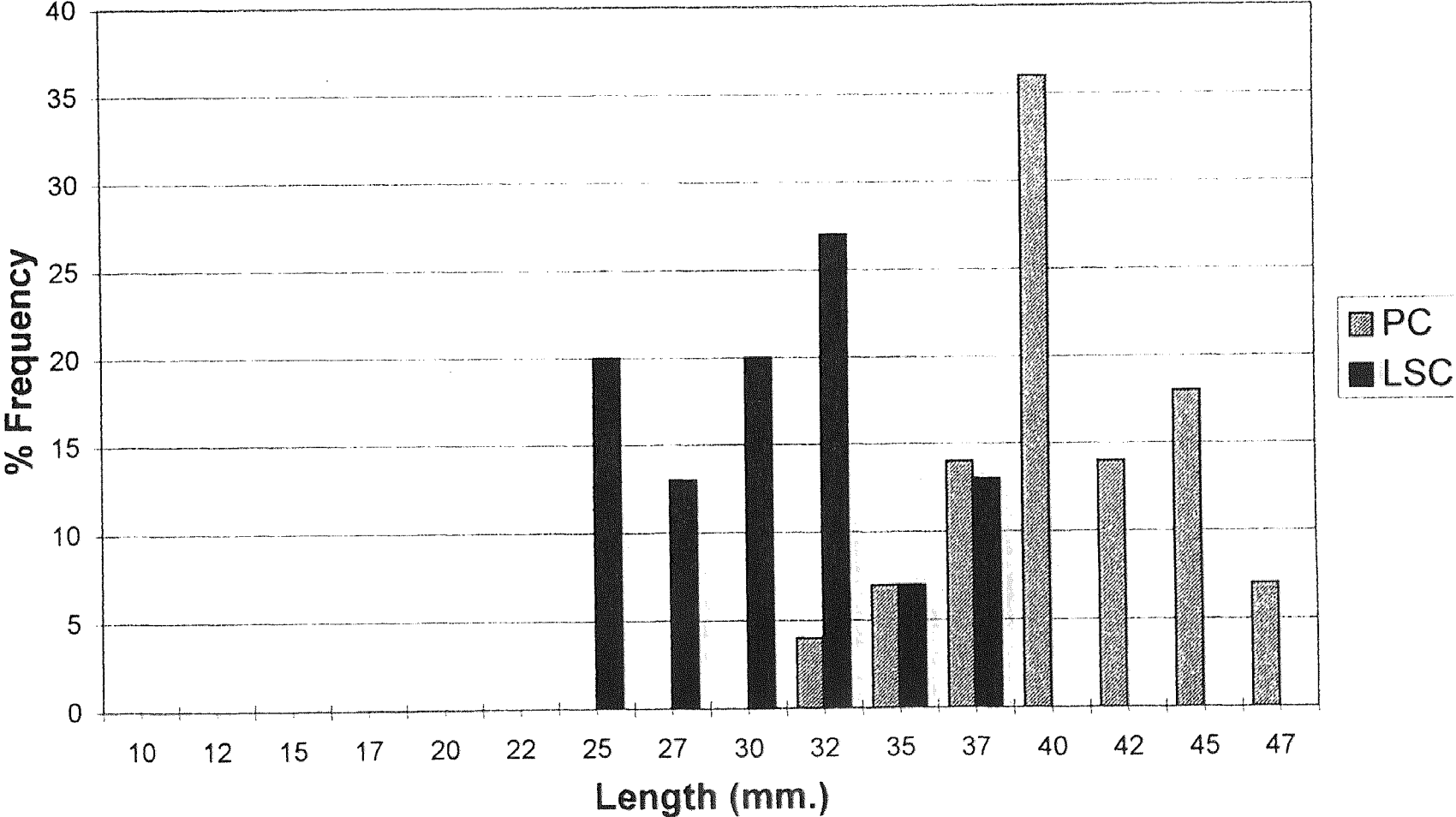


Figure 8 Week 2 Shrimp Lengths (June 5th, 6th)

Week 3 Shrimp Lengths

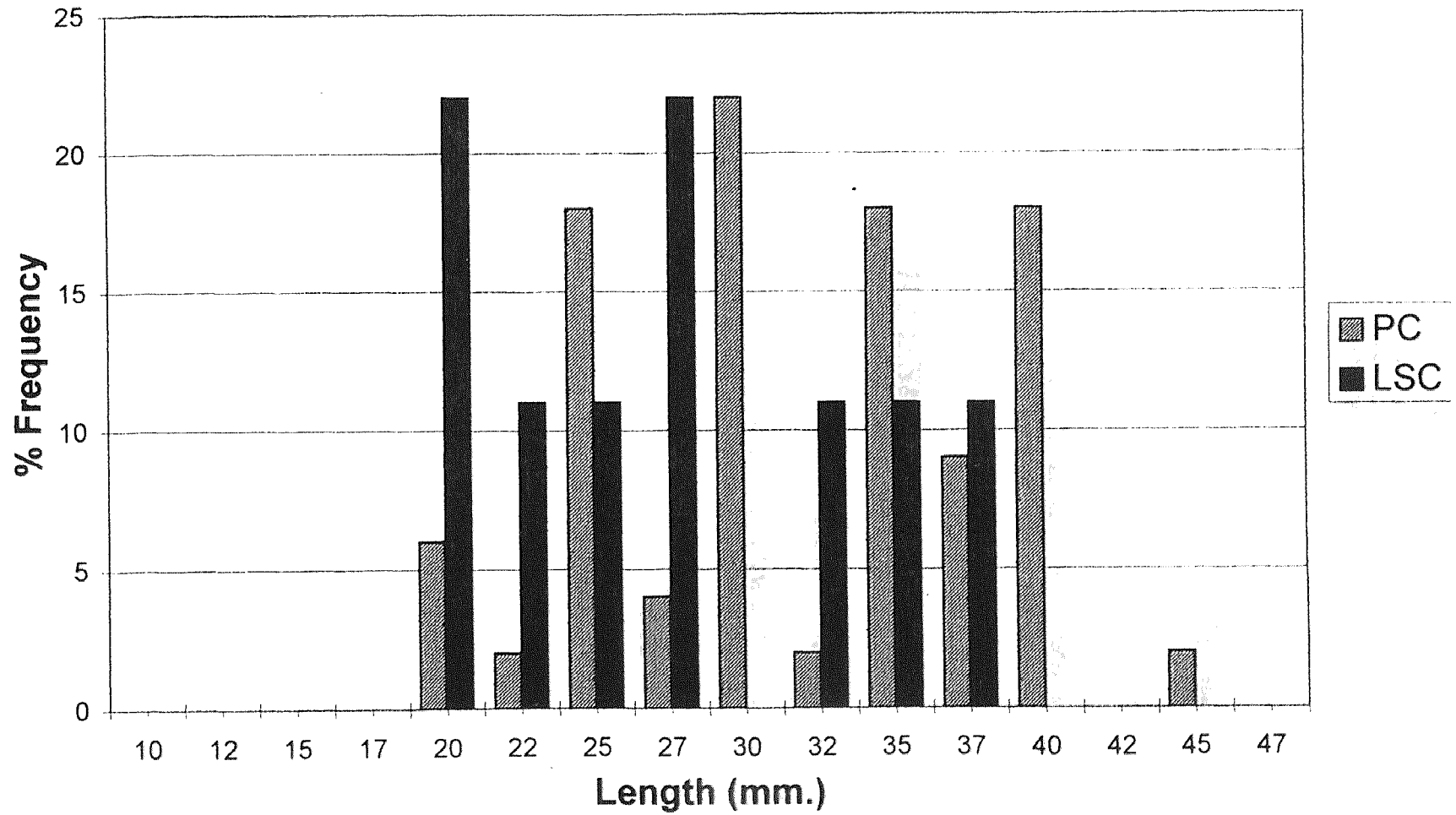


Figure 9 Week 3 Shrimp Lengths (June 10th, 11th)

Week 4 Shrimp Lengths

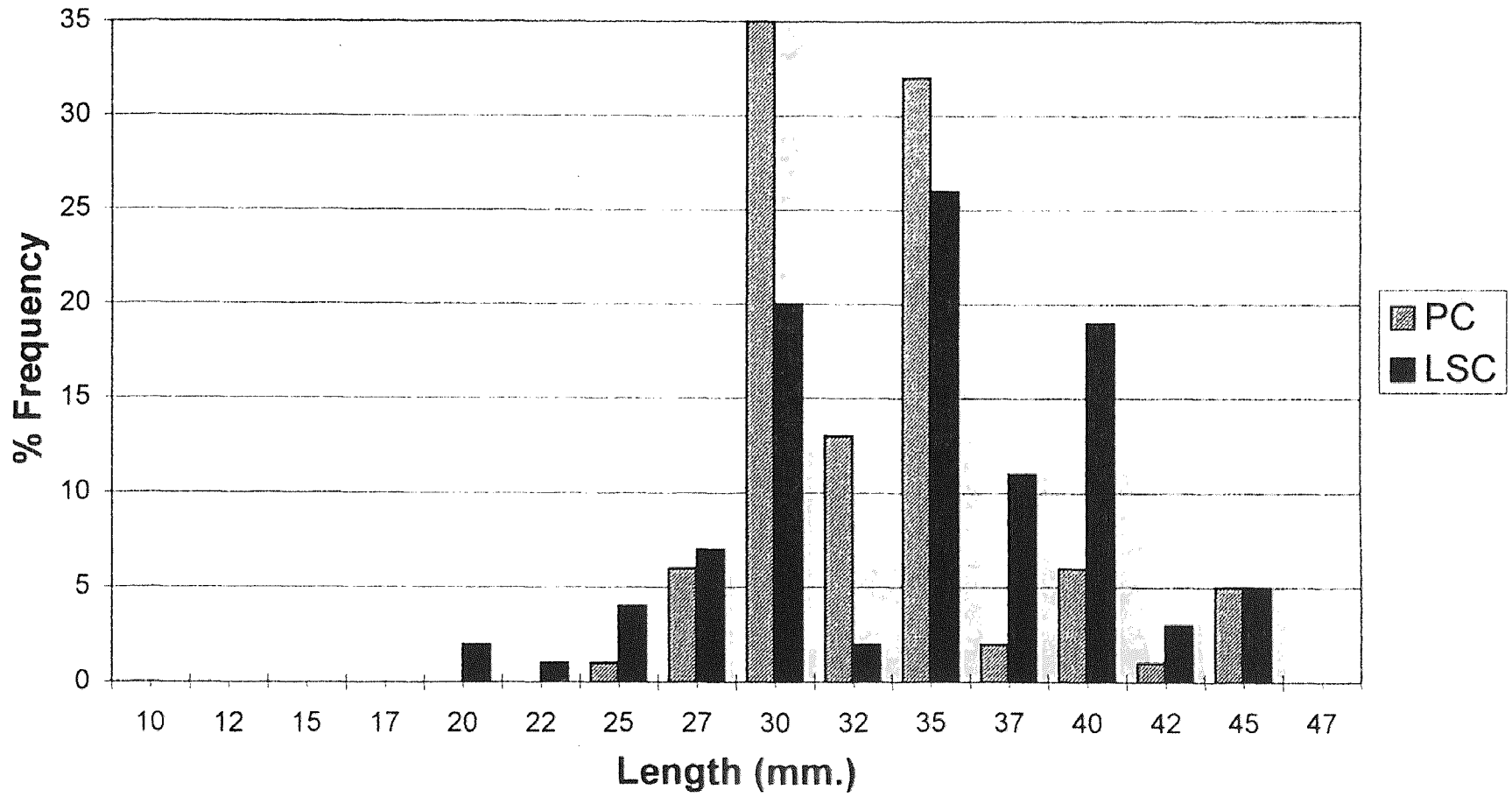


Figure 10 Week 4 Shrimp Lengths (June 18th, 19th)

Week 5 Shrimp Lengths

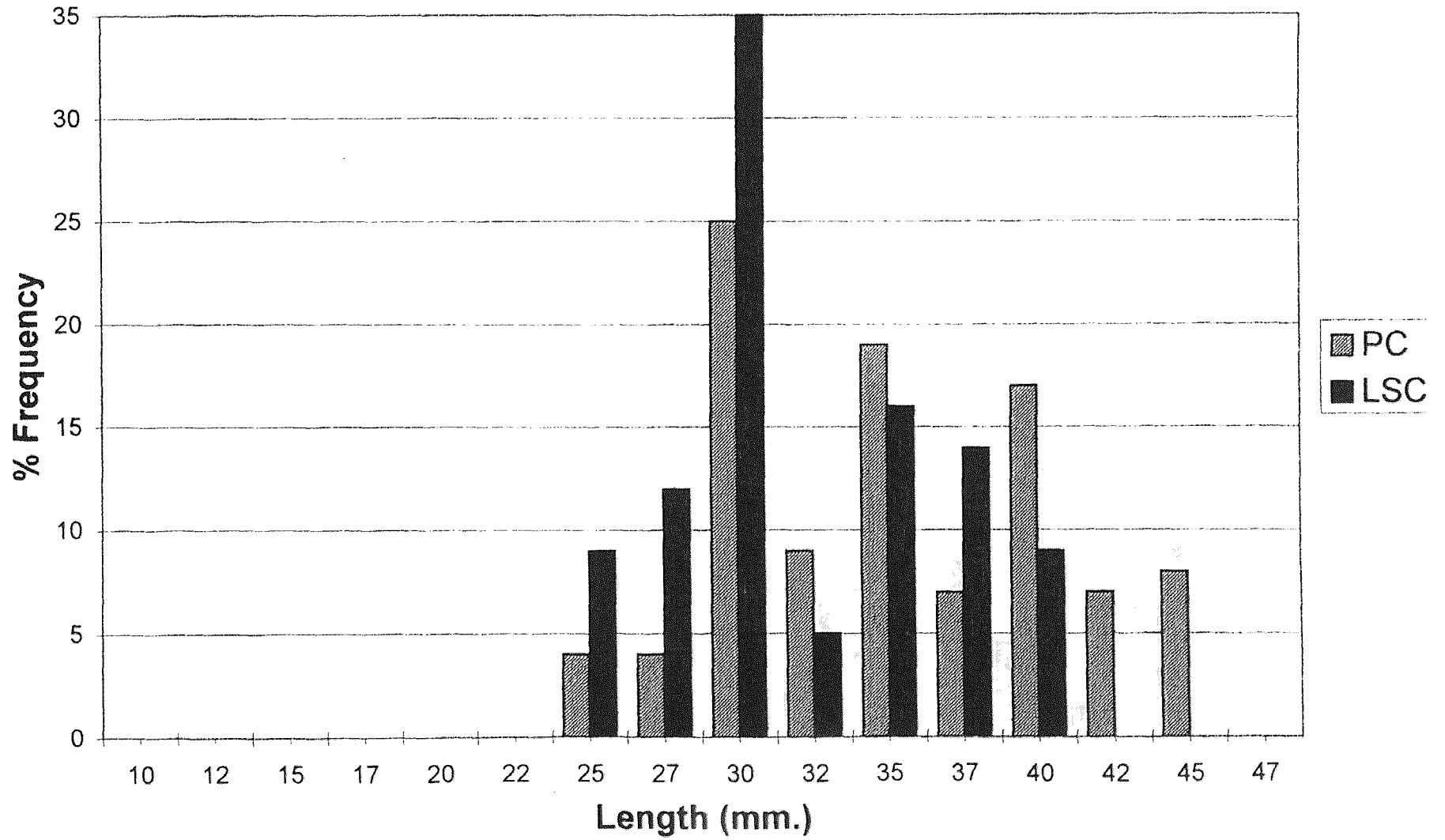


Figure 11 Week 5 Shrimp Lengths (June 24th, 26th)

Week 6 Shrimp Lengths

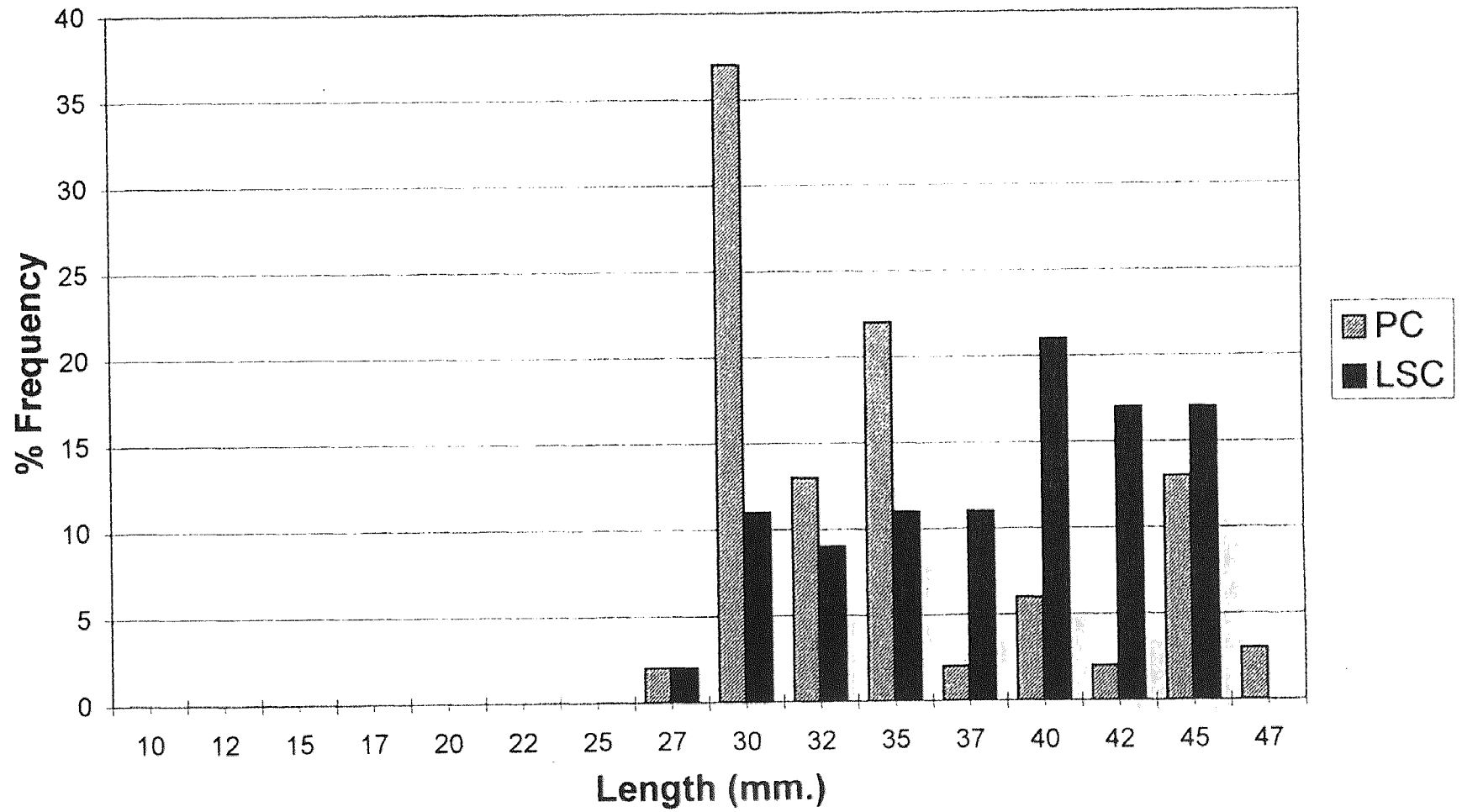


Figure 12 Week 6 Shrimp Lengths (July 8th, 9th)

Week 7 Shrimp Lengths

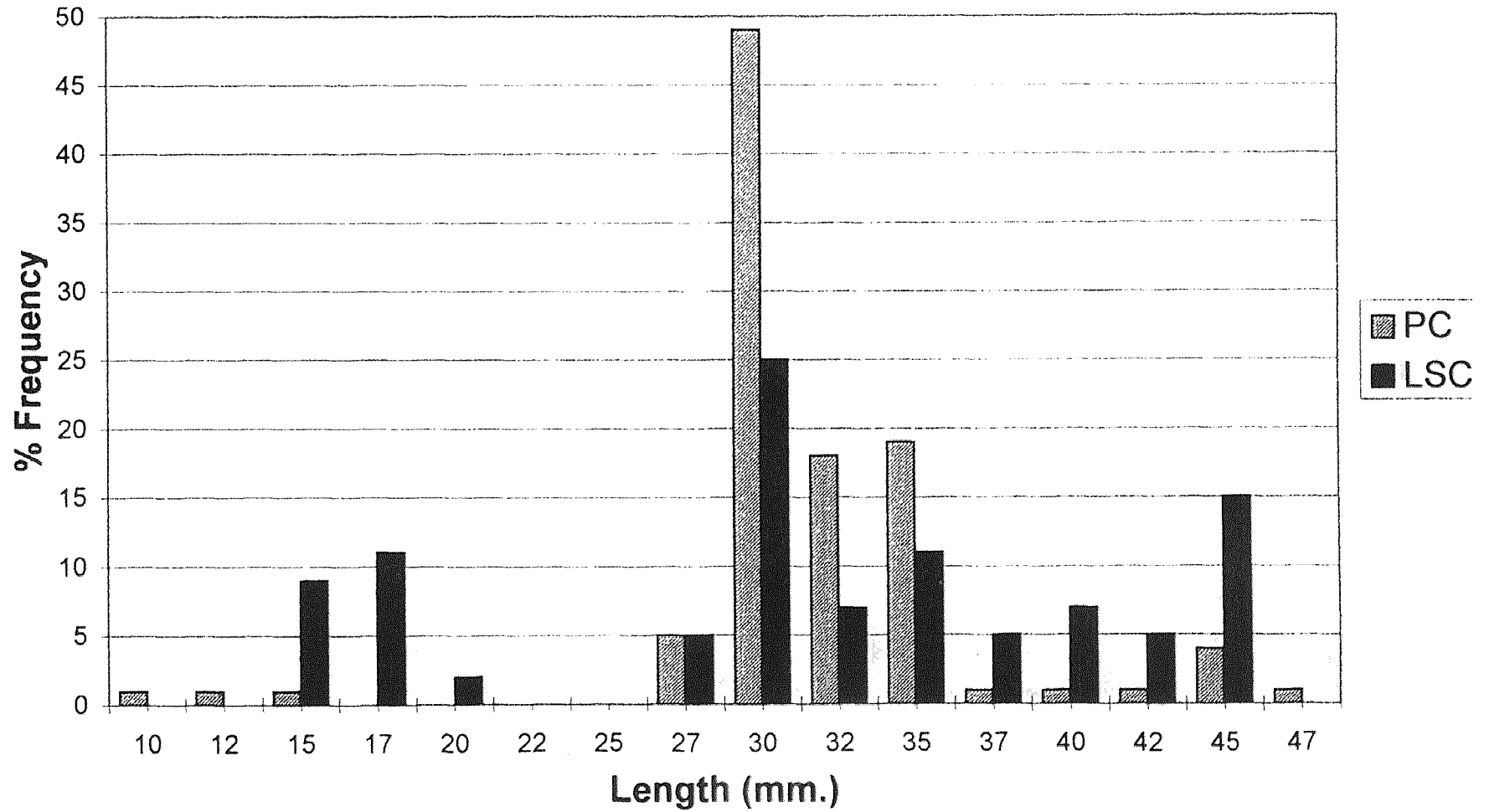


Figure 13 Week 7 Shrimp Lengths (July 15th, 16th)

Week 8 Shrimp Lengths

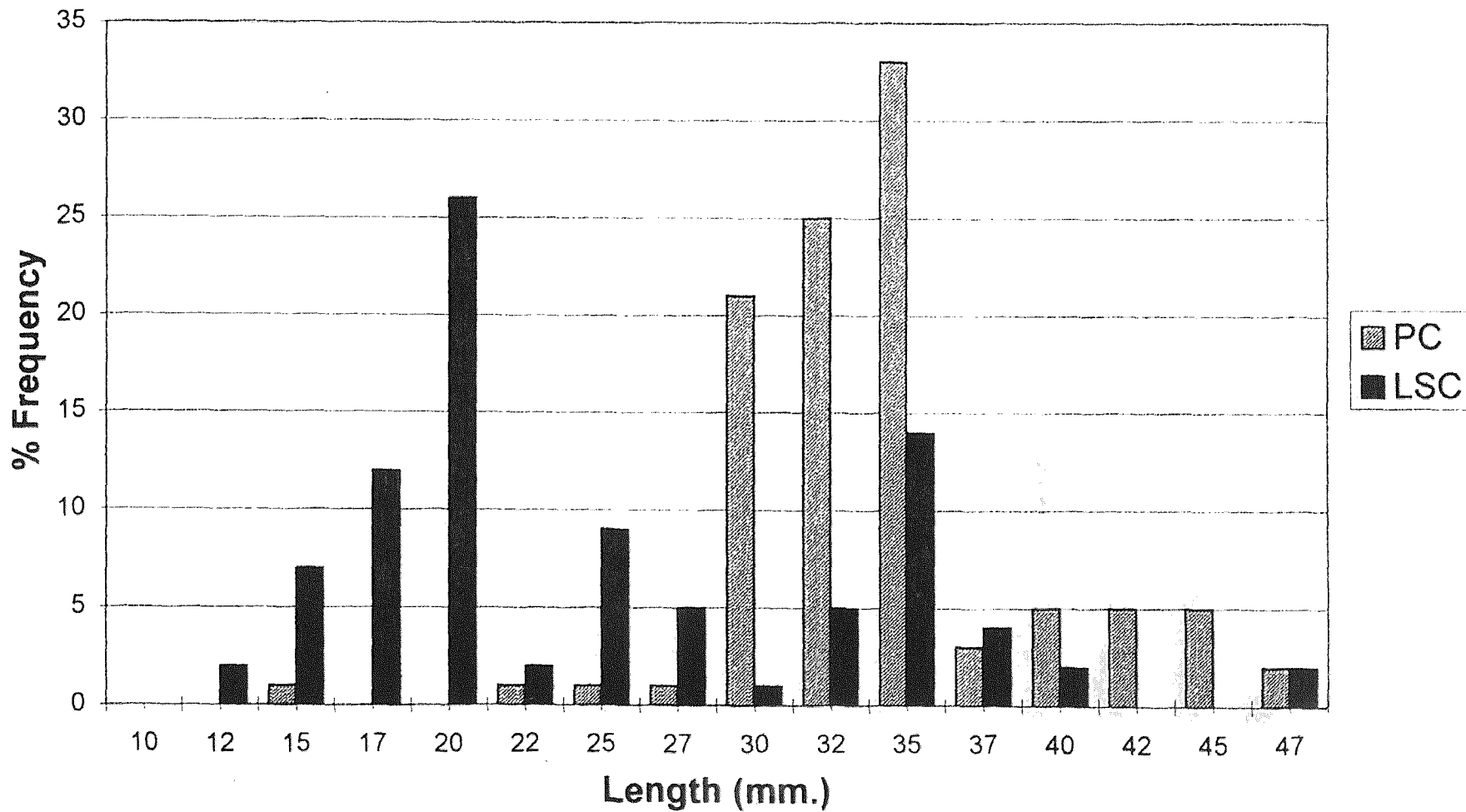


Figure 14 Week 8 Shrimp Lengths (July 23rd, 24th)

Week 9 Shrimp Lengths

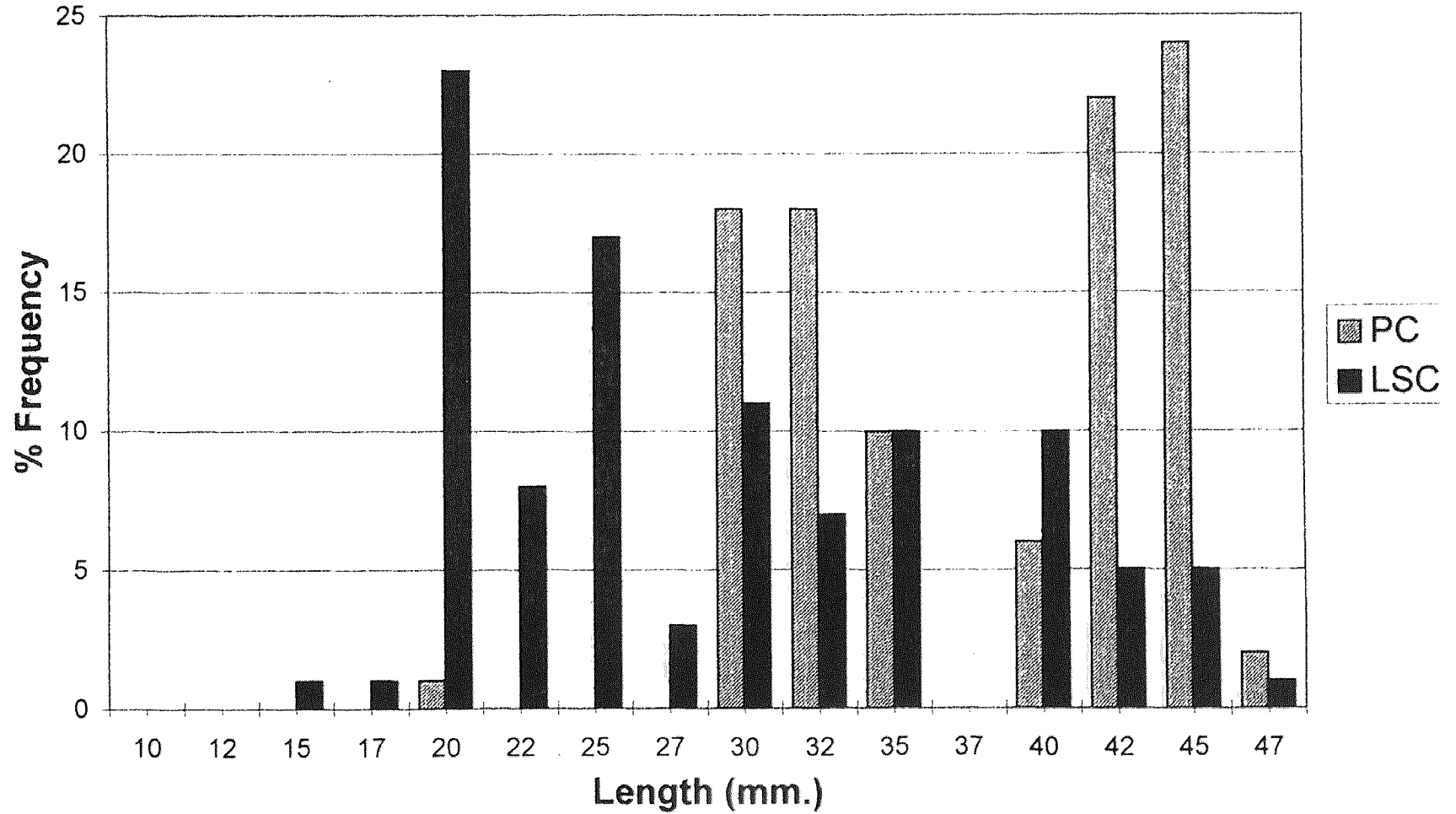


Figure 15 Week 9 Shrimp Lengths (July 29th, 30th)

Week 10 Shrimp Lengths

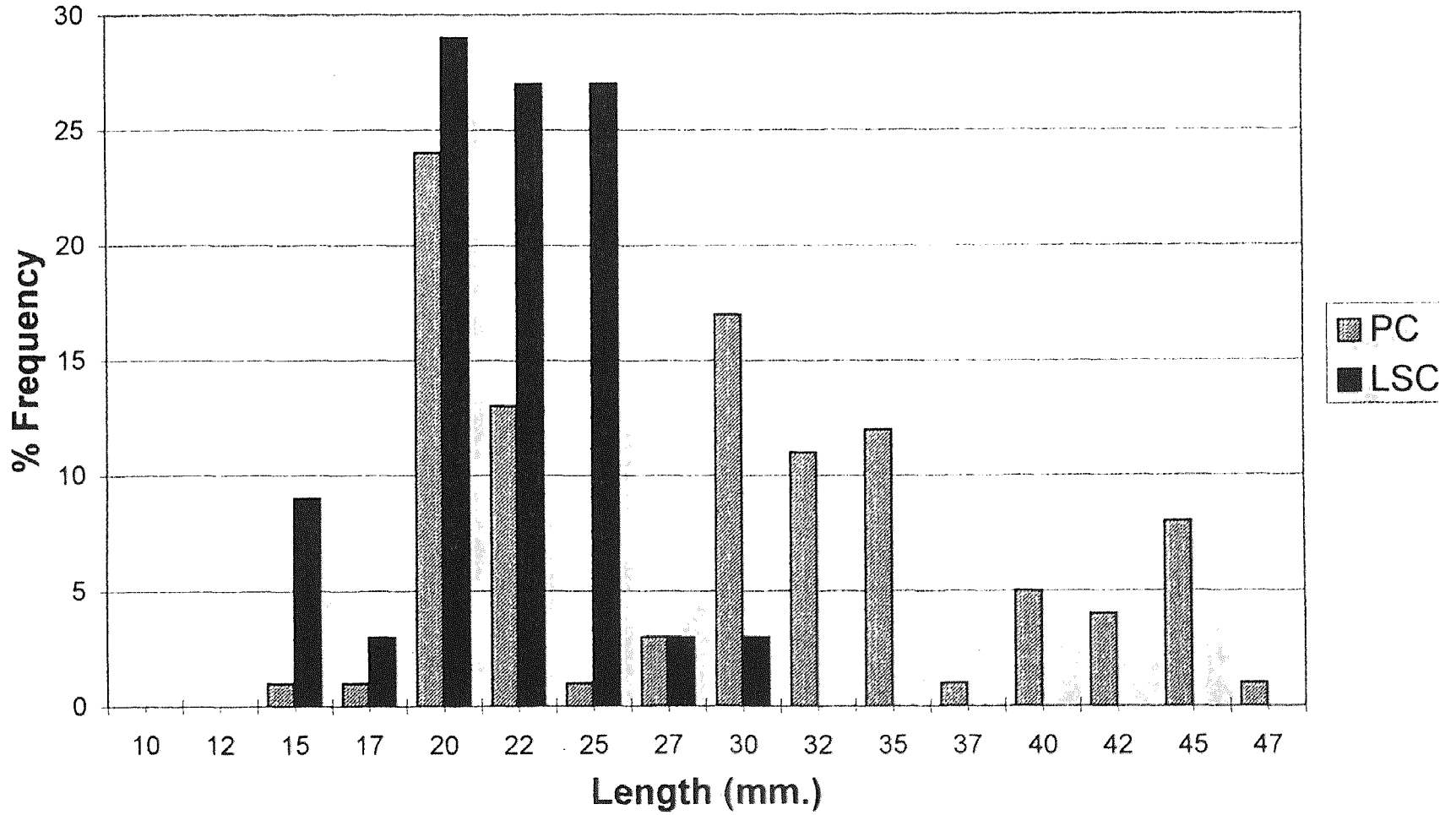


Figure 16 Week 10 Shrimp Length (August 6th, 7th)

Week 11 Shrimp Lengths

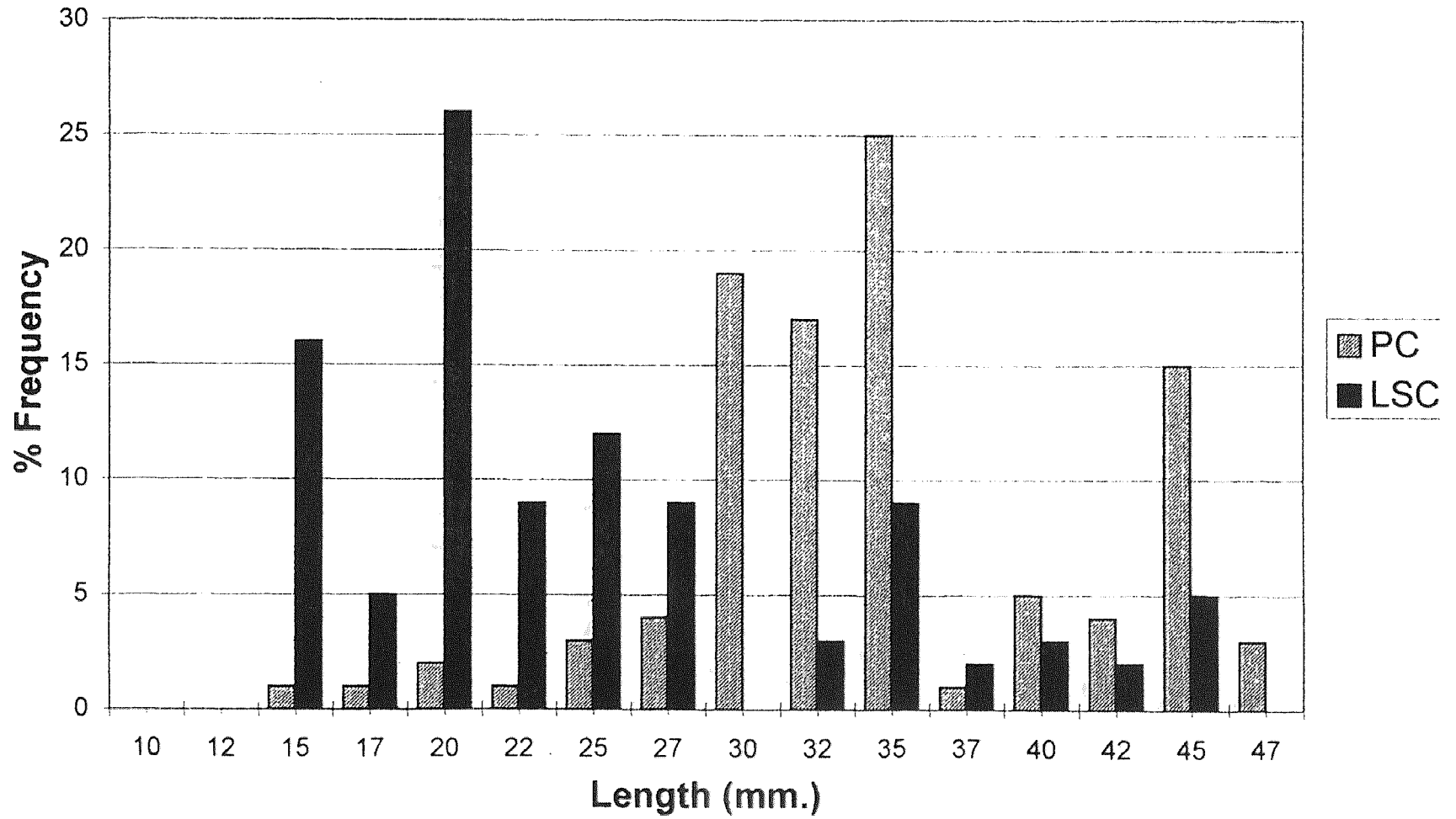


Figure 17 Week 11 Shrimp Lengths (August 12th, 13th)

Week 12 Shrimp Lengths

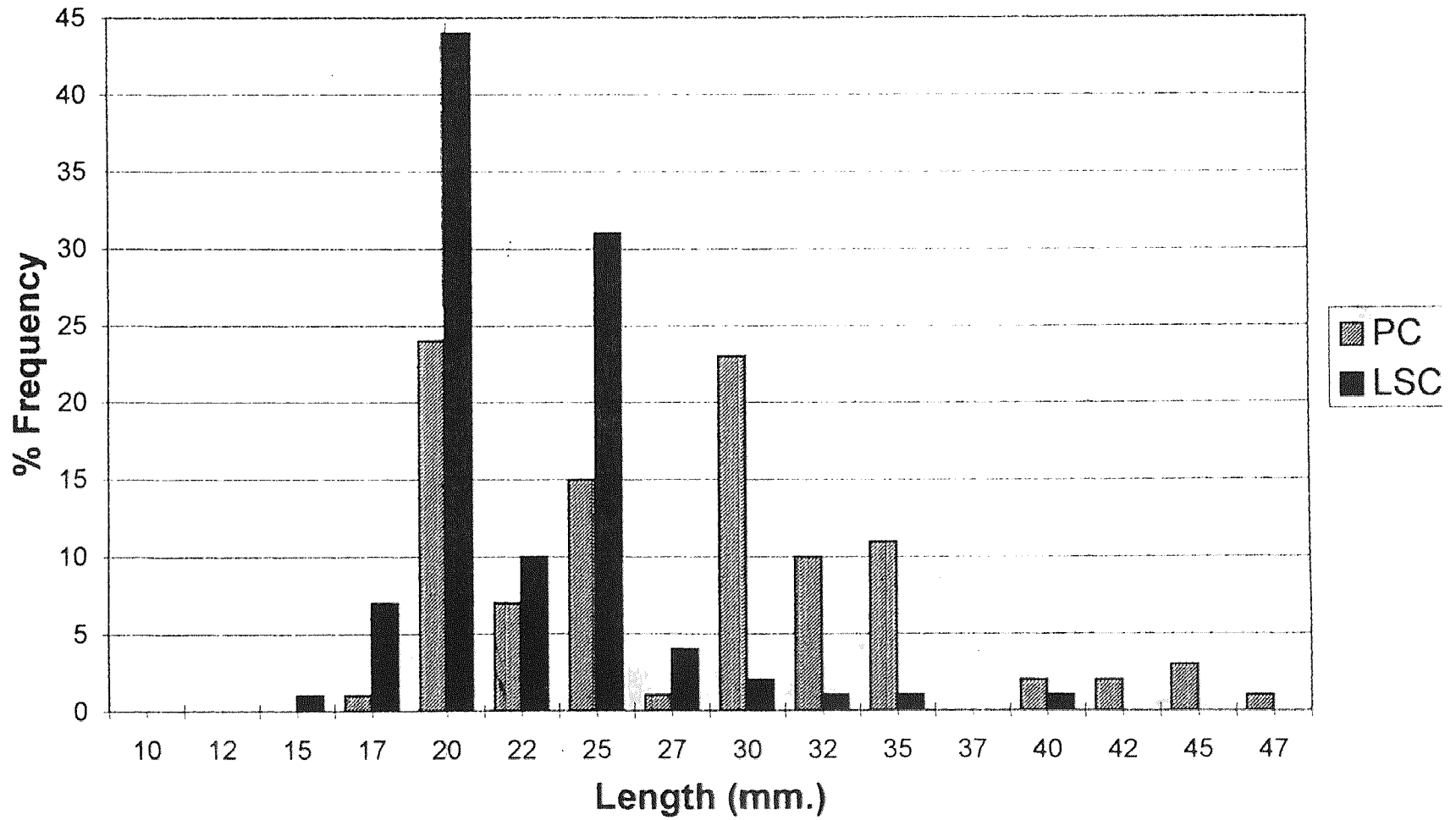


Figure 18 Week 12 Shrimp Length (August 19th, 20th)

September Shrimp Lengths

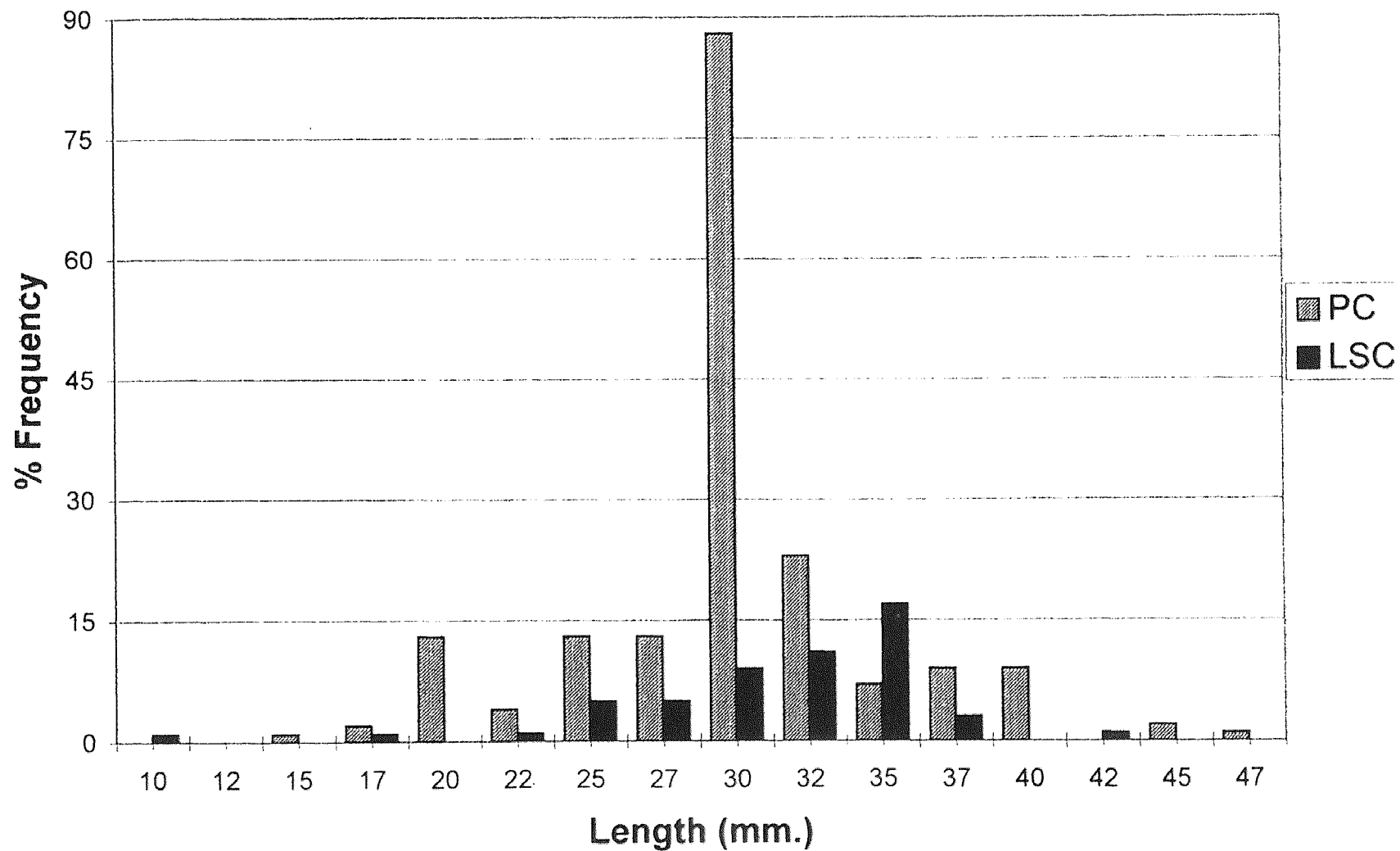


Figure 19 September Shrimp Lengths (September 29th, 30th)

CHAPTER 4

DISCUSSION

4.1 Environmental Conditions

Over the course of the study, there were key differences observed between the two sample populations of *F. heteroclitus* and *P. pugio*. Data showed that there were three times as many killifish in LSC than there were in PC, and three times as many grass shrimp in PC than there were in LSC. Additionally, it was found that grass shrimp were generally larger at PC, despite the discovery that LSC shrimp started to reproduce earlier in the season than did shrimp inhabiting PC.

4.1.1 Temperature and Salinity

Both temperature and salinity affect metabolism, and hence growth and distribution of all cold-blooded animals, such as the grass shrimp (Wood 1965). The large fluctuations in temperature and salinity recorded for PC and LSC are most likely due to the highly variable weather conditions encountered during the data collection period. In addition to unseasonably mild weather, I encountered a great deal of rain and high wind during this time. Wood (1965) reported similar findings in that water temperature was considerably influenced during the day by cloudiness, wind velocity and the height of waves.

The lowest temperatures (13° C at LSC, and 19° C at PC) were recorded during the first two weeks of the study and reflect the prolonged spring-like temperatures that the northeast region experienced early in the study. The low number of *P. pugio* accounted for during weeks 1 through 4 at PC, and weeks 1 through 3 at LSC, are most likely a reflection of the environmental conditions sustained at the two sites, particularly

cooler water temperatures. When water temperatures are unfavorable or extreme, grass shrimp tend to retreat from the edge of the shore and move to deeper waters (Wood 1965).

Salinity plays a major role in grass shrimp growth and distribution (Morgan 1980, Knowlton et al. 1994). The lowest salinity readings at PC and LSC of 9 ‰ (week 3) and 12 ‰ (week 11) respectively, were both taken while it was raining which would decrease the salinity readings at the creek's surface. Wood (1965) found that the largest grass shrimp were found when salinity was between 10 to 22 ‰. In general, conditions found in PC fit this criteria. S. Bhan (personal communication) noted a slight positive impact on PC shrimp growth when placed in the high salinity range found in LSC, with no change in LSC shrimp growth when placed in salinity conditions of PC. However, statistics showed that the differences in growth were numerically insignificant. Therefore, both temperature and salinity may be ruled out as major factors contributing to growth differences.

4.1.2 Inherent Environmental Components

Inherent environmental components in PC were also thought to possibly contribute to the larger mean size of the grass shrimp. This hypothesis was tested by S. Bhan in which microcosms of each site were assembled in laboratory tanks. In the first trial (without any added nutrients or food), S. Bhan (personal communication) concluded that there was equal growth among surviving conspecifics and no calculated significant difference in mean length.

In the second trial, it was reported that PC sediment and water played no positive role in growth for either PC or LSC shrimp. In fact, it seemed as though PC sediment and water inhibited LSC growth to some extent. However, there was a significant difference between PC and LSC shrimp placed in tanks with LSC sediment and water. *P. pugio* from LSC grew better than their counterparts in PC microcosms, with LSC shrimp exhibiting the greatest growth of the two sites in controlled laboratory conditions.

In the laboratory, LSC shrimp had a higher rate of growth than did PC shrimp when using LSC sediment and water; however, in the field, it is the PC shrimp that are generally significantly larger than LSC. This can be explained by the absence of predators in the controlled laboratory experiment whereas in the field under natural conditions, predators are present.

4.2 Reproductive Effort and Timing

The reproductive flexibility of *P. pugio* enhances its ability to persist in a variety of environments (Alon and Stancyk 1982). I hypothesized that *P. pugio* from PC may have had an advantage over shrimp in LSC by benefiting from either an increased reproductive potential or the ability to reproduce earlier. Having a “head start” would confer to the organism a prolonged period of growth.

Although both sites show ovigerous females during the same sampling period (week 3), LSC had a greater number of young recruiting into the population than PC for three consecutive weeks (weeks 7, 8, and 9). Even though LSC had a three week “head start” in recruitment, which would have granted the shrimp an extended period of

growth, PC shrimp remain significantly larger 9 out of the 12 weeks studied including September.

Some weeks reflected a larger percentage of ovigerous females in PC at times and in LSC at others. When calculating the percentage of YOY recruiting into each population, it became obvious that LSC had a higher reproductive effort than did PC, averaging 54% YOY at LSC (vs. 25% in PC) from week 7 when they first recruited into the population, through the last sampling date in September. Theoretically, this increased reproductive potential should conceivably result in increased survivorship, hence, increased potential to maximize body size for *P. pugio* and increased numbers of individuals found in LSC. The data shows that this was obviously not the case, as PC remained consistently larger in numbers and in individual sizes throughout the sampling period. The reproductive strategy implemented in LSC is reminiscent of an idealized textbook example of an r-selected population when compared to PC. The heavy predation that LSC shrimp encounter (three times as many killifish than in PC) has caused them to compensate by reproducing at an earlier age and having a larger number of offspring. Generally, organisms yielding larger clutch sizes tend to produce smaller offspring. Additionally, PC shrimp may have decreased their reproductive effort when compared to LSC as a direct result of decreased predation. Consequently, the two hypotheses regarding increased reproductive effort in PC may be rejected.

4.3 Role of Competition

Growth is a sensitive index of available resources and is most probably the parameter through which intra- and interspecific competition is expressed. Since a higher growth

rate reduces the time it takes to reach reproductive size, often increases survivorship, and/or increases size (and therefore generally fecundity) at first reproduction, it has often been argued that there is strong selection for maximizing growth rates (Werner and Gilliam 1984). PC grass shrimp may not in fact be experiencing an increased growth rate, it may be that LSC individuals are experiencing reduced or stunted growth as a consequence of increased competition. The data collected suggests otherwise. If competition were the major contributor to the differences in overall mean size of *P. pugio*, I would have caught the greater number of shrimp in LSC and the lesser amount in PC. This was not the case as there were almost three times as many shrimp captured in PC than in LSC. Therefore, competition may be ruled out as a factor as well.

4.4 Role of Predation

F. heteroclitus, due to their size and abundance, are one of the most potentially important predators to shallow zone species (Ruiz et al. 1993). The overall discrepancy reported between PC and LSC with respect to the total number of killifish caught can be explained primarily as a result of human interference. PC is overwhelmed by heavy fishing pressure. Tens of gallons of killifish are removed from the creek on a weekly basis by fisherman for personal use and for sale to sport shops as bait (personal observation and discussion with fishers).

In PC, weeks 10 and 12 illustrated the largest number of killifish collected over the course of study. I also noted that toward the end of the sampling period (weeks 10, 11, and 12), the traps in PC contained small, young-of-the-year mummichogs exclusively. This surge in number is due to the recruitment of young-of-the-year killifish into the

population that is exacerbated by the tremendous fishing pressure which eliminated almost all of the larger adults from the population over the course of the sampling period. This dominance of YOY has also been noted in freshwater (Samaritan and Schmidt 1982) and in salt-marshes (Valiela et al 1977) where the older, larger 3 year olds disappear from the population by October, with samples predominantly consisting of small fry in the fall months. LSC also experienced an influx of YOY toward the end of the sampling period; however, in contrast to PC, the site was relatively consistent in the number of fish caught per week and maintained an assorted size range of mummichogs (age classes 0 to 3+) throughout the study.

Palaemonetes are commonly reported as abundant or important in the diets of mummichogs from salt marshes. An analysis of the gut contents of *F. heteroclitus* in a study by Kneib (1986) suggested that *P. pugio* densities were controlled by large mummichogs, particularly in cages with high fish densities. However, *P. pugio* are too large to occur frequently in the diets of small (< 50 mm.) mummichogs but are common in the guts of larger fish (Nixon and Oviatt 1973). The fact that there are nearly three times as many killifish in LSC than in PC, most of which are larger, supports the hypothesis that LSC grass shrimp are preyed upon more frequently than are grass shrimp in PC and that size selective predation is limiting the number of LSC adult shrimp from ultimately reaching their maximum length. There are too few large fish to prey on and consume the large grass shrimp in PC.

CHAPTER 5

CONCLUSION

As a result of weekly sampling it was found that in most weeks, shrimp were significantly larger in PC relative to LSC and were more numerous. Several possible causes for differences in the size frequency distribution were investigated: environmental conditions, inherent environmental components, reproductive effort and timing, the role of competition, and the role of predation.

Optimum temperature and salinity conditions were thought to be positively impacting PC shrimp growth. Although there was a difference in salinities between the two sites, there was no significant difference in temperatures. Laboratory studies (Bhan personal communication) showed that the differences found between the salinities had no significant role in increasing mean shrimp length. In lab microcosms, all shrimp grew better in LSC conditions and in fact, conditions in PC seemed to negatively impact growth of shrimp.

Reproductive effort and timing were shown to differ between the two sites; however, contrary to the initial hypothesis, it was LSC that demonstrated the higher reproductive potential and earlier breeding, not PC. Competition was also investigated as a possible contributor to the differences in mean shrimp length. There was overwhelming evidence that there is a difference in population size between the two sites. However, the greatest number of shrimp were caught in PC which is the direct opposite of what was hypothesized.

Lastly, size-selective predation was thought to be impacting the population of *P. pugio*. This hypothesis was substantiated by sampling the number of *F. heteroclitus* relative to the number of *P. pugio*. It was found that there are three times as many grass shrimp in PC than in LSC (3:1), yet there are three times as many mummichogs in LSC than there are in PC (3:1). Therefore, it is reasonable to conclude that predation is in fact the primary factor involved in the differences found in size-frequency distribution as well as relative numbers.

BIBLIOGRAPHY

- Allen, E. A., P. E. Fell, M. A. Peck, J. A. Gieg, C. R. Guthke, and M. D. Newkirk. 1994. Gut Contents of Common Mummichogs, *Fundulus heteroclitus* L., in a Restored Impounded Marsh and in Natural Reference Marshes. *Estuaries* 17(2):462-471.
- Alon, N. C., and Stancyk, S. F. 1982. Variation in Life-history Patterns of the Grass Shrimp *Palaemonetes pugio* in Two South Carolina Estuarine Systems. *Mar. Bio.* 68:265-276.
- Anderson, G. 1985. Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (Gulf of Mexico) - Grass Shrimp. *U.S. Fish Wildl. Serv., Biol. Rep.* 82(11.35):19 pp.
- Backstrom, J. 1969. Distribution Studies of Mercuric Pesticides in Quail and Some Fresh-water Fishes. *Acta. Pharm. Toxicol.* 27:1-103.
- Bigelow, H. G. and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. *U.S. Fish Wildl. Serv. Fish. Bull.* 53:162-164.
- Boesch, D. F., and R. E. Turner. 1984. Dependence of Fishery Species on Salt Marshes: The Role of Food and Refuge. *Estuaries* 7(4A):460-468.
- Broad, A. C. 1957. The Relationship Between Diet and Larval Development of *Palaemonetes*. *Biol. Bull. Mar. Biol. Lab., Woods Hole* 112:162-170.
- Csanyi, V., and A. Doka. 1993. Learning Interactions Between Prey and Predator Fish. *Mar. Behav. Physiol.* 13:63-78.
- Denoncourt, R., J. C. Fisher, and K. M. Rapp. 1978. A freshwater Population of the Mummichog, *Fundulus heteroclitus*, from the Susquehanna River Drainage in Pennsylvania. *Estuaries* 1(4):269-272.
- Fernandez-Delgado, C. 1989. Life-history Patterns of the Salt Marsh Killifish *Fundulus heteroclitus* (L.) Introduced in the Estuary of the Guadalquivir River (South West Spain). *Estuarine, Coastal and Shelf Science* 29:573-582.
- Foreman, K., I. Valiela, and R. Sarda. 1995. Controls of Benthic Marine Food Webs. *Sci. Mar.* 59(Supl. 1):119-128.
- Formanowicz Jr., D. R., and M. S. Bobka. 1988. Predation Risk and Microhabitat Preference: An Experimental Study of the Behavioral Responses of Prey and Predator. *Am. Midl. Nat.* 121:379-386.

- Gibson, R. N. 1988. Patterns of Movement in Intertidal Fishes. In: Chelazzi, G., Vannini, M. (eds.) *Behavioral Adaptation to Intertidal Life*. Plenum Publishing Corp., New York, pp. 55-63.
- Gibson, R. N., M. C. Yin, and L. Robb. 1995. The Behavioral Basis of Predator-prey Size Relationships Between Shrimp (*Crangon crangon*) and Juvenile Plaice (*Pleuronectes platessa*). *J. Mar. Biol. Ass. U.K.* 75:337-349.
- Heck, K. L., Jr., and R. J. Orth. 1980. Seagrass Habitats: The Roles of Habitat Complexity, Competition and Predation in Structuring Associated Fish and Motile Macroinvertebrate Assemblages. In, *Estuarine Perspectives*, edited by V. S. Kennedy. Academic Press, New York, pp. 449-464.
- Heck, K. L., Jr. and T. A. Thoman. 1981. Experiments on Predator-prey Interactions in Vegetated Aquatic Habitats. *J. Exp. Mar Biol. Ecol.* 53:125-134.
- Huddart, R., and D. R. Arthur. 1971. Shrimps in Relation to Oxygen Depletion and its Ecological Significance in a Polluted Estuary. *Environ. Pollut.* 2:13-35.
- Hunter, M. D., and P. W. Price. 1992. Playing Chutes and Ladders: Heterogeneity and the Relative Roles of Bottom-up and Top-down Forces in Natural Communities. *Ecology* 73(3):724-732.
- Jenson, S., and A. Jernelov. 1969. Biological Methylation of Mercury in Aquatic Organism. *Nature.* 223:753-754.
- Kerfoot, W. C., and A. Sih. 1987. Predators and Prey Lifestyles: An Evolutionary and Ecological Overview. In, *Predation: Direct and Indirect Impacts on Aquatic Communities*. U. Press of New England, Hanover, London, pp. 203-224.
- Khan, A. T., J. S. Weis, and L. D'Andrea. 1989. Bioaccumulation of Four Heavy Metals in Two Populations of Grass Shrimp, *Palaemonetes pugio*. *Bull. Environ. Contam. Toxicol.* 42:339-343.
- Kitchell, J. F., L. A. Eby, X. He, D.E. Schindler, and R. A. Wright. 1994. Predator-Prey Dynamics in an Ecosystem Context. *Journal of Fish Biology* 45(Supl. A):209-226.
- Kneib, R. T. 1988. Testing for Indirect Effects of Predation in an Intertidal Soft-bottom Community. *Ecology* 69(6):1795-1805.
- Kneib, R. T. 1987a. Predation Risk and Use of Intertidal Habitats by Young Fishes and Shrimp. *Ecology* 68(2):379-386.
- Kneib, R. T. 1987b. Seasonal Abundance, Distribution and Growth of Postlarval and Juvenile Grass Shrimp (*Palaemonetes pugio*) in a Georgia, USA, Salt Marsh. *Mar. Bio.* 96:215-223.

- Kneib, R. T. 1984. Patterns of Invertebrate Distribution and Abundance in the Intertidal Salt Marsh: Causes and Questions. *Estuaries* 7(4A):392-412.
- Kneib, R. T. 1986. The Role of *Fundulus heteroclitus* in Salt Marsh Trophic Dynamics. *Amer. Zool.* 26:259-269.
- Kneib, R. T., and M. K. Knowlton. 1995. Stage-structured Interactions Between Seasonal and Permanent Residents of an Estuarine Nekton Community. *Oecologia* 103:425-434.
- Kneib, R. T., and A. E. Stiven. 1982. Benthic Invertebrate Responses to Size and Density Manipulations of the Common Mummichog, *Fundulus heteroclitus*, in an Intertidal Salt Marsh. *Ecology* 63(5):1518-1532.
- Kneib, R. T., and S. L. Wagner. 1994. Nekton Use of Vegetated Marsh Habitats at Different Stages of Tidal Inundation. *Mar. Ecol. Prog. Ser.* 106:227-238.
- Knowlton, R. E., R. N. Khan, P. M. Arguin, T. A. Aldaghas, and R. Sivapathasundram. 1994. Factors Determining Distribution and Abundance of Delmarva Grass Shrimp (*Palaemonetes* spp.). *Virginia J. Sci.* 45(4):231-247.
- Kraus, M. L., J. S. Weis, and P. Weis. 1988. Effects of Mercury on Larval and Adult Grass Shrimp (*Palaemonetes pugio*). *Arch. Environ. Contam. Toxicol.* 17:355-362.
- Morgan, M. D. 1980. Grazing and Predation of the Grass Shrimp *Palaemonetes pugio*. *Limnol. Oceanogr.* 25(5):896-902.
- Nelson, W. G. 1981. Experimental Studies of Decapod and Fish Predation on Seagrass Macrobenthos. *Mar. Biol. Prog. Ser.* 5:141-149.
- Nixon, S. W., and C. A. Oviatt. 1973. Ecology of a New England Salt Marsh. *Ecol. Monogr.* 43:463-498.
- Odum, W. E., and E. J. Heald. 1972. Trophic Analysis of an Estuarine Mangrove Community. *Bull. Mar. Sci.* 22:671-738.
- Paine, R. T. 1980. Food Webs: Linkage, Interaction Strength and Community Infrastructure. *J. Ani. Ecol.* 49:667-685.
- Paine, R. T. 1966. Food Web Complexity and Species Diversity. *The American Naturalist* 100(910):65-75.
- Posey, M. H., and A. H. Hines. 1991. Complex Predator-prey Interactions Within an Estuarine Benthic Community. *Ecology* 72(6):2155-2169.

- Prinslow, T. E., I. Valiela, and J. M. Teal. 1974. The Effect of Detritus and Ration Size on the Growth of *Fundulus heteroclitus* (L.). *J. Exp. Mar. Biol. Ecol.* 16:1-10.
- Ruiz, G. M., A. H. Hines, and M. H. Posey. 1993. Shallow Water as a Refuge Habitat for Fish and Crustaceans in Non-vegetated Estuaries: An Example From Chesapeake Bay. *Mar. Biol. Prog. Ser.* 99:1-16.
- Samaritan, J. M., and R. E. Schmidt. 1982. Aspects of the Life History of a Freshwater Population of the Mummichog, *Fundulus heteroclitus* (Pisces: Cyprinodontidae), in the Bronx River, New York, USA *Hydrobiologia* 94:149-154.
- Smith, G., and J. S. Weis. In press. Predator-prey Relationships in Mummichogs (*Fundulus heteroclitus*): Effects of Living in a Polluted Environment. *J. Exper. Mar. Biol. Ecol.*
- Toppin, S. B., M. Heber, J. S. Weis, P. Weis. 1987. Changes in Reproductive Biology and Life History in *Fundulus heteroclitus* in a Polluted Environment. In, *Pollution Physiology of Estuarine Organisms*, eds. W. Vernberg, A. Calabrese, F. Thurberg, and F. J. Vernberg, University of South Carolina Press, Columbia, S. C. pp. 208-211.
- Troccaz, O., F. Giraud, G. Bertru, and J. C. Lefeuvre. 1994. Methodology for Studying Exchanges Between Salt Marshes and Coastal Marine Waters. *Wetl. Ecol. Managem.* 3(1):37-48.
- Turner, A. M., and G. G. Mittelbach. 1990. Predator Avoidance and Community Structure: Interactions Among Piscivores, Planktivores, and Plankton. *Ecology* 71(6):2241-2254.
- Valiela, I., J. E. Wright, J. M. Teal, and S. B. Volkmann. 1977. Growth, Production and Energy Transformations in the Salt-marsh Killifish *Fundulus heteroclitus*. *Marine Biology* 40:135-144.
- Vince, S., I. Valiela, N. Backus, and J. M. Teal. 1976. Predation by the Salt Marsh Killifish *Fundulus heteroclitus* (L.) in Relation to Prey Size and Habitat Structure: Consequences for Prey Distribution and Abundance. *J. Exp. Mar. Biol. Ecol.* 23:255-266.
- Weis, J. S., and A. A. Khan. 1990. Effects of Mercury on the Feeding Behavior of the Mummichog, *Fundulus heteroclitus*, From a Polluted Habitat. *Mar. Envir. Res.* 30:243-249.
- Weis, J. S., and P. Weis. 1989. Tolerance and Stress in a Polluted Environment: The Case of the Mummichog. *Bioscience* 39:89-96.

- Weisberg, S. B., R. Whalen, and V. A. Lotrich. 1981. Tidal and Diurnal Influence on Food Consumption of a Salt Marsh Killifish, *Fundulus heteroclitus*. *Mar. Bio.* 61:243-246.
- Welsh, B. L. 1975. The Role of Grass Shrimp, *Palaemonetes pugio*, in a Tidal Marsh Ecosystem. *Ecology* 56:513-530.
- Werner, E. E., and J. F. Gilliam. 1984. The Ontogenetic Niche and Species Interactions in Size-structured Populations. *Ann. Rev. Ecol. Syst.* 15:393-425.
- Wiltse, W. I., K. H. Foreman, J. M. Teal, and I. Valiela. 1984. Effects of Predators and Food Resources on the Macrobenthos of Salt Marsh Creeks. *J. Mar. Res.* 42:923-942.
- Wood, C. E. 1967. Physioecology of the Grass Shrimp, *Palaemonetes pugio*, in the Galveston Bay Estuarine System. *Contrib. Mar. Sci.* 12:54-79.
- Wright, R. A., L. B. Crowder, and T. H. Martin. 1993. The Effects of Predation on the Survival and Size-distribution of Estuarine Fishes: An Experimental Approach. *Environ. Bio. Fishes* 36:291-300.