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A comparison of life histories and ecological aspects among snappers (Pisces: Lutjanidae)

Fernando Martinez-Andrade

Louisiana State University and Agricultural and Mechanical College, fmartin@lsu.edu

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A COMPARISON OF LIFE HISTORIES AND ECOLOGICAL ASPECTS AMONG
SNAPPERS (PISCES: LUTJANIDAE)

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State university and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Oceanography and Coastal Sciences

by

Fernando Martinez-Andrade

B.S., Universidad Autonoma Metropolitana, 1992

M.S., Instituto Tecnologico y de Estudios Superiores de Monterrey, 1997

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GENERAL INTRODUCTION

Life-history variables influence the economic importance of individual species and are of obvious interest to the management of fisheries and other natural resources because they are fundamental determinants of population dynamics. To achieve a sustainable exploitation of any species, these variables must be considered and fully understood (Stearns 1980, Winemiller and Rose 1992). Studies of life-history variables for a particular population or species usually require direct on-site observation and sampling, which involves a considerable amount of time and effort from the scientists who plan and conduct these studies. The resulting publications of all this research have the primary purpose of serving the scientific community in the future by contributing to the scientific knowledge base. This study reviews most of the extensive information available for a fish family of world-wide importance, the snappers, to analyze variability among species and subfamilies and focuses on ten life-history variables. It also examines two ecological factors addressing their distribution and feeding habits.

The snapper family, Lutjanidae, belongs to the order Perciformes, the largest order of vertebrates, with 148 families and nearly 9,300 species. The Perciformes is a huge group of spiny-rayed fishes that are especially common in tropical and subtropical seas, and are usually found in coastal areas; however, it also includes a few families restricted to fresh water (Nelson 1994).

The family Lutjanidae is composed of 17 genera and 103 species of mostly reef-associated marine fishes, several deep-water (>100 m) species and three freshwater species. The family is divided in four subfamilies. The largest is the subfamily Lutjaninae with three monotypic genera (*Hoplopagrus*, *Ocyurus*, and *Rhomboplites*), the

genera *Macolor* and *Pinjalo* with two species each, and the genus *Lutjanus* with 66 species. Three smaller subfamilies include the Paradicichthyinae with two monotypic genera (*Symphorus* and *Symphorichthys*), the Etelinae with five genera (*Aphareus*, *Aprion*, *Etelis*, *Pristipomoides* and *Rhandallichthys*) and 18 species, and the Apsilinae with four genera (*Apsilus*, *Lipocheilus*, *Paracesio* and *Parapristipomoides*) and 10 species (Allen 1985).

Several new species of snappers and even genera have been described recently (Anderson 1981, Akazaki 1983, Randall *et al.* 1987, Iwatsuki *et al.* 1993, Allen 1995); however, there is still debate within the scientific community about the validity of these species and biological information about them is extremely limited.

The fish family most closely related to snappers is the Caesionidae, a small family of about 20 semi-pelagic and planktivorous species restricted to the Indo-west Pacific Ocean and commonly called fusiliers. The Caesionidae and Lutjanidae families compose the superfamily Lutjanoidea and in the past fusiliers have been included in the snapper family by some authors (Johnson 1980). Other closely related families are the grunts (Haemulidae), porgies (Sparidae), picarels (Centracanthidae), emperors (Lethrinidae), and threadfin breams (Nemipteridae). The first two families have world-wide distributions and over 100 species each, the latter three families are smaller with more restricted distributions, all these families are marine (Johnson 1980, Nelson 1994).

The subfamily Lutjaninae represents about two thirds of the species in the family and it is the best known; however, the other three subfamilies also deserve attention and are relevant aquatic resources in many regions of the world. The species in the subfamily Lutjaninae constitute an important component of the reef fisheries in tropical and sub-

tropical latitudes throughout their geographical range, while the deep-water subfamilies Apsilinae and Etelinae represent by far the most important component of the deep-bottom fishery in Hawaii and other areas of the Pacific, Atlantic, and Indian oceans. One possible reason of the underestimated role of the latter subfamilies is the manner in which landings data of individual species in different subfamilies are lumped together. Such is the case of the black snapper (*Apsilus dentatus*) and the black-fin snapper (*Lutjanus buccanella*) in the Gulf of Mexico, the black snapper belongs to the subfamily Apsilinae, while the black-fin snapper belongs to the subfamily Lutjaninae; however, landing reports combine these two species together.

Landings of snappers are of significant volume and economic value due to the excellent quality of the meat and high demand, making them some of the most appreciated species in the market today. However, there is concern about the status of several fisheries. In the Gulf of Mexico alone, red snapper (*Lutjanus campechanus*) and vermilion snapper (*Rhomboplites aurorubens*) are currently over-fished (Coleman *et al.* 1999). Cubera snappers (*L. cyanopterus*) and mutton snapper (*L. analis*) are listed as vulnerable by the International Union for Conservation of Nature, and considered at risk of extinction (IUCN 2002).

Decreases in natural populations of snappers have motivated new interest in developing techniques for reproducing them in captivity, either for fishery enhancement or for commercial cultivation. Research in this area has focused on understanding the life cycle and nutritional requirements of selected species to find protocols for producing reliable sources of eggs and fingerlings and to determine the best rearing conditions. Currently, *Lutjanus argentimaculatus*, *L. johnii*, *L. russelli*, and *L. sebae* are successfully

farmed in floating net cages in Pakistan, China, Singapore, Malaysia, Thailand, and the Philippines (Doi *et al.* 1994, Emata *et al.* 1999, Hussain and Khatoon 2000, Tucker 2000, Hong and Zhang 2002). In the U.S.A., aquaculture research has been conducted on *L. campechanus*, *L. analis* and *L. griseus* among others (Watanabe *et al.* 2001, Chigbu *et al.* 2002).

The objectives of this study are (1) to review some important concepts in life-history theory; (2) to acquire, standardize and analyze information on ten selected life-history variables to describe patterns of variation among species of snappers and subfamilies; (3) to review aspects of the physical distribution of snappers in different environments; and (4) to acquire, standardize and analyze information related to the feeding habits of different species of snappers to describe the patterns of variation related to ten selected prey categories commonly found in their diets.

CHAPTER 1

A BRIEF REVIEW OF LIFE-HISTORY CONCEPTS RELEVANT TO SNAPPERS

Life-history theory helps us to understand the way natural selection acts on living organisms and how genetic variation will be expressed. It deals with trade-offs among demographic and reproductive variables and the manner in which these trade-offs shape life-history strategies for dealing with different kinds of environments. These trade-offs may have physiological, demographic, ecological or phylogenetic bases (Winemiller and Rose 1992).

A life-history strategy is defined as a set of co-adapted variables designed by natural selection to solve particular ecological problems (Roff 1992). Evolution of life-history strategies determines the population dynamics of interacting species and can only be measured on populations and not on individuals; however, variance among individual patterns is one of the most important elements of a strategy (Stearns 1976). Such variance is the product of selection acting on individual organisms, not on populations. The evolution of life-history strategies is strongly influenced by the variation in space and time of relevant environmental variables. The most relevant of these variables are prey availability, temperature, breeding sites, shelter areas, competitors, and predators. These environmental variables have a direct impact on the life-history variables of the populations which results in changing strategies (Stearns 1976).

Scientists doing broad surveys of life-history variables on genera, families, and even phyla have been more successful in perceiving broader life-history strategies than other scientists studying intra-specific variability. For example, within a single species covariance among two variables is more likely than is covariance among three variables.

However, comparisons among congeneric species might detect covariance of three variables and comparisons of genera within a family might detect four variables. Stearns (1980) concluded that allometrical constraints within lineages and punctuated equilibrium are two processes responsible for increases in the number of co-varying life history variables within ascending taxonomic hierarchies.

For fish species Winemiller and Rose (1992) identify three major strategies. Opportunistic strategists are typically species that are small in size, with early maturation and short life span. Periodic strategists include species that are larger, generally higher in fecundity with longer life spans. And equilibrium strategists which are fishes of intermediate size that often exhibit parental care and produce fewer but larger offspring. Not all fish species fit into these categories, many species have intermediate strategies.

Some of the most important life-history variables are growth rate, age and size at maturity, characteristics of the offspring (number, size and sex ratio), age and size-specific reproductive effort, age and size-specific mortality, and longevity. These variables interact together by many trade-offs, including those between reproductive effort and survival or growth, current reproduction and future reproduction, or the number and size of the offspring (Roff 1992, Stearns 1992). Life-history variables are fundamental determinants of population fitness (Winemiller and Rose 1992). Stearns (1976) defines fit organisms as those better represented in future generations than their relatively less fit competitors. Growth and reproduction are important components of fitness. In fishes, growth is of particular significance as fecundity is an increasing function of body size and energy channeled into the gonads reduces somatic growth and affects future fecundity (Roff 1983).

Growth is defined as the change in size (length and weight) over a period of time, or as the change in calories stored in somatic and reproductive tissues. Growth is one of the most intensely studied aspects of fish biology because it is a good indicator of health in individuals and populations. Most fishes grow throughout their entire lives; however, the growth rate among individuals is highly variable because it is dependent on several environmental factors such as temperature, levels of dissolved oxygen and ammonia, salinity, and photoperiod. These factors interact with each other and with other factors such as the degree of competition, amount and quality of food ingested, and the age and state of maturity. Fishes typically have a high growth rate in the first few months or years of life (depending on the longevity of the species), until maturation. When maturation is achieved, increasing amounts of energy are diverted from growth of somatic tissues to gonadal growth, resulting in much slower somatic growth rate in mature fishes than in immature (Moyle and Cech 1996).

Age at maturity is important in determining the growth rate (K) of a population (Stearns 1976). In fishes, and animals in general, maturity is defined as the age of first reproduction not the age when some morphological or physiological criterion is met (Stearns 1992). Maturity may range from early to late age with varying benefits and costs; benefits of an early maturity are a shorter generation time and a higher survival rate to maturity because of a shorter period as a juvenile. Early maturity leads to a cost in lower life-time fecundity, which may translate in less reproductive success, and lower quality of the offspring produced with the consequent increase in juvenile mortality. The advantage of an earlier maturity is greater for species with large clutches than for those with small clutches, and greater for species that only reproduce once and then die

(semelparous species) than for species that reproduce multiple times (iteroparous species) (Stearns 1976). Benefits of a later age at maturity are higher initial clutch size through longer juvenile growth, lower instantaneous juvenile death rates and ultimately higher fecundity through longer growth achieved during a prolonged adult life. The costs of delayed maturity are longer generation time and lower survival of juveniles to maturity (Stearns 1992). Delayed maturity is favored when juvenile survival is higher than adult survival, when the reproductive success depends on age, size, or social status, or in species where the investment in reproductive effort is considerable (e.g., salmon). When a population declines, the individuals usually delay reproduction to slow down the rate of decrease. The mean age at maturity can vary considerably among populations of the same species due to environmental factors. For example, the age at maturity for the American shad (*Alosa sapidissima*) increases with latitude from Florida to Canada (Leggett and Carscadden 1978). Another factor affecting maturity within species is the social interaction of the sexes. In polygynous species for example, males compete for females so the males tend to delay maturity, grow larger, and gain experience before attempting to reproduce, this pattern is called “bimaturism”. Age at maturity and fecundity generally increase with adult body size but since growth usually slows down with age, the age-specific fecundity also slows down (Roff 1992).

Clutch size or fecundity refers to the number of offspring and there are several alternative hypotheses to explain the most productive clutch size; one theory states that there are trade-offs between demands for resources directed to reproduction versus other functions. In temperate climates, organisms direct most of their energy into increasing the reproductive rate and the number of the offspring per reproductive event, while in

tropical climates smaller clutches should occur. A second hypothesis involves the trade-offs between clutch size and adult mortality; for perennial species, where the act of reproduction implies a mortality risk, large clutch sizes reduce the parents' chances of future survival and reproduction (Charnov and Krebs 1973). Another hypothesis is called "bet-hedging" because of the uncertainty related to conditions during the breeding season, where making a great reproductive effort could result in a total disaster (Stearns 1976); reproductive effort and risks are spread over time to increase chances of success. Regarding the size of the offspring, one hypothesis focuses on the size-number trade-off, where the proportional increase in fitness resulting from the production of larger offspring equals the proportional decrease in fitness resulting from fewer offspring and the increased expenditure on each offspring. Another hypothesis implies that variation in size is an adaptation to an unpredictable environment (Stearns 1992).

Other biological factors, such as predation, can affect the size and number of the offspring produced within species. Reznick (1982) demonstrated that some populations of the guppy *Poecilia reticulata*, a small (1-4 cm), viviparous, sexually dimorphic freshwater fish, matured earlier, made a larger reproductive effort, and had more, smaller offspring in sites where its main predator was a cichlid fish (*Crenicichla alta*) than in sites where its main predator was a killifish (*Rivulus hartii*). The cichlid selects large, mature guppies, while the killifish eats mostly small juvenile guppies (Stearns 1992).

All organisms utilize energy for three different purposes: maintenance, growth, and reproduction. Reproductive effort is a measure of the amount of energy and time invested by an organism, over a specific and biologically meaningful time, in the production of offspring. The age schedule of reproduction and survival is dependent

upon the use of energy for growth versus reproduction (Roff 1992). Several methods have been used to estimate how the organism is using its energy for reproduction or “reproductive effort”. One limited way to estimate the reproductive effort in fishes is taking the “gonadosomatic index” (GSI), which is the relative weight of the eggs and associated gonadal tissue to the total biomass or somatic weight of the individual. Besides the obvious investment in gonadal tissue, the reproductive effort of many organisms also includes investment in the offspring after birth (or after egg laying in oviparous species). Parental care is profitable if it increases the survival rate of the offspring without incurring an excessive cost, such as increased mortality of the parents, or missed breeding or feeding opportunities. One or both sexes participate when parental care is involved, with fish species showing the greatest variety among vertebrates. Clutton-Brock (1991) suggested that parental care in ectotherms might be present when environmental conditions are harsh, predation is heavy, or competition for resources is intense (Roff 1992). The number of offspring alone is not a good indicator of reproductive effort (Stearns 1976). Time invested and forgone opportunities for foraging should also be accounted for when measuring reproductive effort.

In living organisms in general, two basic reproductive strategies can be distinguished: semelparity and iteroparity. Semelparity is usually known as “big bang” reproduction because it describes the situation where an organism breeds once and then dies soon after reproducing. In this strategy, the amount of energy and time that must be allocated for reproduction (reproductive effort) drains the organism’s resources for maintenance until the point where it dies. There are relatively fewer examples of fishes (e.g., Pacific salmon, European eel, and American eel) with this type of reproduction than

organisms which breed more than once. Semelparity in these fish species may be, in part, a consequence of difficulties in migration, and it may explain why Pacific salmon *Oncorhynchus* spp. are in fact, semelparous, while the Atlantic salmon *Salmo salar* is iteroparous. Other explanations as to whether semelparity is present or not are the differences in physiology and/or phylogenetic constraints (Roff 1992). Iteroparous organisms breed more than once, allocate fewer energetic resources for reproduction than semelparous species, and are more common in general (Roff 1992). Iteroparity is favored by age-specific mortality and also when the risk of total reproductive failure in any given year is significant (Stearns 1976).

There are many examples of iteroparity among fishes. Snappers, groupers, tunas, sharks, drums, and flatfishes are all iteroparous organisms. The distinction between semelparity and iteroparity is not always clear because in several species some of the individuals die after the first spawning, but others survive to spawn more than once (e.g., blackhead minnow, *Pimephales promelas*). Difficulties in migration can also account for the “degree” of iteroparity present in some species. For example, the proportion of repeat spawners in sea-run brown trout, *Salmo trutta*, increases with the length of passable river and the water discharge. And finally, the relative allocation of energy to migration may be responsible for a latitudinal gradient in the proportion of repeat spawners present in the American shad (Roff 1992).

The life span or longevity of different species is affected by external factors which change the relative value of offspring and adults. Natural selection for further survival and reproduction is expected when the investment in the adult soma tends to maintain its value as the organism ages, resulting from low and constant adult mortality

relative to juvenile mortality. Selection for further survival and reproduction is weak when the adult soma loses value as it ages because adult mortality is high and variable relative to juvenile mortality and the effects of ageing accumulate (Stearns 1992).

Mortality has two different sources, extrinsic and intrinsic. Extrinsic sources of mortality are those that are not sensitive to changes in reproductive decisions. Intrinsic sources of mortality are those influenced by changes in allocations among reproduction, maintenance, and defensive structures and behaviors. Ageing is defined as an increase in the intrinsic component of mortality with age (Stearns 1992).

A theoretical approach developed to explain this variability in life-history traits, called r-and K-selection, involves the effect of physical versus biological factors when determining the age at maturity. The basic idea of r- and K-selection originated fifty years ago with a paper by Dobzhansky (1950) and was elaborated later when MacArthur and Wilson (1967) coined the term. The basic concept of this theory states that natural selection operates in a fundamentally different ways in the tropics than it does in temperate areas. In r-selection, physical factors are most frequently limiting and act in a density-independent way. Life-history characteristics associated with r-selection include early age at maturity, large clutch size, semelparity, no parental care, a large reproductive effort, small and numerous offspring, low assimilation efficiency, and a short generation time. Thus r-selection occurs in environments favoring rapid population growth and is typical of temperate areas where the climate is variable or unpredictable (Stearns 1976). In K-selection, biological interactions predominate, leading to selection for ability to compete and to avoid predation; it is most common in tropical areas with stable environments, favoring ability to compete and to avoid predation. In K-selection,

reproduction is delayed. Characteristics include small clutches, a high degree of parental care, low reproductive effort in a given year, a few, large offspring, and high assimilation efficiency. Stearns (1976) at first supported this theory but later rejected it as incorrect. He argues that it involves population regulation rather than a demographic mechanism, and that it fails about half of the time to correctly classify life histories of species when reliable data are available, and that it has failed when tested in artificial selection experiments (Stearns1992).

CHAPTER 2

COMPARISON OF LIFE HISTORY FACTORS AMONG SNAPPERS

Introduction

Snappers are generally medium (300 – 600 mm) to large (> 600 mm) fishes with some species reaching total lengths well over 1000 mm. Previously snappers were characterized as short-lived (< 11 years), fast growing fishes with relatively high rates of natural mortality (Newman 1996a & b), but new age and growth data from validated studies of sectioned otoliths indicate that snappers are often long-lived (up to 53 years), slow growing fishes with low rates of natural mortality (Newman 2000a, b, Wilson and Nieland 2001). Snappers are in the family Lutjanidae, which is composed of 103 species in four subfamilies. The largest subfamily is the Lutjaninae with 73 species and the smallest is the subfamily Paradicichthyinae with two species. The subfamilies Etelinae and Apsilinae have 18 and 10 species, respectively (Allen 1985).

Regarding their reproductive biology, snappers are dioecious and gonochoristic organisms; this means that they have separate sexes and that the sexual differentiation remains constant throughout their life span. Sexual dimorphism in structure or color pattern is rare and only reported in two species (genus *Pristipomoides*) from the Indo-west Pacific (Grimes 1987).

A key reproductive feature displayed by several species of inshore-dwelling lutjanids that has not been well documented until recently, is an extensive migration to select offshore areas along outer reefs to form seasonal spawning aggregations in the week or so prior to the full moon. This behavior has been known for decades in other tropical reef fish families like the groupers (family Serranidae), and this characteristic alone has huge potential implications for the management of several snapper fisheries (Thresher 1984).

Not all species within the snapper family display this extensive migratory behavior during the spawning season. Domeier *et al.* (1996) characterized two different spawning strategies for inshore snappers: medium sized, schooling species do not migrate or form spawning aggregations, while large and solitary species do migrate and form aggregations during the spawning season. The adult populations of deeper water species (>100 m), which are normally found off-shore, on the continental slope, apparently move little or not at all to spawn (Thresher 1984).

Migrations and aggregations related to spawning have been reported for several species of the subfamilies Lutjaninae and Paradicichthyinae from both sides of the Atlantic and the Indo-Pacific oceans. Bortone and Williams (1986), Domeier *et al.* (1996), Domeier and Colin (1997) and Dahlgren *et al.* (2001) witnessed spawning aggregations of mutton and grey snappers (*L. analis* and *L. griseus*, respectively). They noted that both species migrate from inshore to offshore waters during the spawning season and remarked that mutton snappers are rarely found in groups or schools in coastal waters. During the spawning season these aggregations, of at least several hundred individuals each, lasted for several weeks, exhibited high site fidelity and spawned regularly on the same days of the lunar calendar. The aggregations were observed at Dry Tortugas, south Florida, off the coast of Turks and Caicos, and off the coast of Belize. All aggregation sites were located on the edge of a steep drop-off where spawning occurred at dusk.

Carter and Perrine (1994), Domeier *et al.* (1996) and Domeier and Colin (1997) observed mass spawning aggregations of dog snapper (*L. jocu*). The aggregation observed by Carter and Perrine (1994) had around 500-1000 individuals, was located off central Belize (about 32 km from the coast line) where water depth was 27 – 30 m and occurred during daylight hours (1400-1500 hrs). Borrero *et al.* (1978), Claro (1982), Bortone & Williams (1986) and Garcia-Cagide *et*

al. (1994) reported that lane snappers (*L. synagris*) form spawning aggregations in Cuba, which migrate against strong currents and spawn where water depth is 30 – 40 m. These migrations are actually famous among Cuban fishermen who call them “lane snapper runs” and they also describe transit areas with individuals of *L. synagris* not quite ready for spawning.

Beaumariage & Bullock (1976), Moran (1988) and Domeier and Colin (1997) reported that red snappers (*L. campechanus*) spawn away from reefs and at a depth of 18 – 37 m over a sand bottom with little relief. Similarly, Thresher (1984) reported two areas of concentrated spawning activity for *L. campechanus* off the northern coast of Florida, each at the edge of deep water, between 20 and 40 m. Domeier *et al.* (1996) and Domeier and Colin (1997) reported that cubera snappers (*L. cyanopterus*) form spawning aggregations and they observed three of these aggregations off the coast of south Florida where water depth was about 67 – 85 m, and another two off the coast of Belize at water depths of 10 – 30 m, all during the months of June and July. Bortone & Williams (1986) documented that yellowtail snappers (*Ocyurus chrysurus*) spawn in groups usually migrating offshore during the spawning season.

Other reports include Caveriviere (1996), who documented frequent spawning aggregations of up to 2,500 large (840 – 1160 mm fork length) African red snappers (*L. agennes*), off the Guinea Gulf coast on western Africa, which were captured by accident by tuna purse seiners in surface waters where depth was up to 3,000 m and about 80 km from the coast line; specimens analyzed were found to be mature. Lieske and Myers (1994) and Domeier and Colin (1997), noted that the Indo-West Pacific sail-fin snappers (*Symphorichthys spilurus*) aggregate to spawn along seaward reefs. Finally, Domeier and Colin (1997) reported spawning aggregations without detailed descriptions for the Indo-West Pacific species of mangrove red snapper (*L. argentimaculatus*), two-spot red snapper (*L. bohar*), humpback red snapper (*L.*

gibbus), black and white snapper (*Macolor niger*) and the Chinaman fish (*Symphorus nematophorus*).

Lunar or semilunar spawning cycles have been recorded for snappers, with increased spawning intensity at full or new moon, or both. Snappers (e.g., *L. vitta*) spawn at various times throughout the day, including dusk, more likely in response to the timing of the tides (Sadovy 1996). There have been few sightings of the actual spawning act, but the general pattern is described by Susuki and Hioki (1979) for *Lutjanus kasmira* in an aquarium. Group spawning of ten or more individuals occurred during the evening and night in August, with water temperatures between 22.2 and 25.2 °C. Males initiated courtship by pecking and rubbing against the body of the female. Eventually other fish joined the activities and initiated a spiral ascent, releasing gametes just below the surface. Hamamoto *et al.* (1992) noted a similar pattern for *L. stellatus* at another aquarium in Japan where the fish formed a spawning aggregation of more than 100 individuals. Spawning behavior occurred every night, from 2000 – 2300 hrs, over a period of one month from mid May to mid June with water temperatures ranging from 24 to 26 °C. The behavior was similar to that reported by other authors, forming small schools with several males following a single female, nuzzling, and finally rushing towards the surface.

Lutjanids are batch spawners with individual females generally spawning several times during the year (Thresher 1984). Batch and annual fecundities are highly variable with female size. For example, a single ripe female red snapper (*L. campechanus*) of 610 mm TL yields over 200 times more eggs than a 420 mm TL individual (Pauly *et al.* 2002). Collins *et al.* (1996) calculated that the annual fecundity for the same species ranges from 0.012 to 59,666 million eggs per female, assuming an equal spawning frequency for all sizes and ages.

Based on larval abundance, two types of seasonal reproductive patterns are common to the family: continental populations and species exhibit a protracted summer spawning, whereas insular populations and species reproduce in a more or less continuous pattern with peak activity in the spring and fall (Allen 1985, Grimes 1987).

Lutjanid eggs are pelagic, spherical in shape, with a diameter ranging from 0.65 to 1.02 mm, and usually contain a single oil droplet 0.12 – 0.20 mm in diameter (except in *L. erythropterus*, where no oil droplet is present) which provides buoyancy. Eggs are similar to most pelagic eggs, which makes them difficult to identify from plankton samples. Eggs hatch after 17 to 36 hours, depending on the species and temperature, and the just-hatched larvae are also similar to the vast majority of larvae coming from pelagic eggs (Leis 1987).

Newly hatched larvae measure less than 2 mm TL, have a large yolk sac, unpigmented eyes, no mouth and limited swimming abilities. The yolk sac reserves last for 3 – 4 days and by this time the eyes are pigmented and the mouth becomes functional. After a few more days, snapper larvae develop spines on the head and some have particularly long dorsal and pelvic fins what make them relatively easy to identify at this point. These spines reach a maximum length when larvae are about 7 – 8 mm SL and then decrease in relative size and remain only slightly elongated at settlement. Larvae of the subfamilies Lutjaninae and Paradicichthyinae are most common in coastal waters while Apsilinae and Etelinae larvae are more common in offshore areas. The larval pelagic stage lasts for 25 – 47 days, when larvae are between 12 and 20 mm TL (Allen 1985, Leis 1987, Lindeman *et al.* 2001).

After settlement juveniles remain on nursery grounds usually for a period of 2 to 4 years, until they reach maturity, and then move to other areas joining the adult population. On average, lutjanids reach their maturity at about 43 to 51 % of the maximum total length, with

males maturing at a slightly smaller size than females (Allen 1985, Everson *et al.* 1989). Populations and species of snappers associated with islands mature at a significantly higher percentage of maximum length (51%) than continental species and populations (43%). Deep-water species and populations mature at a significantly higher percentage of maximum size (49%) than shallow-water species (43%) (Grimes 1987). Size at maturity is a particularly important parameter used to assess and evaluate the impact of fishing mortality on the spawning stock biomass and to determine levels of optimum fishery yield (Froese and Pauly 2000).

The objectives of this Chapter are (1) to collect all available information on life-history and reproductive variables in populations of snappers; (2) standardize all information obtained from the literature into a single format; (3) estimate missing values from other related variables; (4) analyze the data set for patterns of variability using a series of Principal Component Analyzes; (5) detect sources of life-history variation among snappers within each subfamily and among subfamilies; and (6) relate the variability of life-history traits to strategies in reproductive biology in snappers.

Methodology

An extensive search for information on life-history variables pertaining to species of the family Lutjanidae was conducted to create a database from peer-reviewed journals, conference proceedings, special reports, and thesis and dissertations. In some instances, the authors were contacted for additional information, to obtain updates on current investigations, or to request permission to use their materials. Ten life-history variables included age at length zero, asymptotic length, maximum length, longevity, asymptotic weight, length and age at maturity, reproductive life span, growth rate, and mortality rate. A preliminary database showed that there was information on some of these variables for a considerable number of species and

populations, but the complete set of all ten variables was available for only a few species. I used published relationships to estimate the missing values from the variables already present in the initial database. Froese and Binohlan (2000) developed and published a series of empirical equations to estimate asymptotic length, length at maturity, and longevity from maximum observed length. Froese and Pauly (2000) also developed other empirical equations to estimate growth rate from life span and the age at length zero from asymptotic length and growth rate. Finally, Pauly (1980) developed an empirical equation to estimate mortality from asymptotic length, growth rate and the annual mean temperature of the surface water where the population lives. Using these equations it was possible to complete all ten variables for each population if (1) either an ageing or a growth study was available and (2) either an estimate of asymptotic length or maximum length existed. Only publications with this minimum of information were included in the database. Original sources were preferred even when several authors cited information on these variables from third parties. As expected the information obtained came in a wide variety of styles and formats, but data were standardized to a single format and the same units before analysis.

Several of the life-history variables investigated here are either components of the von Bertalanffy growth equation (VBGE) or were estimated using a manipulation of the same equation, its basic form to estimate length at any age is:

$$L_t = L_{inf} (1 - e^{-K(t-t_0)}),$$

where L_t is the length at age t , L_{inf} is the asymptotic length, K is the growth rate per year, and t_0 is the hypothetical age at length zero. These components are explained in detail below. The definitions of the selected life-history variables and the methodology to estimate them if not obtained from the literature are the following:

Age at length zero (t_0) is defined as the hypothetical age in years when the individuals would have had at a length equal to zero, if their early life stages grew in the manner described by the VBGE. The values of this variable for snappers are usually between 0 to -1. When not available, values of t_0 were estimated from asymptotic length (L_{inf}) and growth rate (K) using the empirical formula by Pauly (1980):

$$\log (-t_0) = -0.3922 - 0.2752 \log L_{inf} - 1.038 \log K.$$

Asymptotic length (L_{inf}) is defined as the length in millimeters that a fish of a given population would reach if they would grow indefinitely (it is also known as length infinity and represented as **L ∞**). If no growth studies were available, L_{inf} was estimated from maximum length (L_{max}) using another empirical relationship between L_{inf} and L_{max} developed by Froese and Binohlan 2000:

$$\log L_{inf} = 0.044 + 0.9841 * \log (L_{max}) \quad (r^2 = 0.959, \text{S.E.} = 0.074, n = 551).$$

Another practical way to estimate L_{inf} is using the mean size of the ten largest fish within the sample (Pauly 1984).

Maximum length (L_{max}) is the maximum total length (TL) observed and reported for each population. Standard lengths (SL) and fork lengths (FL) were transformed to total length using conversion formulas (Appendix A). Most of these formulas were estimated by Froese and Pauly (2000). For five species of the genus *Pristipomoides*, the conversion formulas were missing and had to be estimated from means of pictures following Froese and Pauly (2000).

L_{max} was estimated using an equation derived from the relationship used to calculate L_{inf} as follows

$$\log L_{max} = (\log L_{inf} - 0.044)/0.9841.$$

Longevity (t_{\max}) is the maximum age reported in years that individuals of a given population would reach. Following Taylor (1958), t_{\max} was calculated as the age at 95% of L_{inf} , and using the parameters of the von Bertalanffy growth equation it was estimated as

$$t_{\max} = t_0 + 3 / K.$$

If a growth rate estimate was not available for a population but the age at maturity was known, then longevity was estimated from the following empirical formula (Froese and Binholan 2000):

$$\log t_{\max} = 0.5496 + 0.957 * \log t_{\text{mat}} \quad (r^2 = 0.77, \text{S.E.} = 0.194, n = 432).$$

Asymptotic weight (W_{inf}) was estimated using the asymptotic length value for each population and the conversion values 'a' and 'b' for each particular species obtained from Froese and Pauly (2000) and the following equation

$$W_{\text{inf}} = a L_{\text{inf}}^b.$$

Length at maturity (L_m) is defined as the smallest length category in which at least 50% of the individuals of a given population are mature (stage II or beyond, $\text{GSI} > 1.5$) for the first time during the spawning season. Missing values of length at maturity were calculated separately for different populations from an empirical relationship between length at maturity (L_m) and asymptotic length (L_{inf}) by Froese and Binohlan (2000).

Mixed genders: $\log L_m = 0.8979 * \log L_{\text{inf}} - 0.0782 \quad (r^2 = 0.888, \text{S.E.} = 0.127, n = 467).$

Male: $\log L_m = 0.8915 * \log L_{\text{inf}} - 0.1032 \quad (r^2 = 0.855, \text{S.E.} = 0.147, n = 115).$

Female: $\log L_m = 0.9469 * \log L_{\text{inf}} - 0.1162 \quad (r^2 = 0.905, \text{S.E.} = 0.122, n = 167).$

Age at maturity (t_m) is the mean age at which fish of a given population mature for the first time. It was calculated from length at maturity by solving the von Bertalanffy growth function for t_m (Froese and Pauly 2000):

$$t_m = t_0 - \ln(1 - L_m / L_{inf}) / K.$$

Reproductive life span (RLS) is the number of years that fish of a given population make a reproductive effort. RLS was estimated subtracting the age at maturity from the maximum reported age for a particular population:

$$RLS = t_{max} - t_m.$$

Growth rate (K) expresses the rate per year at which the asymptotic length is approached (it is also known as the Brody coefficient). The value of K was calculated using data on length at maturity (L_m) and age at maturity (t_m) if available for a species, from the following equation (Froese and Pauly 2000):

$$K = -\ln(1 - L_m / L_{inf}) / (t_m - t_0).$$

If there were no available growth and maturity data, but an estimate of maximum age (t_{max}) was available, K was calculated from the equation (Froese and Pauly 2000):

$$K = 3 / (t_{max} - t_0).$$

Natural mortality rate (M) refers to the mortality during the late juvenile and adult phases of a population per year, excluding mortality attributed to fishing activities (F). It was calculated from an empirical equation based on asymptotic length (L_{inf}) and the mean annual water temperature in degrees Celsius (T) (Froese and Pauly 2000):

$$M = 10^{(0.566 - 0.718 * \log(L_{inf}) + 0.02 * T)}.$$

All estimated data were labeled and compared with data from publications; separate minimum, maximum and mean values were determined for data from the literature and for the estimates made here to corroborate the precision of the equations employed. In addition to the quantitative values of each variable, records were kept providing information for each population about the geographic location of the study population, literature reference, ageing method

employed by the author (i.e., whole or sectioned otoliths, scales, vertebrae, urohyals, length frequency analysis, radiometric analysis, aquarium observation or maturity study), and whether the analysis was gender specific or based on mixed genders. For further comparison, the information about these variables for species of snappers available on the FishBase website (www.fishbase.org) was also included.

Principal Component Analysis

A Principal Component Analysis (PCA) of ten life-history variables was performed to explore variance patterns among subfamilies and among species within subfamilies of snappers. The PCA was conducted using the Factor Procedure in SAS (SAS Institute 1996) and the first four factors were rotated using the Varimax option to facilitate the interpretation of each separate component. The PCA was configured to resolve ten inter-correlated life-history variables into four orthogonal factors to facilitate interpretation and comparisons among species and subfamilies. Life-history variables in 408 snapper stocks without missing data were used to estimate variable loadings and generate principal component scores for each species. The mean value of the variables for each species was obtained from the populations through the Means Procedure in SAS (SAS Institute 1996). The subfamilies and species within subfamilies were plotted as centroids in three-dimensional life-history space with radii adjusted to one standard error. The interpretation was based on eigenvalues of the correlation matrix that were greater than or equal to 1.0 and rotated factor loadings that were greater than or equal to 0.50 (Grossman 1991). Other methods to analyze the data included correlation, statistical and graphic analyses.

Results

Age or growth studies were available for 408 different lutjanid stocks, representing 51 species of snappers in all four subfamilies. Publications provided approximately half of the

values (after standardization) and permitted estimation of all other missing values from the life-history database, resulting in 408 complete stocks. The values reported in literature and the estimates developed from empirical equations were very similar since all estimates were near or within the same limits as the values from the literature (Table 2.1). Separate correlation analyses of the initial database (values from literature only) and the expanded database (estimates included) showed similar values (Table 2.2).

Table 2.1 Mean value (\pm S.D., (n)) and range for ten variables reported in literature and overall for the family Lutjanidae.

Variable	Literature	Overall
t₀	-0.73 \pm 0.86 (226)	-0.72 \pm 0.68 (408)
Range	-4.04 to 1.60	-4.04 to 1.60
L_{inf}	701.16 \pm 273.69 (367)	698.88 \pm 269.07 (408)
Range	205 to 1773	205 to 1773
L_{max}	673.38 \pm 279.13 (224)	689.79 \pm 267.93 (408)
Range	224 to 1600	224 to 1739
t_{max}	16.75 \pm 10.35 (250)	15.93 \pm 9.33 (408)
Range	3 to 53	3 to 53
W_{inf}	6149.47 \pm 7728.39 (161)	6957.03 \pm 8771.06 (408)
Range	177 to 57000	116 to 118000
L_m	352.13 \pm 150.58 (144)	365.51 \pm 139.34 (408)
Range	92 to 811	92 to 873
t_m	2.77 \pm 1.36 (109)	3.30 \pm 1.61 (408)
Range	1 to 8	0 to 10
RLS	11.70 \pm 7.84 (105)	12.70 \pm 8.77 (408)
Range	2 to 51	0 to 51
K	0.24 \pm 0.16 (363)	0.24 \pm 0.16 (408)
Range	0.06 to 1.46	0.06 to 1.46
M	0.43 \pm 0.29 (186)	0.55 \pm 0.29 (408)
Range	0.08 to 1.9	0.08 to 1.9

t₀ = age at length zero, L_{inf} = asymptotic length, L_{max} = maximum length, t_{max} = longevity, W_{inf} = asymptotic weight, L_m = length at maturity, t_m = age at maturity, RLS = reproductive life span, K = growth rate and M = mortality rate.

Table 2.2 Correlation analyses of ten life-history variables in the initial and expanded databases for the family Lutjanidae.

	t 0	L_{inf}	L_{max}	t max	W inf	L_m	t m	RLS	K	M
t 0	1	0.01	0.06	-0.21	-0.01	-0.03	-0.31	-0.16	0.40	0.05
L_{inf}	0.08	1	0.95	0.13	0.77	0.90	0.26	0.09	-0.35	-0.51
L_{max}	0.18	0.92	1	0.18	0.76	0.88	0.26	0.14	-0.34	-0.49
t max	0.02	0.00	0.21	1	0.09	0.13	0.41	0.98	-0.40	-0.28
W inf	0.08	0.84	0.78	0.14	1	0.70	0.19	0.06	-0.23	-0.33
L_m	-0.05	0.81	0.82	0.07	0.77	1	0.42	0.05	-0.33	-0.43
t m	-0.23	0.30	0.36	0.42	0.25	0.47	1	0.22	-0.52	-0.31
RLS	-0.16	0.07	0.15	0.99	0.04	0.02	0.28	1	-0.31	-0.23
K	0.33	-0.34	-0.32	-0.17	-0.26	-0.20	-0.50	-0.29	1	0.52
M	0.12	-0.18	-0.13	-0.54	-0.30	-0.21	-0.41	-0.37	0.62	1

t_0 = age at length zero, L_{inf} = asymptotic length, L_{max} = maximum length, t_{max} = longevity, W_{inf} = asymptotic weight, L_m = length at maturity, t_m = age at maturity, RLS = reproductive life span, K = growth rate and M = mortality rate. Correlation coefficients below the diagonal are based on observed literature data; while those above the diagonal are based on the expanded database including the estimates generated from published relationships. Sample size for literature data are given in Table 2.1, the sample size for the expanded data set is 408.

The correlation analysis of the initial database of life-history variables for the family Lutjanidae (Table 2.2) revealed several distinctive patterns. High correlations were available among and between size variables (asymptotic, maximum and length at maturity and asymptotic weight) and for longevity and reproductive life span. Growth and mortality rates were moderately correlated, and longevity had a low correlation with all size variables and with age at maturity. Most of the correlations among size variables suggested redundancy between them and required little analysis; however, the correlations between length at maturity and other size variables indicated that the size at which a particular species matured was dependent upon the asymptotic or maximum size it reached later in life. In contrast, the low correlation between size

variables and longevity indicated that size is not dependent upon life span, so small species could achieve long life spans and vice versa.

The high correlation between longevity and reproductive life span and the low correlations of age at maturity with longevity and the different size variables suggest that snappers mature at about the same age regardless of the life span, length at maturity or maximum length. This assumption was made because the difference between longevity and reproductive life span is age at maturity and is supported by the relatively low standard deviation of the mean age at maturity. The mean overall age at maturity for snappers in the four subfamilies was 3.3 years (Table 2.1).

The PCA for the species in the family Lutjanidae resolved ten life-history variables into four factors that explained over 85 % of the variability among the species (Table 2.3). The first three factors had eigenvalues values > 1.0 . The first Principal Component (PC1) accounted for 43.5 % of the variation and loaded heavily ($= 0.50$) and positively for the four measures of size (i.e., asymptotic, maximum, maturity and length and asymptotic weight), which were all positively related. The second Principal Component (PC2) accounted for 22.6 % of the variation and loaded heavily and positively for longevity and reproductive life span. The third Principal Component (PC3) explained 12.0 % of the variation and loaded heavily and positively for age at length zero and growth rate and negatively for age at maturity. The fourth Principal Component (PC4) explained 7.7 % of the variation and loaded heavily and positively for mortality and growth rates.

The plots of subfamily centroids in three dimensional life-history space (Figure 2.1) characterized the subfamily Lutjaninae as having smaller species with intermediate life spans. It had the second longest lived species after the subfamily Paradicichthyinae, which has only two

species and both appear to be long lived; the latter subfamily is characterized as large, long-lived, and slow growing, and late maturing. The single species representing this subfamily has a large asymptotic length (932 mm TL). The subfamilies Etelinae and Apsilinae are characterized by intermediate size; the subfamily Etelinae is intermediate in size between the subfamilies Lutjaninae and Paradicichthyinae and shorter in life span. Finally, the subfamily Apsilinae was the shortest-lived group and smaller in size than the Etelinae.

Table 2.3 Loadings, eigenvalues and variance explained by factor from the Principal Component Analysis of the life-history variables for all subfamilies.

Variables	Factor 1	Factor 2	Factor 3	Factor 4
Asymptotic length	0.93795	0.03320	-0.02709	-0.25294
Maximum length	0.93433	0.09726	0.01826	-0.23533
Length at maturity	0.90726	-0.00023	-0.14654	-0.20093
Asymptotic weight	0.88019	0.03255	-0.05833	-0.00502
Reproductive life span	0.02395	0.98868	-0.07263	-0.08904
Longevity	0.06426	0.96314	-0.19555	-0.15915
Age at length zero	0.05704	-0.07209	0.89462	-0.07708
Age at maturity	0.21325	0.19196	-0.62094	-0.35677
Growth rate	-0.17426	-0.19856	0.54934	0.64032
Natural mortality rate	-0.31074	-0.13288	-0.00654	0.86329
Eigenvalue	4.35448	2.25990	1.20147	0.76966
Proportion of variation	0.4354	0.2260	0.1201	0.0770
Cumulative variance	0.4354	0.6614	0.7816	0.8586

The species centroids in three dimensional life-history space for 34 species within the subfamily Lutjaninae in relation to the ten variables analyzed (Figure 2.2) show that PC1 placed the species by adult size variables, while PC2 separated the species by life span variables (redundant with RLS) and PC3 by age at maturity (negatively), age at zero length and growth rate. Most of the species within this subfamily were located in a single central group with several species overlapping with others. This indicates a homogeneous group of species with similar life-history characteristics; however, some small snappers (*L. fulviflamma*, *L.*

quinquelineatus and *L. adetii*) had considerably longer life spans than larger species (*L. sanguineus*, *L. sebae* and *L. argentimaculatus*). Cubera snapper (*L. cyanopterus*) had the most evident separation from all other species because it is considerably larger than the rest of the species.

The species centroids in three dimensional life-history space for 14 species within the subfamilies Paradicichthyinae, Etelinae and Apsilinae (Figure 2.3) showed the formation of three different groups. The first group is centrally located on PC1 and has three species from the subfamily Etelinae (genera *Pristipomoides*, *Etelis* and *Aprion*) and the only species from the subfamily Paradicichthyinae (*Symphorus nematophorus*). These species have an intermediate size and longer life spans than the other groups. The second group of smaller species (PC1) includes five species from the subfamily Etelinae (all *Pristipomoides*) and the only species from the subfamily Apsilinae (*Apsilus dentatus*). These species are small, short lived and two (*Apsilus dentatus* and *Pristipomoides zonatus*) have high growth and mortality rates. The third group includes all Etelinae species (genera *Etelis* and *Aphareus*) and can be characterized as large species with short life spans and relatively low growth and mortality rates.

Subfamily Lutjaninae

For the subfamily Lutjaninae data for 322 stocks and 37 species were available. Age at length zero values were available for 186 stocks and an additional 136 were estimated using the empirical equation. The mean from the literature was -0.789 years with a minimum value of -4.04 years for *L. buccanella* and a maximum of 1.48 years for *L. peru*. The mean estimate from the equation was -0.717 years with a minimum value of -1.847 years for *L. malabaricus* and a maximum of -0.154 years for a population of *L. Lutjanus*.

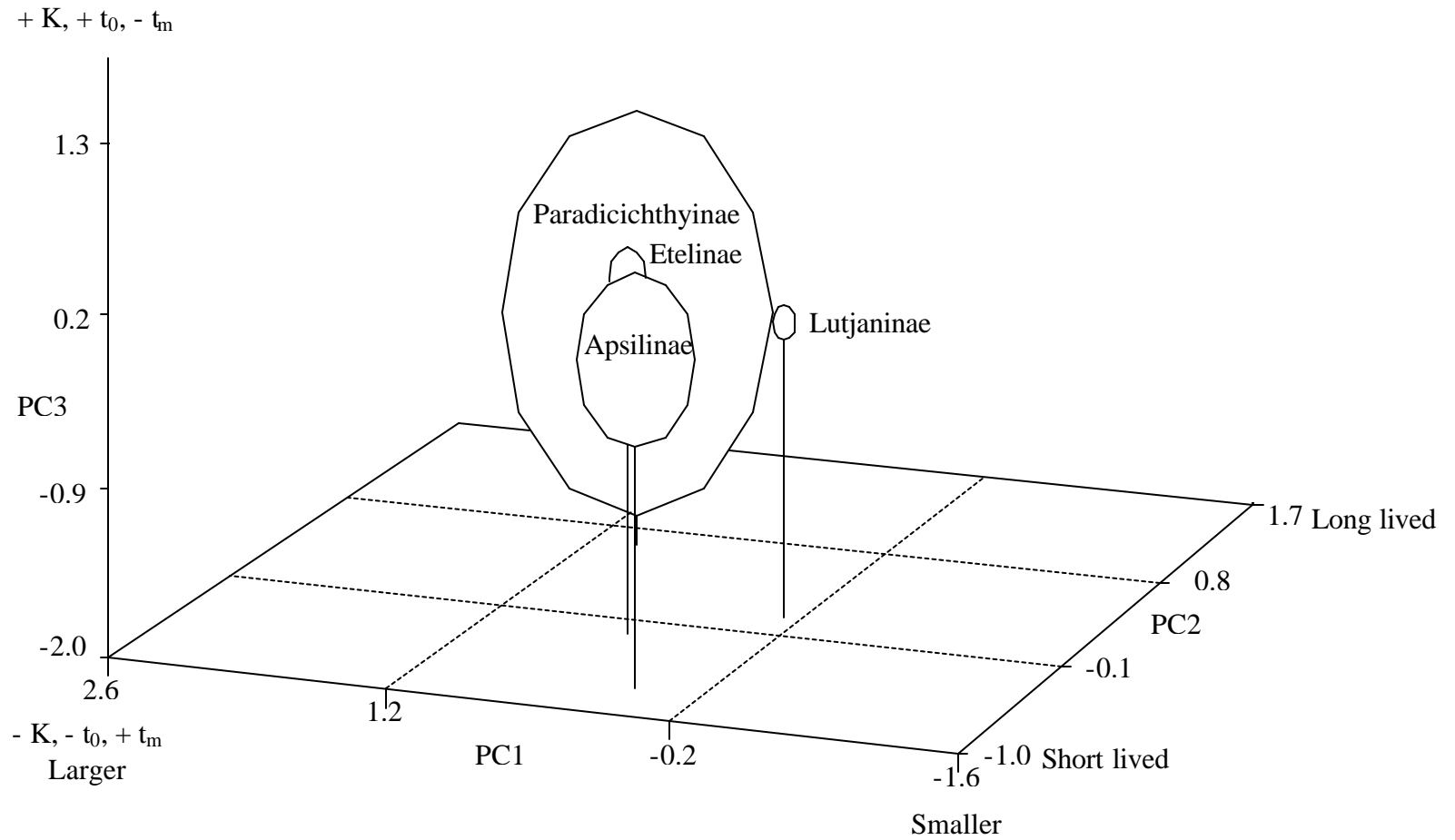


Figure 2.1 Life-history data for the family Lutjanidae. Subfamilies in 3-dimensional life-history space.

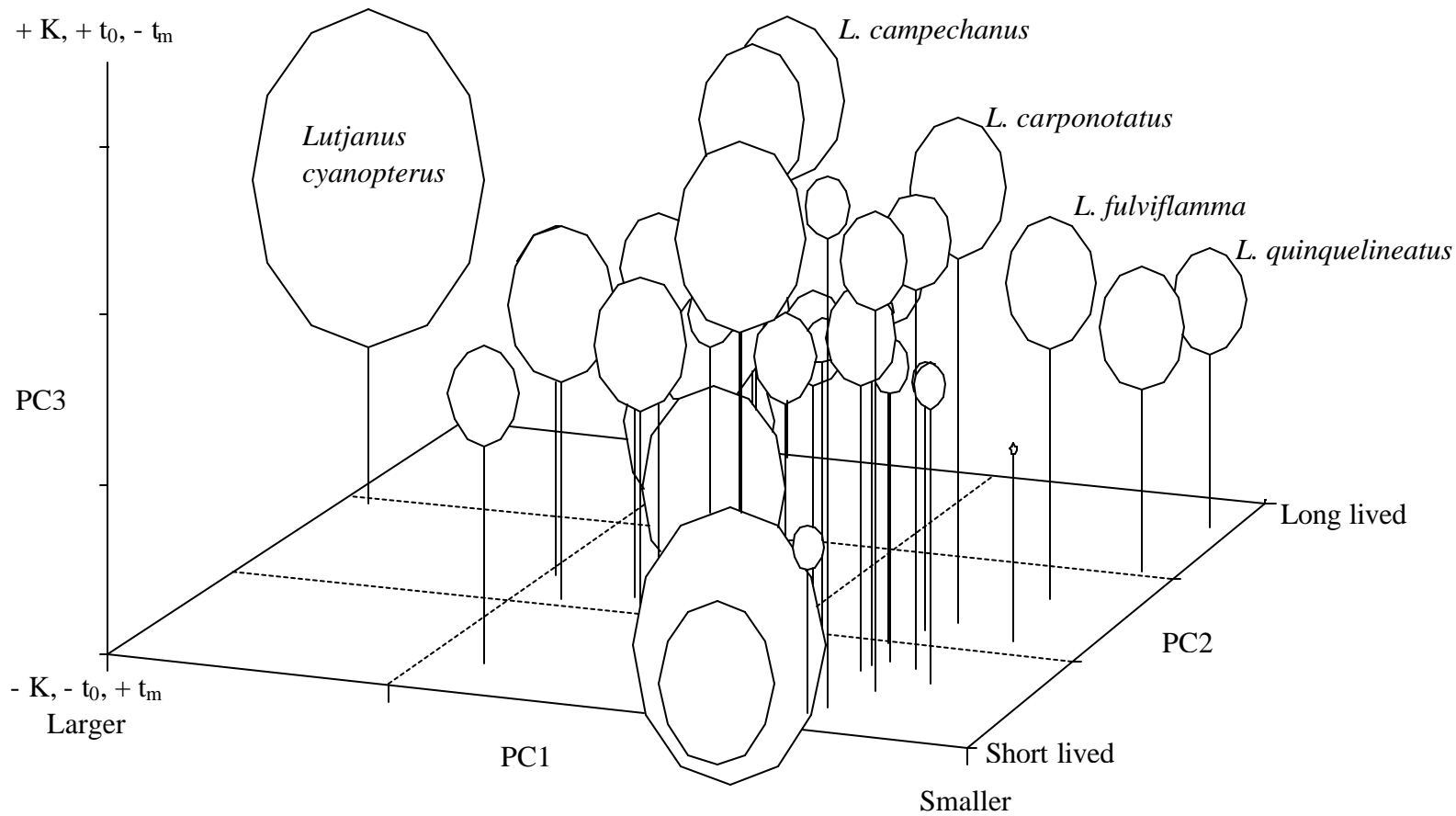


Figure 2.2 Life-history data for species in the subfamily Lutjaninae. Species in 3-dimensional life-history space.

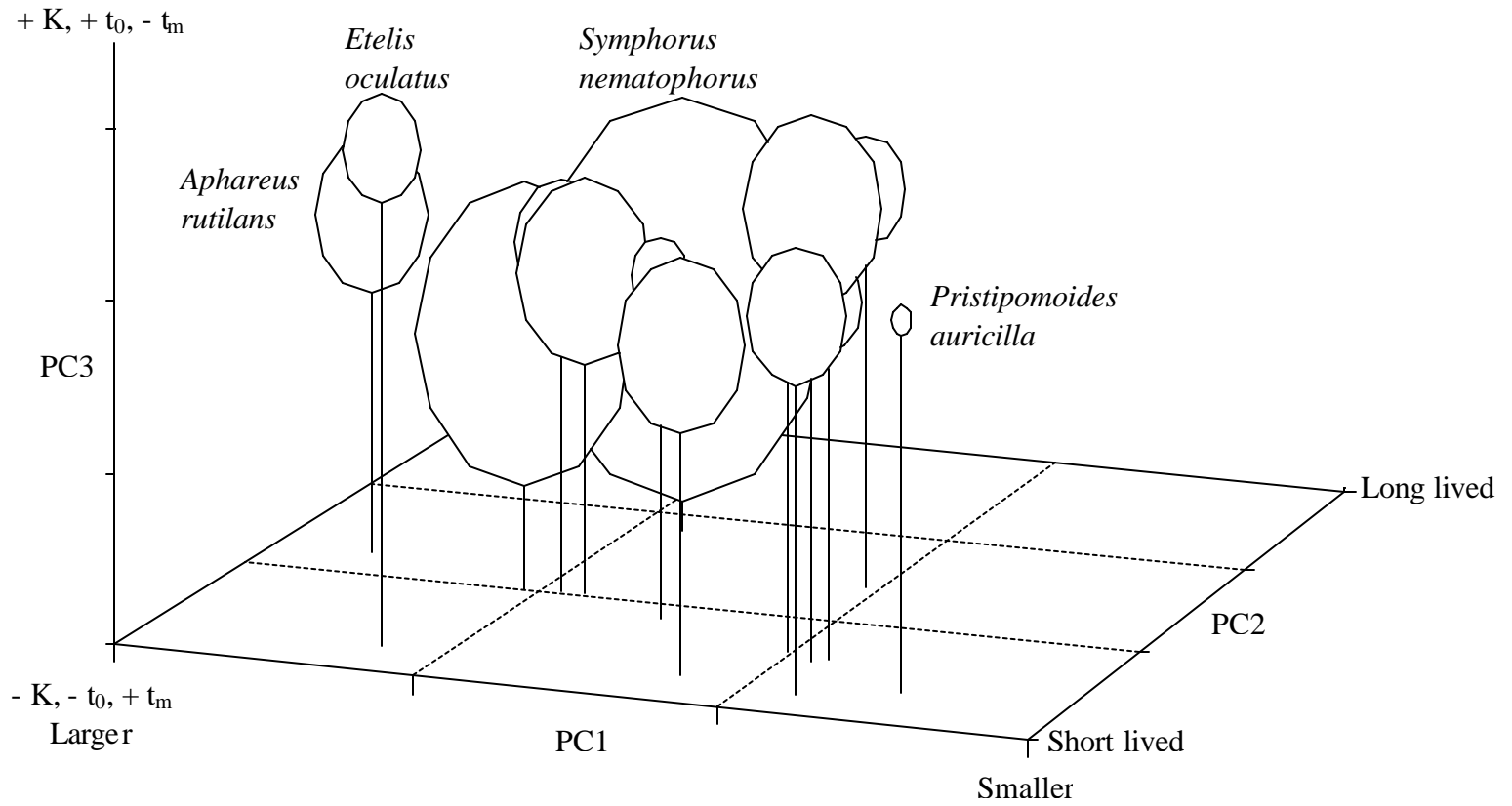


Figure 2.3 Life-history data for species in the subfamilies Paradicichthyinae, Etelinae and Apsilinae. Species in 3-dimensional life-history space.

Asymptotic length values (mm TL) were available for 288 stocks and only 34 were estimated using the empirical equation. The mean from publications was 673 mm with a minimum value of 205 mm for *L. quinquelineatus* and a maximum of 1,773 mm for *L. sebae*. The mean estimate was 614 mm with a minimum value of 313 mm for *L. synagris* and a maximum of 1,028 mm for *L. malabaricus*. Maximum length values (mm TL) were available for 176 stocks and 146 were estimated using the empirical equation. The mean from publications was 634 mm with a minimum value of 224 mm for *L. quinquelineatus* and a maximum of 1,600 mm for *L. cyanopterus*. The mean estimate was 686 mm with a minimum value of 239 mm for *L. lutjanus* and a maximum of 1,739 mm for *L. sebae*. Asymptotic weight values were available for 126 stocks and 196 were estimated using the empirical equation. The mean from publications was 5,748 g with a minimum value of 177 g for *L. quinquelineatus* and a maximum of 57,000 g for *L. cyanopterus*. The mean estimate was 6,877 g with a minimum value of 116 g for *L. quinquelineatus* and a maximum of 118,000 g for *L. sebae*.

Longevity values were available for 213 stocks and 109 were estimated using the empirical equation. The mean from publications was 17.1 years with a minimum value of 3 years for *L. lutjanus* and a maximum of 53 years for *L. campechanus*. The mean estimate was 15.4 years with a minimum value of 4 years for populations of *L. buccanella*, *L. lutjanus*, *L. notatus*, and *L. vitta* and a maximum of 33 years for a population of *L. vivanus*. Length at maturity information was available for 106 stocks and 216 were estimated using the empirical equation. The mean from publications was 313 mm with a minimum value of 92 mm for some populations of *L. synagris*, and a maximum of 811 mm for a population of *L. cyanopterus*. The mean estimate was 365 mm with a minimum value of 103 mm for *L. quinquelineatus*, and a maximum of 873 mm for a population of *L. sebae*.

Age at maturity information was available for 86 stocks and 236 were estimated using the empirical equation. The mean from publications was 2.9 years with a minimum value of 1 year for some populations of *L. quinquelineatus*, *L. lutjanus*, *L. notatus*, *L. synagris*, *L. vitta*, *L. kasmira*, and *Rhomboplites aurorubens* and a maximum of 8 years for a population of *L. buccanella*, *L. peru* and also *L. quinquelineatus*. The mean estimate was 3.7 years with a minimum value of 0 years for a population of *Ocyurus chrysurus* and *L. synagris*, and a maximum of 10 years for a population of *L. campechanus*. Reproductive life span values were estimated for all 322 population stocks of Lutjaninae species. The mean was 13.1 years with a minimum value of 0 years for populations of *L. buccanella* and *L. sebae* and a maximum of 51 years for a population *L. campechanus*. Growth rate values were available for 287 stocks and 35 were estimated using the empirical equations. The mean from publications was 0.23/year with a minimum value of 0.06/year for *L. sebae* and a maximum of 1.46/year for *L. peru*. The mean estimate was 0.282/year with a minimum value of 0.07/year for *L. malabaricus* and a maximum of 1/year for a population *L. lutjanus*. Mortality rate values were available for 134 stocks and 188 were estimated using the empirical equation. The mean from publications was 0.38/year with a minimum value of 0.112/year for *L. malabaricus* and a maximum of 1.83/year for *L. buccanella*. The mean estimate was 0.68/year with a minimum value of 0.249/year for *Lutjanus adetii* and a maximum of 1.46/year for a population of *L. quinquelineatus*.

The mean size at which species in the subfamily Lutjaninae reach maturity is 52% of their asymptotic length (Figure 2.4) and the values of these variables from the literature are highly correlated ($r = 0.81$) (Table 2.2). Other results indicated that there was no correlation between longevity and the age at maturity for species of the subfamily Lutjaninae (Table 2.2). There was little correlation between age at maturity and longevity ($r = 0.42$) or size

measurements ($r = 0.30, 0.36, 0.25$). The mean age at maturity for species in the subfamily Lutjaninae is 3.5 years with relatively little variation (Figure 2.5). Finally, although mortality and growth rates among species of the subfamily Lutjaninae showed a moderate correlation ($r = 0.62$) (Table 2.2) a graphic analysis indicated dependency on each other (Figure 2.6). Except for cubera snapper (*Lutjanus cyanopterus*) there were no clear cut points to separate the species within this subfamily by size; however, species ranged in asymptotic size from 232 mm TL to 1171 mm TL.

To compare the growth rates of snappers of different sizes, growth models (Figure 2.7) of three arbitrary categories (small, medium, and large) were constructed using the von Bertalanffy growth equation, and the mean values of the life-history variables for selected species (Table 2.4) as input values. The smallest species (*L. quinquelineatus*, *L. lutjanus*, *L. fulviflamma*, *L. decussatus*, *L. notatus*, *L. adetii*, *L. vitta*, *L. kasmira* and *L. carponotatus*) had asymptotic lengths of 232 – 383 mm TL (mean 315 mm TL); medium species (*L. apodus*, *L. buccanella*, *L. erythropterus*, *L. griseus*, *L. mahogoni*, *L. monostigma*, *L. russelli*, *L. stellatus*, *L. synagris*, and *Rhomboplites aurorubens*) had asymptotic lengths of 465 – 670 mm TL (mean 578 mm TL); and the largest species (*L. cyanopterus*, *L. argentimaculatus*, *L. sanguineus*, *L. campechanus*, *L. purpureus*, *L. analis*, *L. sebae*, *L. jocu*, *L. johnii* and *L. malabaricus*) had asymptotic lengths of 830 – 1171 mm TL (mean 952 mm TL). Further comparison of these three groups of snappers within the subfamily Lutjaninae indicated that larger species had a considerably lower growth rate (0.163/year) than medium (0.212/year), and small species (0.397/year), and lower mortality rates (0.39, 0.56 and 0.84/year, respectively). Large species matured later and at larger sizes (mean values of 4 years and 494 mm TL) than medium (3.8 years and 324 mm TL) and small species (2.5 years and 186 mm TL); and had longer life spans (mean of 19.7 years) than medium

(13.3 years), and small species (14.4 years). A second growth model (Figure 2.8) was constructed to show the contrast in growth patterns between small and large snappers that are particularly long lived. Selected species were the yellow-banded snapper (*L. adetii*), a small species from the Indo-west Pacific, which can live up to 40 years, and the red snapper (*L. campechanus*), a large species inhabiting the Gulf of Mexico and the eastern coast of the U.S.A., which can live up to 53 years. Input values were the species mean asymptotic length, growth rate and age at length zero (Table 2.4).

Subfamily Paradicichthyinae

For the subfamily Paradicichthyinae, published data were available on one species (*Symphorus nematophorus*) of two, but included information on three different stocks. The only datum on age at length zero reported in published literature was -0.53 years. The mean estimate of age at length zero was -1.195 years with a minimum value of -1.85 years and a maximum of -0.539 years. Mean asymptotic length of the data in published literature was 942 mm with a minimum value of 910 mm and a maximum of 974 mm; the estimated value was 912 mm. The mean maximum length in published literature was 1,037 mm with a minimum value of 885 mm and a maximum of 1,188 mm; the estimated value was 883 mm. Mean longevity reported in published literature was 28 years with a minimum value of 13 years and a maximum of 43 years, the only estimated longevity value was 13 year. The asymptotic weight in published literature was 15,724 g, while the expanded mean estimate was 13,790 g with a minimum value of 11,080 g and a maximum of 16,500 g. Length at maturity reported in published literature was 510 mm. The estimated was 480 mm. Age at maturity reported in published literature was 3 years and the estimated age at maturity was 5.8 years. The reproductive life span estimated was 18.2 years.

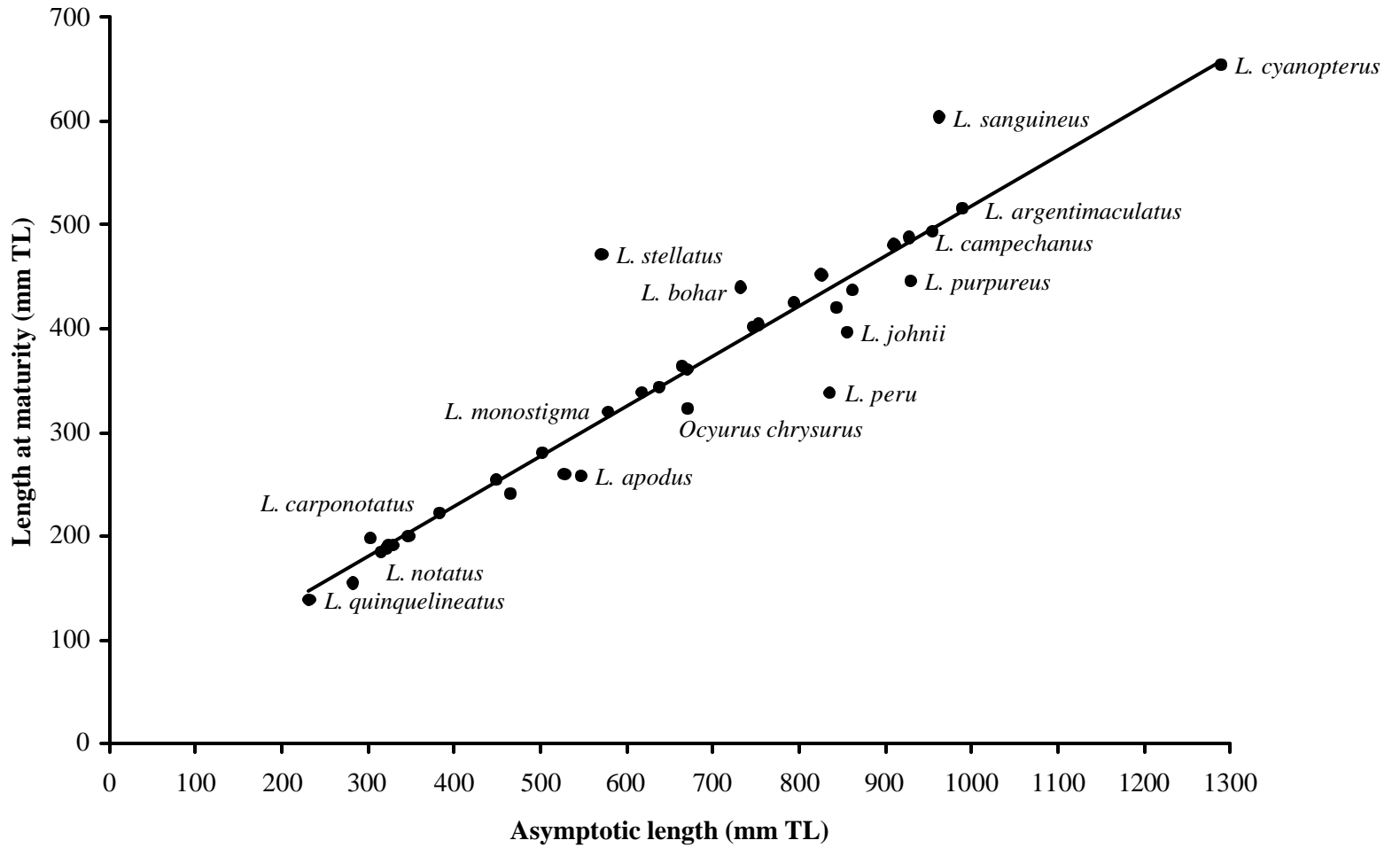


Figure 2.4 Length at maturity vs. asymptotic length in species of the subfamily Lutjaninae.

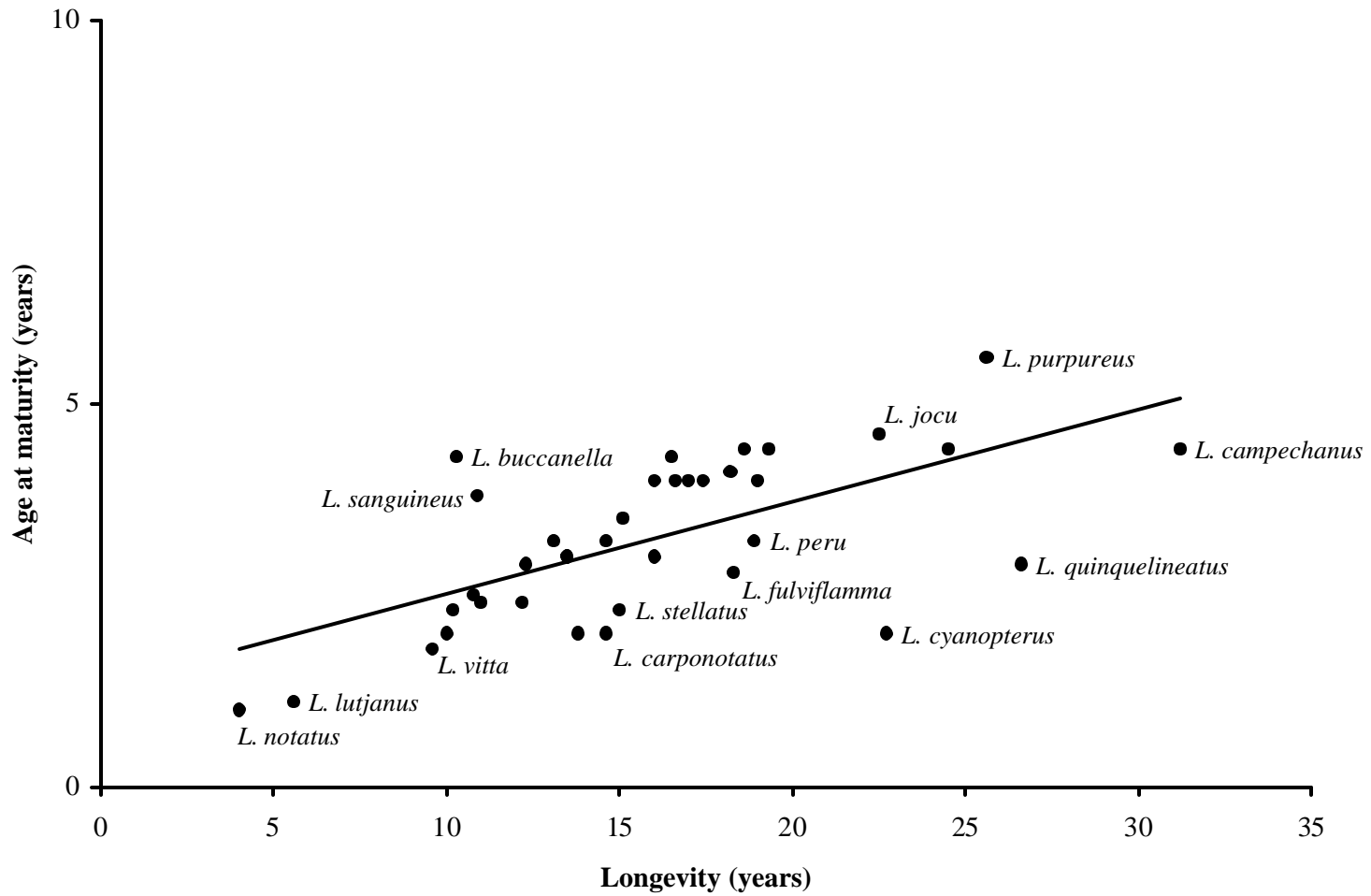


Figure 2.5 Age at maturity vs. longevity in species of the subfamily Lutjaninae.

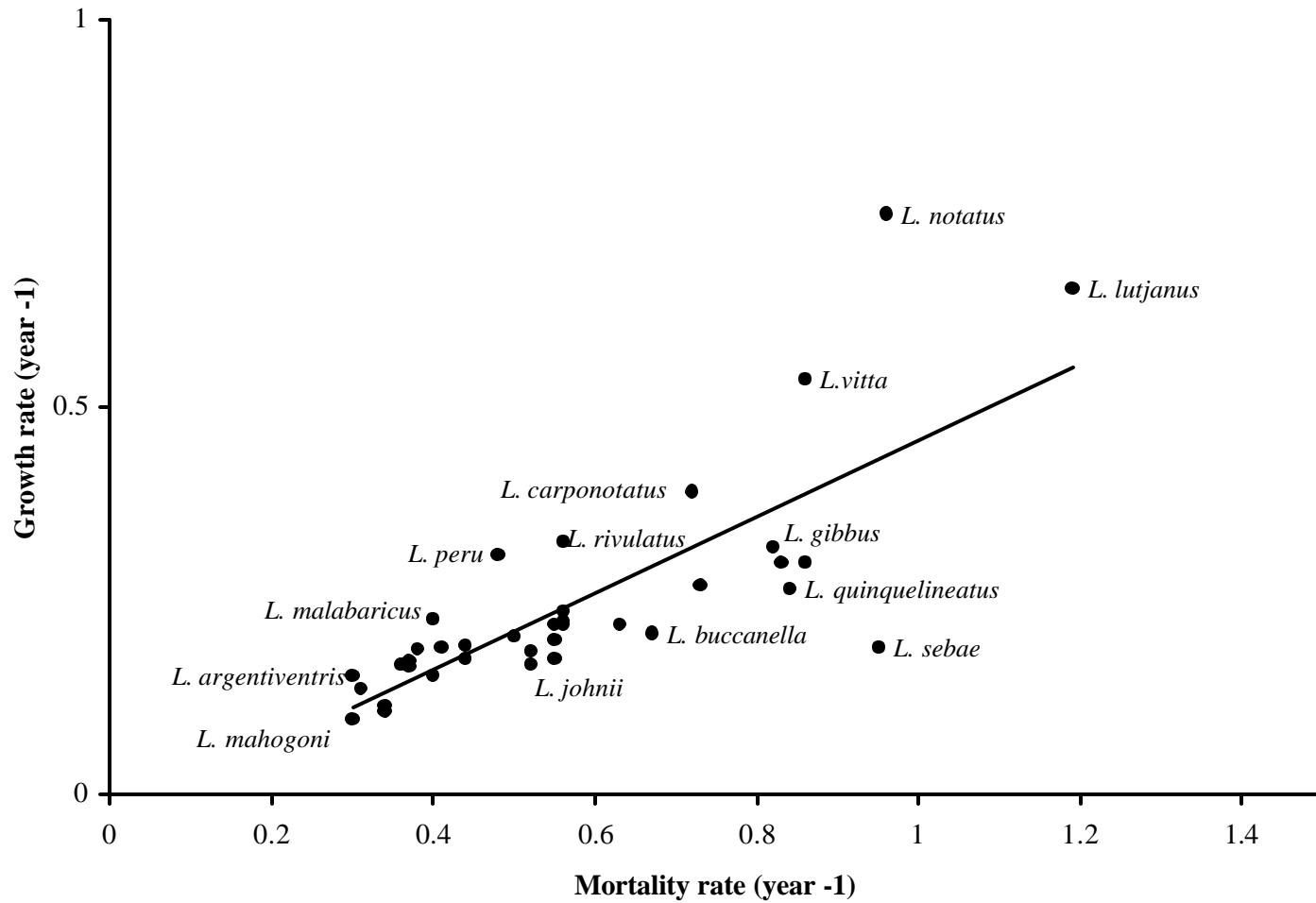


Figure 2.6 Growth rate vs. mortality rate in species of the subfamily Lutjaninae

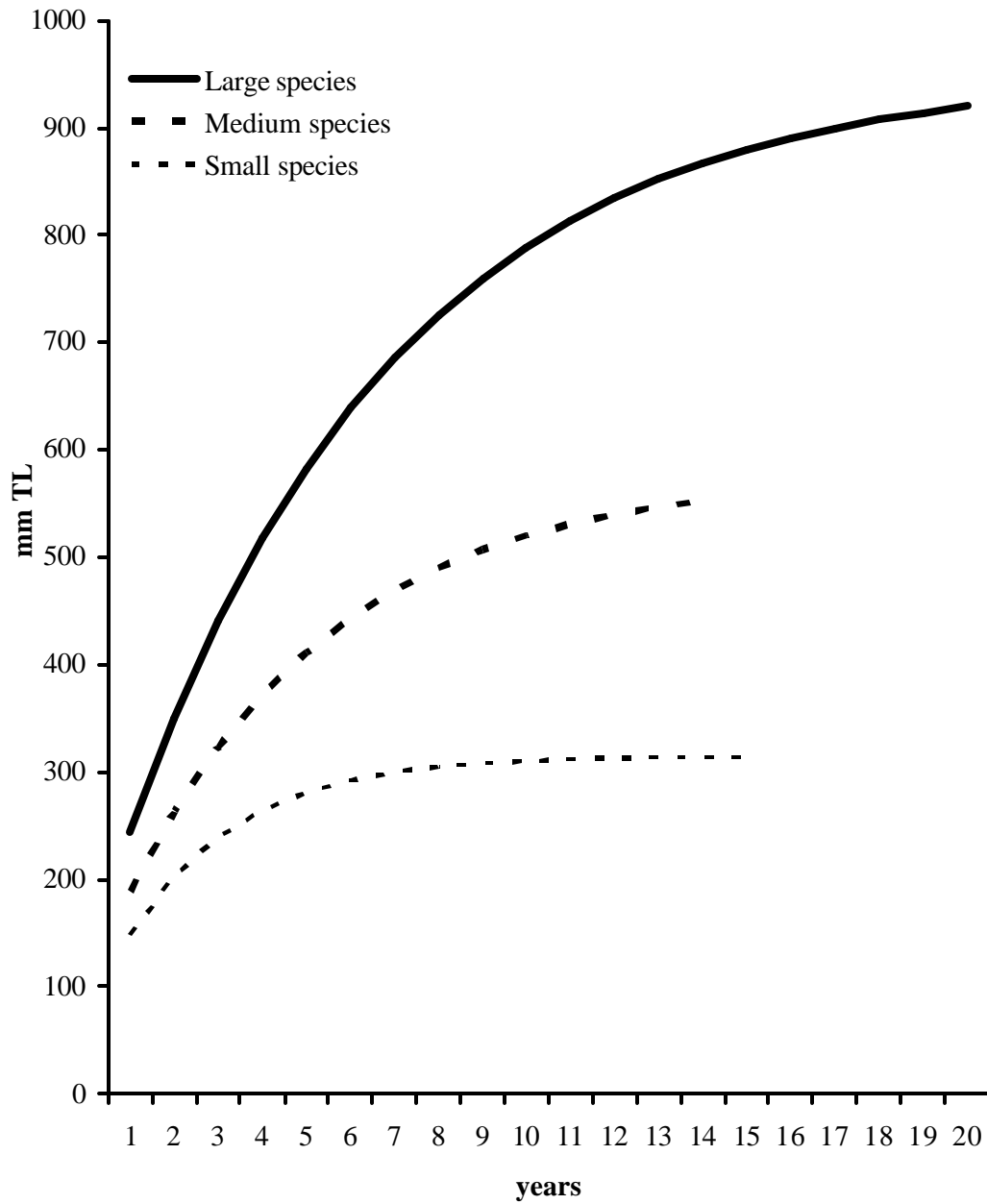


Figure 2.7 Growth models of large, medium and small species in the subfamily Lutjaninae.

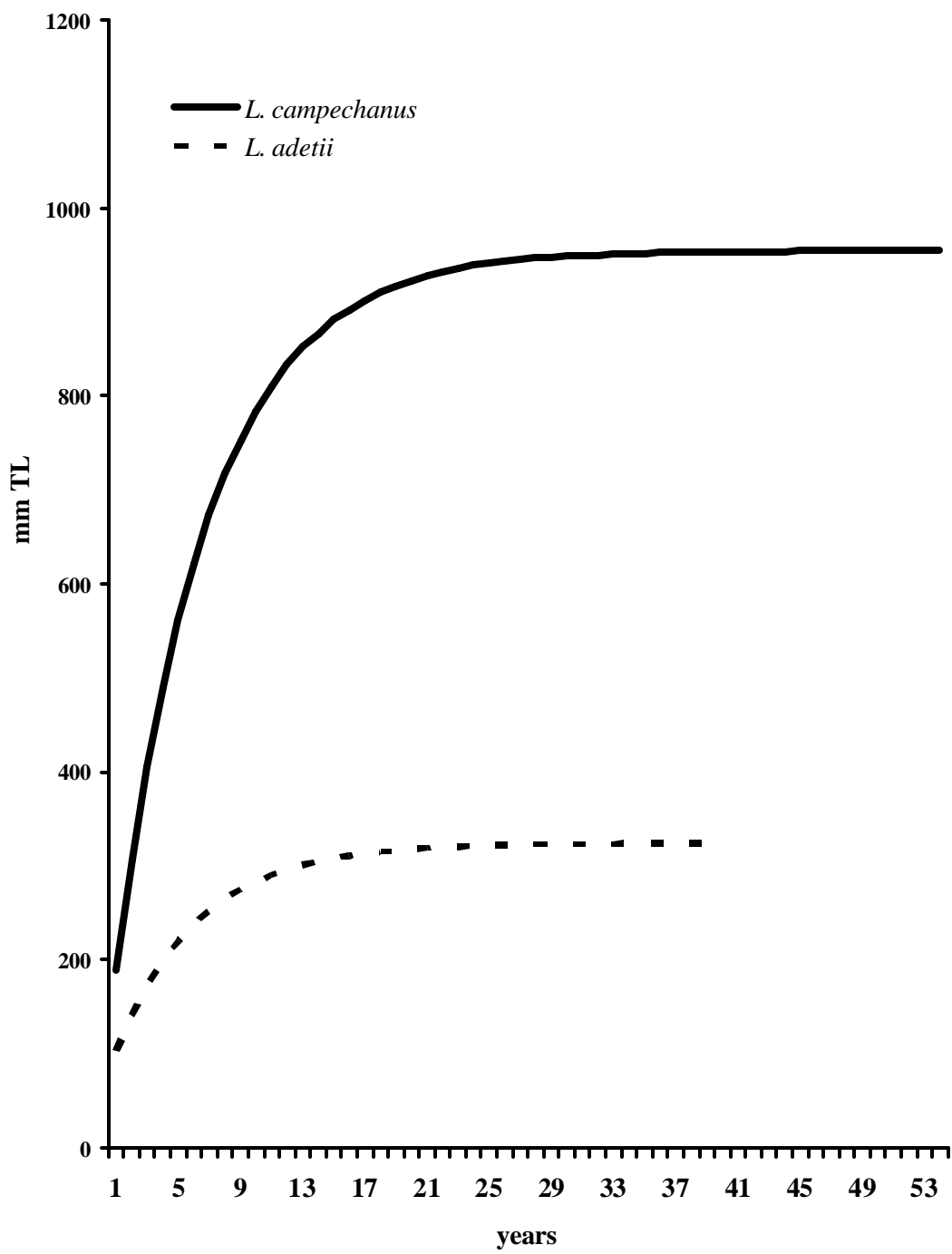


Figure 2.8 Growth model of *Lutjanus campechanus* and *L. adetii*.

Table 2.4 Mean values of the life-history variables for each species from the populations available by subfamily.

Species	t 0 years	Linf mm	Lmax mm	t max years	W inf (g)	Lm mm	t m years	RLS years	K yr -1	M yr -1
Lutjaninae										
<i>Lutjanus adetii</i>	-1.031	324	370	24.5	528	192	4.4	20.2	0.188	0.38
<i>L. analis</i>	-0.927	928	894	18.2	9893	488	4.1	14.1	0.154	0.4
<i>L. apodus</i>	-0.497	547	512	13.8	2926	258	2	11.2	0.223	0.56
<i>L. argentimaculatus</i>	-0.766	989	1106	19.3	13745	516	4.4	14.9	0.172	0.37
<i>L. argentiventris</i>	-0.873	753	752	19	9338	404	4	15	0.153	0.3
<i>L. bohar</i>	-0.567	732	758	16.5	7441	440	4.3	12.2	0.237	0.56
<i>L. buccanella</i>	-2.094	638	606	10.3	1997	344	4.3	6	0.208	0.67
<i>L. campechanus</i>	-0.311	955	939	31.2	12934	494	4.4	26.8	0.167	0.36
<i>L. carponotatus</i>	-0.185	383	423	14.6	1638	223	2	12.6	0.391	0.72
<i>L. cyanopterus</i>	-0.714	1289	1171	22.7	32460	654	2.7	20	0.137	0.31
<i>L. decussatus</i>	-0.879	315	300	16	1083	185	4	12	0.19	0.95
<i>L. erythropterus</i>	-0.213	664	609	11	4190	364	2.4	8.6	0.327	0.56
<i>L. fulviflamma</i>	-0.552	303	327	18.3	488	198	2.8	15.5	0.3	0.86
<i>L. gibbus</i>	-0.526	449	452	10.8	1644	254	2.5	8.3	0.32	0.82
<i>L. griseus</i>	-0.695	670	651	17.4	4627	361	4	13.4	0.168	0.52
<i>L. guttatus</i>	-0.675	794	769	16	2944	425	3	13	0.192	0.44
<i>L. jocu</i>	-1.573	862	927	22.5	13050	437	4.6	18.1	0.108	0.34
<i>L. johnii</i>	-0.837	856	830	14.6	10923	397	3.2	11.4	0.185	0.52
<i>L. kasmira</i>	-0.732	347	337	10.2	752	200	2.3	8	0.299	0.83
<i>L. lutjanus</i>	-0.311	283	291	5.6	360	155	1.1	4.5	0.653	1.19
<i>L. mahogoni</i>	-1.728	618	418	10	3200	339	2	8	0.097	0.3

(Table continued)

Species	t 0 years	Linf mm	Lmax mm	t max years	W inf (g)	Lm mm	t m years	RLS years	K yr -1	M yr -1
<i>L. malabaricus</i>	-0.49	843	838	15.1	9440	420	3.5	11.7	0.226	0.4
<i>L. monostigma</i>	-0.64	579	577	13.5	3112	320	3	10.5	0.22	0.63
<i>L. notatus</i>	-0.211	322	308	4	1079	188	1	3	0.75	0.96
<i>L. peru</i>	-0.04	836	849	18.9	8454	338	3.2	15.7	0.31	0.48
<i>L. purpureus</i>	-1.059	929	920	25.6	10797	446	5.6	22	0.115	0.34
<i>L. quinquelineatus</i>	-1.17	232	251	26.6	208	139	2.9	23.9	0.265	0.84
<i>L. rivulatus</i>	-0.59	747	736	13.5	4639	402	3	10.5	0.22	0.56
<i>L. russelli</i>	-0.828	502	483	17	2256	281	4	13	0.175	0.55
<i>L. sanguineus</i>	-0.805	962	934	10.9	12611	604	3.8	7.1	0.175	0.44
<i>L. sebae</i>	-0.664	910	916	16.6	17630	481	4	12.6	0.19	0.41
<i>L. stellatus</i>	-0.708	571	550	15	1963	472	10.8	4.2	0.2	0.55
<i>L. synagris</i>	-0.815	465	447	12.2	1795	241	2.4	9.8	0.27	0.73
<i>L. vitta</i>	-0.335	329	339	9.6	602	191	1.8	7.8	0.536	0.86
<i>L. vivanus</i>	-1.587	826	698	18.6	7765	452	4.9	13.7	0.165	0.37
<i>Ocyurus chrysurus</i>	-0.781	671	661	13.1	2921	323	3.2	10	0.204	0.5
<i>Rhomboplites aurorubens</i>	-0.436	528	504	12.3	2304	260	2.9	9.4	0.22	0.55
Paradicichthyinae										
<i>Symphorus nematophorus</i>	-0.973	932	985	23	14435	490	4.8	18.2	0.177	0.44
Etelinae										
<i>A. rutilans</i>	-0.543	1288	1257	18	21159	655	3.8	14.3	0.163	0.32
<i>Aprion virescens</i>	-0.585	1009	1012	15.6	9833	559	3.3	12.3	0.251	0.45
<i>Etelis carbunculus</i>	-0.761	918	930	15.2	16884	467	2.8	12.3	0.22	0.45
<i>E. coruscans</i>	-0.441	1054	1027	18.6	14677	598	7	11.6	0.166	0.31

(Table continued)

Species	t ₀ years	L _{inf} mm	L _{max} mm	t _{max} years	W _{inf} (g)	L _m mm	t _m years	RLS years	K yr ⁻¹	M yr ⁻¹
<i>E. oculatus</i>	-0.263	1027	977	6.7	16625	534	1.3	5.3	0.503	0.47
<i>P. auricilla</i>	-0.587	431	424	8	1381	245	1.8	6.2	0.347	0.68
<i>P. filamentosus</i>	-0.593	858	827	13.8	8674	460	3	10.8	0.243	0.49
<i>P. flavipinnis</i>	-0.625	602	584	10.8	2750	323	2.3	8.5	0.295	0.6
<i>P. multidentis</i>	-0.375	708	747	18.2	3966	374	3.2	15	0.226	0.35
<i>P. sieboldii</i>	-0.351	548	589	8	3898	302	3	5	0.298	0.58
<i>P. typus</i>	-0.524	679	674	11.3	3870	343	2.7	9	0.252	0.56
<i>P. zonatus</i>	-0.436	498	479	7.8	1933	285	1.8	6	0.667	0.82
Apsilinae										
<i>Apsilus dentatus</i>	-0.644	643	566	7.3	3209	425	2	5.3	0.424	0.98

t₀ = age at length zero, L_{inf} = asymptotic length, L_{max} = maximum length, t_{max} = longevity, W_{inf} = asymptotic weight, L_m = length at maturity, t_m = age at maturity, RLS = reproductive life span, K = growth rate, and M = mortality rate.

The only growth rate (i.e., Brody coefficient) value available in the published literature was 0.23/year and the estimated growth rate was 0.07/year. Mortality rate values reported in published literature were 0.43/year and the expanded mean estimate for mortality rate was 0.45/year with a minimum value of 0.43/year and a maximum of 0.47/year.

Subfamily Etelinae

For the subfamily Etelinae 79 stocks and 12 species were available. Age at length zero values were available for 35 stocks and 44 were estimated using the empirical equation. The mean age at length zero reported in publications was -0.44 years with a minimum value of -1.67 years for *Pristipomoides filamentosus* and a maximum of 1.6 years for *Etelis coruscans*; the mean estimate of age at length zero was -0.63 years with a minimum value of -1.79 years for *Etelis carbunculus* and a maximum of -0.127 years for a population *P. zonatus*.

Asymptotic length values were available for 70 stocks and only 9 were estimated using the empirical equation. The mean asymptotic length of the data on publications was 825 mm with a minimum value of 426 mm for *Pristipomoides auricilla* and a maximum of 1446 mm for *Aphareus rutilans*; the mean estimate of asymptotic length was 810 mm with a minimum value of 622 mm for *P. sieboldii* and a maximum of 1193 mm for *P. filamentosus*. Maximum length values were available for 42 stocks and 37 were estimated using the empirical equation; the mean maximum length in published literature was 434 mm with a minimum value of 450 mm for *Pristipomoides auricilla* and a maximum of 1,383 mm for *Etelis carbunculus*; the mean estimate of maximum length was 800 mm with a minimum value of 408 mm for *P. auricilla* and a maximum of 1414 mm for *Aphareus rutilans*.

Longevity values were available for 28 stocks and 51 were estimated using the empirical equation. The mean reported in published literature was 14.1 years with a minimum value of 3 years for *P. zonatus* and a maximum of 30 years for *P. multidentis*. The mean estimate was 13.5 years with a minimum value of 3 years for *P. zonatus* and a maximum of 43 years for a population of *Etelis carbunculus*.

Asymptotic weight values were available for 23 stocks and 56 were estimated using the empirical equation. The mean in published literature was 10,063 g with a minimum value of 1,560 g for *P. sieboldii* and a maximum of 39,000 g for *Etelis carbunculus*. The mean estimate was 8,721 g with a minimum value of 1,050 g for *P. auricilla* and a maximum of 34,700 g for *Etelis carbunculus*.

Length at maturity information was available for 33 stocks and 46 were estimated using the empirical equation. The mean reported in published literature was 466 mm with a minimum value of 248 mm for *Pristipomoides auricilla*, and a maximum of 670 mm for one population of

Etelis carbunculus. The mean estimate of length at maturity was 422 mm with a minimum value of 243 mm for *P. auricilla* and a maximum of 727 mm for a population *Aphareus rutilans*.

Age at maturity information was available for 19 stocks and 60 were estimated using the empirical equation. The mean from published literature was 2.4 years with a minimum value of 1 year for *Etelis carbunculus*, *E. oculatus* and *Pristipomoides zonatus* and a maximum of 5 years for *Aprion virescens*. The mean estimate was 3.3 years with a minimum value of 0.5 years for one population of *P. zonatus* and a maximum of 18 years for a population *E. coruscans*.

Reproductive life span values were estimated for all 79 population stocks of Etelinae species, the mean was 10.6 years with a minimum value of 1 year for *P. sieboldii* and a maximum of 40 years for a population of *Etelis carbunculus*.

Growth rates were available for 70 stocks and 9 were estimated using the empirical equation. The mean from published literature was 0.285/year with a minimum value of 0.07/year for *Etelis carbunculus* and a maximum of 1.1/year for *P. zonatus*. The mean estimate was 0.18/year with a minimum value of 0.12/year for *P. filamentosus* and a maximum of 0.254/year for a population *P. typus*.

Mortality rates were available for 47 stocks and 32 were estimated using the empirical equation. The mean from publications was 0.5/year with a minimum value of 0.08/year for *Etelis carbunculus* and a maximum of 1.55/year for the same species. The mean estimate was 0.48/year with a minimum value of 0.28/year also for *Etelis carbunculus* and a maximum of 0.68/year for a population of *P. sieboldii*.

Subfamily Apsilinae

For the subfamily Apsilinae information on one species (*Apsilus dentatus*) out of ten was available and included four different stocks. Mean age at length zero in published literature was

-0.96 years with a minimum value of -1.73 years and a maximum of -0.2 years. The mean estimate was -0.32 years with a minimum value of -0.45 years and a maximum of -0.2 years. Mean asymptotic length in published literature was 643 mm with a minimum value of 618 mm and a maximum of 670 mm, no estimations were made. The mean maximum length in published literature was 566 mm, with a minimum value of 418 mm and a maximum of 650 mm, no estimations were made.

The mean longevity in published literature was 7 years, with a minimum value of 4 years and a maximum of 10 years. The estimated mean was 7.5 years, with a minimum value of 5 years and a maximum of 10 years. The mean estimate asymptotic weight was 3,209 g with a minimum value of 2,617 g and a maximum of 4,092 g.

Mean length at maturity in published literature was 454 mm, with a minimum value of 434 mm and a maximum of 477 mm; the estimated was 339 mm. Mean age at maturity in published literature was 1.5 years with a minimum value of 1 year and a maximum of 2 years. The estimated mean was 2.5 years with a minimum value of 1.5 years and a maximum of 3.5 years. The reproductive life span estimate was 5.3 years.

The mean growth rate value in published literature was 0.424/year with a minimum value of 0.097/year and a maximum of 0.65/year, no estimations were made. The mean mortality rate in published literature was 0.98/year with a minimum value of 0.3/year and a maximum of 1.9/year, no estimations were made.

Results indicated that asymptotic length and length at maturity are highly correlated (Figure 2.9). On average, species in the subfamily Paradicichthyinae mature when they reach 52.6 % of their asymptotic length; species in the subfamily Etelinae mature at 53.4 %, and species in the subfamily Apsilinae at 66%.

For species of the Paradicichthyinae, Etelinae and Apsilinae subfamilies, results showed a moderate correlation between longevity and the age at maturity (Figure 2.10). This suggests that there is relatively little variation in the age at which snappers reach maturity regardless of the variation in longevities. On average, the species of Paradicichthyinae reach maturity at 4.8 years, Etelinae at 3 years and Apsilinae at 2 years.

Results from the correlation analysis for all subfamilies (Table 2.2) indicated a also a moderate correlation between mortality and growth rates and the graphic analysis for the subfamilies Paradicichthyinae, Etelinae and Apsilinae (Figure 2.11) shows some degree of correlation between these variables.

Finally, growth models for these subfamilies (Figure 2.12) showed similar patterns among them for early growth; however, the mean growth rates are considerably different (0.177/year for Paradicichthyinae, 0.303/year for Etelinae and 0.424/year for Apsilinae).

Discussion

Results of the analysis of life-history variables for species of snappers indicated that (1) the size at which a particular species matures is dependent upon the maximum size it reaches later in life; (2) different species of snappers presented little variation in age at maturity and age did not depend on size at maturity, maximum size or life span; (3) the maximum size of a species was a poor indicator of life span, and (4) growth and mortality rates were also correlated. The high correlation between length at maturity and size variables indicated that the maximum or asymptotic lengths are good predictors of length at maturity and agrees with the findings of other authors. Longhurst and Pauly (1987) first related the maximum length and length at maturity of a species based on the gill surface area; however, they later determined that the gill surface area is also highly correlated with maximum length (Pauly 1998), indicating that a relationship

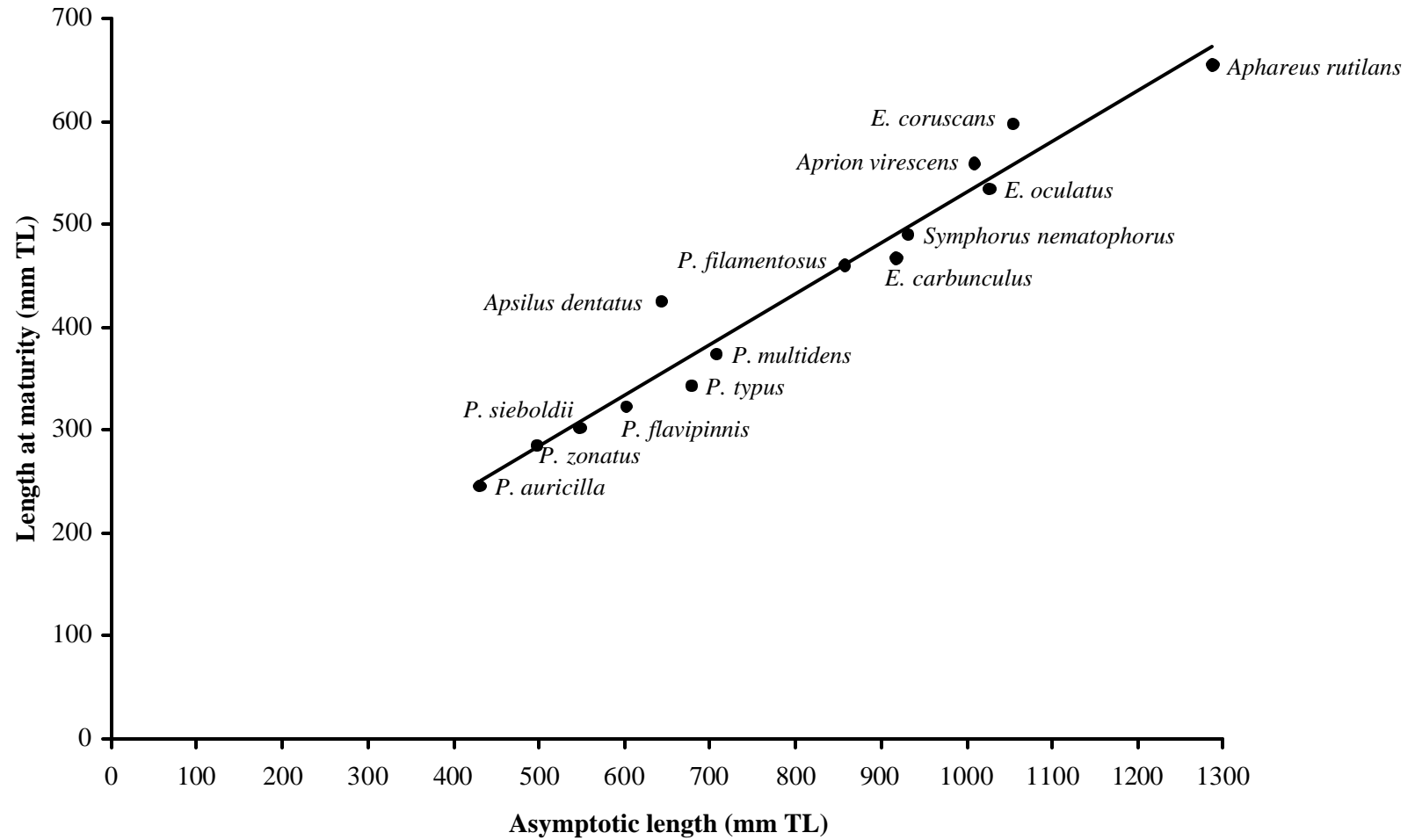


Figure 2.9 Length at maturity vs. asymptotic length in species of the subfamilies Paradicichthyinae, Etelinae, and Apsilinae.

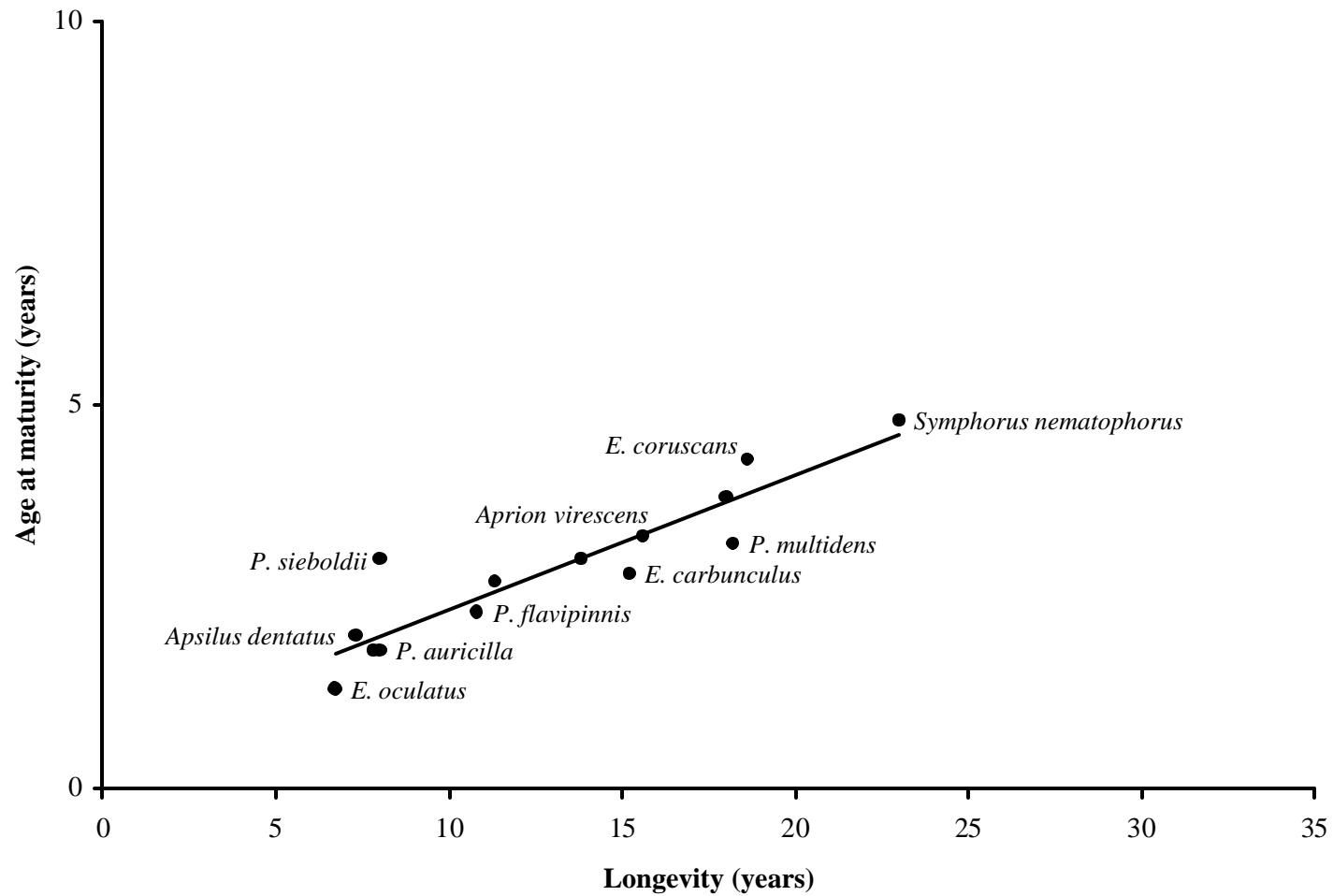


Figure 2.10 Age at maturity vs. longevity in species of the subfamilies Paradicichthyinae, Etelinae, and Apsilinae.

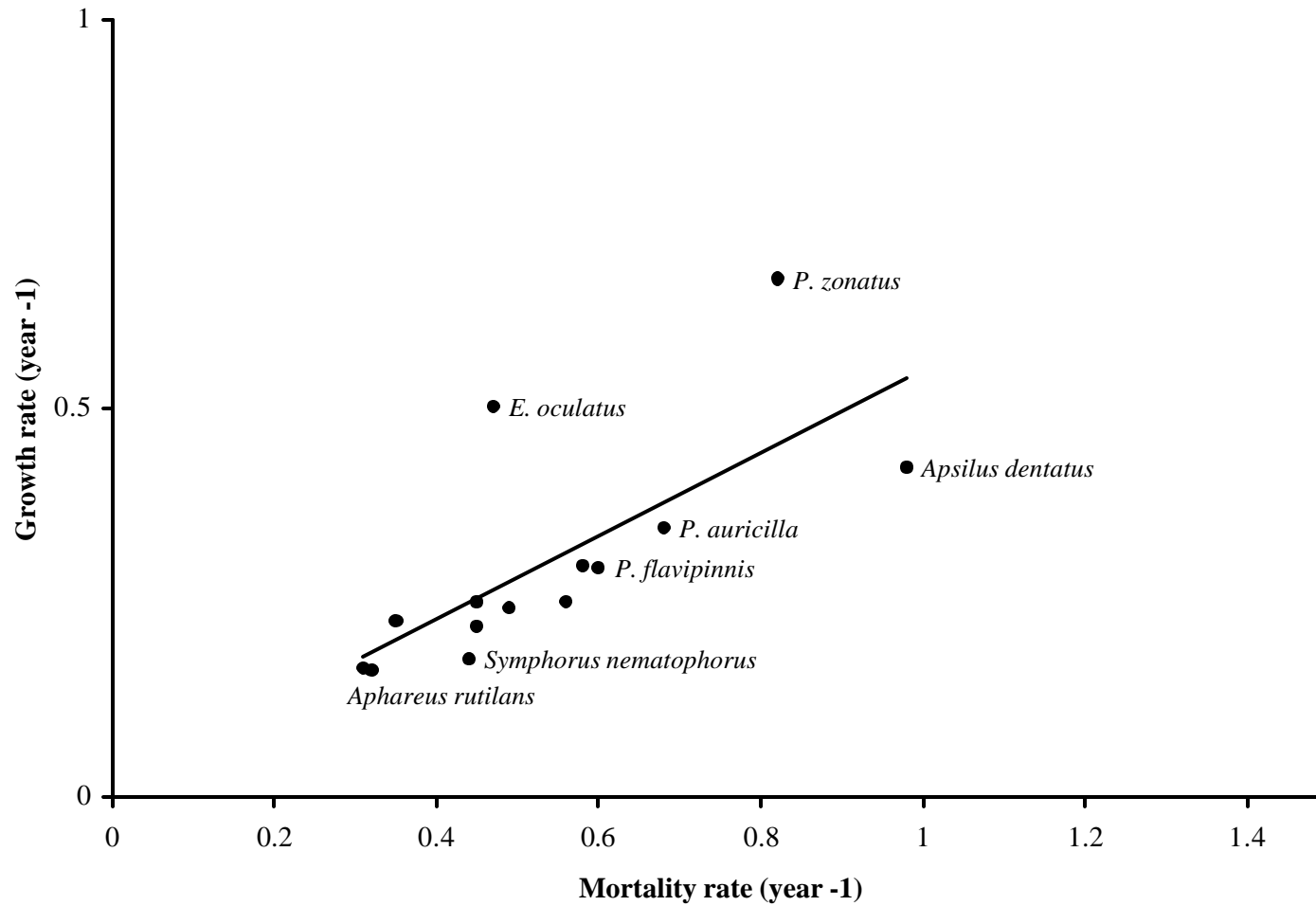


Figure 2.11 Growth rate vs. mortality rate in species of the subfamilies Paradicichthyinae, Etelinae, and Apsilinae.

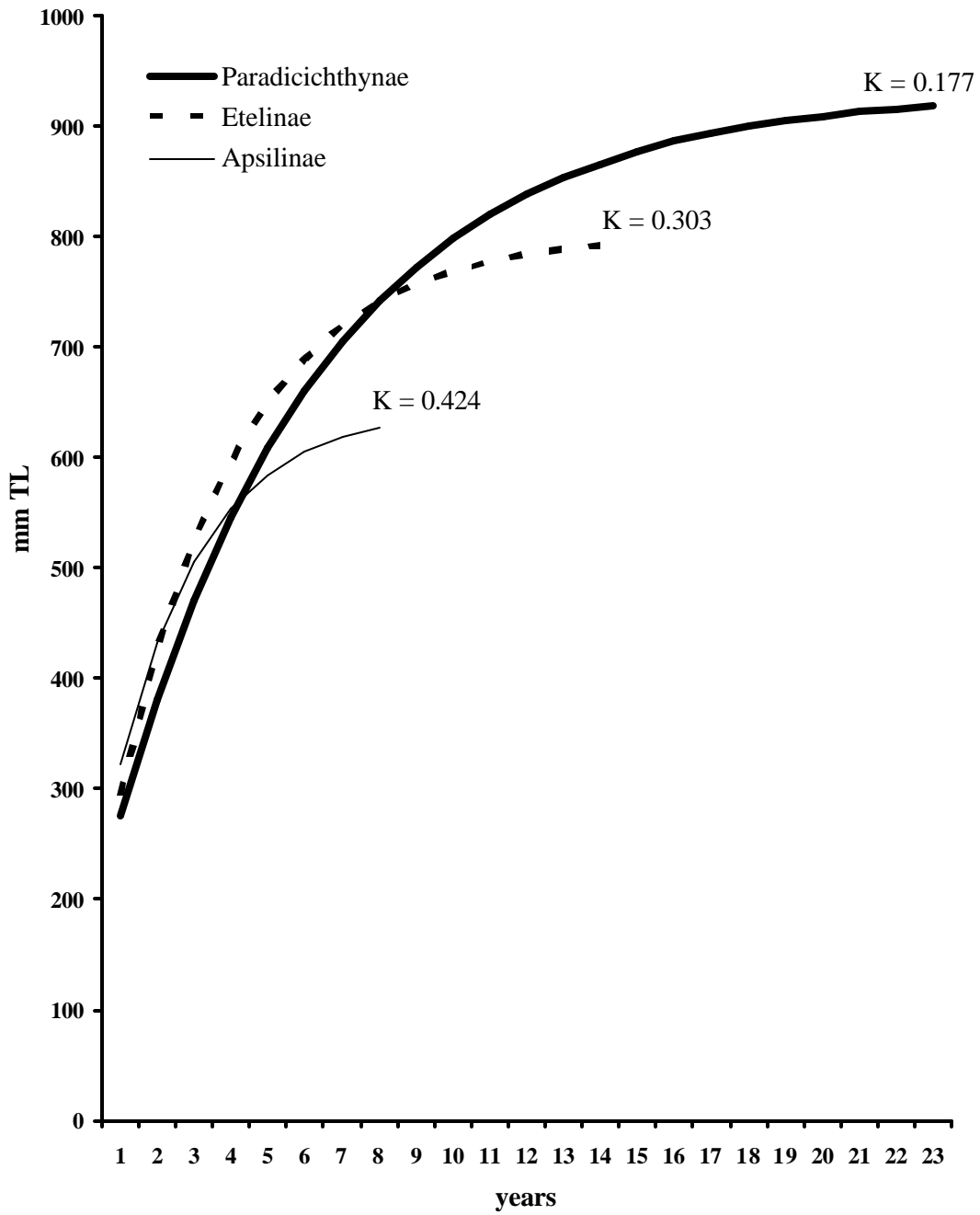


Figure 2.12 Growth models for species in the subfamilies Paradicichthynae, Apsilinae and Etelinae.

Table 2.5 Life history variables available in literature and estimations (bold) for populations within species of snappers.

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Lutjaninae													
<i>Lutjanus adetii</i>													
GBR, Australia	Newman et al. 1996a	O	M	-1.039	291	326	24	337	170	4	20	0.165	0.235
GBR, Australia	Newman et al. 1996a	O	F	-1.276	341	308	23	541	216	6	17	0.13	0.235
GBR, Australia	Newman et al. 1996a	O	B	-1.191	287	326	24	323	159	4	20	0.145	0.235
Rib reef, GBR	Newman et al. 1996b	O	B	-1.304	315	308	24	427	185	5.5	18.5	0.13	0.179
John Brewer, GBR	Newman et al. 1996b	O	B	-1.335	289	326	23	330	171	5.5	17.5	0.13	0.304
Lodestone, GBR	Newman et al. 1996b	O	B	-1.294	292	315	21	341	173	5	16	0.134	0.225
Kelso reef, GBR	Newman et al. 1996b	O	B	-1.201	321	315	22	454	188	5	17	0.14	0.286
All reef data, GBR	Newman et al. 1996b	O	B	-1.191	287	326	24	323	170	5	19	0.145	0.249
New Caledonia	Loubens 1980a & b	O	M	-0.589	415	550	40	1140	231	3	37	0.26	0.77
New Caledonia	Loubens 1980a & b	O	F	-0.458	364	475	37	760	238	3	34	0.343	0.84
Pooled data	Froese & Pauly 2000	C	U	-0.46	367	500	8	834	212	2	6	0.34	0.69
<i>L. analis</i>													
E Florida	Mason & Manooch 1985	O	U	-0.579	862	824	14	11500	400	3.5	10.5	0.153	0.15

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
E Florida	Burton 2002	O	M	-0.94	860	834	29	6118	418	3	26	0.17	0.39
E Florida	Burton 2002	O	F	-1.41	929	902	29	7717	559	5	24	0.14	0.39
E Florida	Burton 2002	O	B	-0.94	869	880	29	6308	460	4	25	0.16	0.39
S Florida	Ault et al. 1998	L	U	-0.738	939	798	14	14100	493	2	12	0.129	0.214
NE Cuba	Perez & Rubio 1986	S, O	U	-0.627	888	861	15	9840	469	3	12	0.2	0.31
NE Cuba	Pozo 1979	V	M	-1.41	871	823	25	7522	423	4	21	0.118	0.52
NE Cuba	Pozo 1979	V	F	-1.43	878	780	26	8020	530	7	19	0.115	0.52
NE Cuba	Pozo 1979	V	B	-1.42	875	823	9	7947	463	5	4	0.116	0.52
NE Cuba	Pozo 1979	L	U	-1.169	878	852	27	8020	464	6	21	0.11	0.52
Cuba	Claro 1981	O	U	-0.817	953	925	9	9913	500	4	5	0.152	0.49
Cuba	Montes, Unpub, In: Manooch 1987	O, U	U	-0.513	845	819	9	7253	449	3	9	0.246	0.53
Cuba	Claro 1976	O	U	-0.715	1276	1240	9	20000	650	4	5	0.16	0.4
N Venezuela	Claro & Garcia -Arteaga 1994		U	-0.62	1030	1010	18	15489	536	4	14	0.17	0.46
Venezuela	Palazon & Gonzales 1986		U	-0.713	1028	1000	8	10524	535	4	4	0.17	0.41
Pooled data	Froese & Pauly 2000	C	U	-0.79	869	940	18	8023	460	4	14	0.16	0.31

L. apodus

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
S Florida	Ault et al. 1998	L	U	0	570	504	12	3300	315	2	10	0.18	0.25
Jamaica	Thompson & Munro 1983	O	M	-0.769	630	601	17	3800	255	2	15	0.18	0.54
Jamaica	Thompson & Munro 1983	O	F	-0.769	630	601	17	3800	255	2	15	0.18	0.54
USVI	Randall 1962		U	-0.451	357	341	9	803	207	2	7	0.35	0.93
<i>L. argentimaculatus</i>													
N Australia	Sheaves 1995		U	-1.416	933	906	32	13046	490	7	25	0.09	0.49
Philippines, in captivity	Emata et al. 1999		M	-0.63	1050	1200	18	11300	496	4	14	0.19	0.34
Philippines, in captivity	Emata et al. 1999		F	-0.63	1050	1200	18	11300	570	5	13	0.19	0.34
Thailand, in captivity	Doi et al. 1994		F	-0.63	1050	1200	18	11300	570	5	13	0.19	0.34
E Malaysia	Ambak et al. 1985		U	-0.642	1050	1021	16	24400	545	3	13	0.187	0.25
New Caledonia	Loubens 1980	O	U	-0.781	738	714	18	5870	397	4	14	0.17	0.51
Pooled data	Froese & Pauly 2000	C	U	-0.63	1050	1500	15	18996	546	3	12	0.19	0.37
<i>L. argentiventris</i>													
W Mexico, Colima	Cruz-Romero et al. 1996		U	-0.835	819	793	19	6676	436	4	15	0.155	0.33
Pooled data	Froese & Pauly 2000	C	U	-0.91	686	710	19	13000	372	4	15	0.15	0.28

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
<i>L. bohar</i>													
Papua, New Guinea	Wright <i>et al.</i> 1986		U	0.013	862	838	9	13230	422	4	5	0.27	0.59
New Caledonia	Loubens 1980		U	-1.287	620	692	38	4240	340	6	32	0.11	0.57
Seychelles	Wheeler & Ommanney 1953		U	-0.404	660	637	9	4923	359	2	7	0.33	0.63
E Africa	Talbot 1960		M	-0.498	660	740	13	4875	517	5	8	0.27	0.64
E Africa	Talbot 1960		F	-0.498	660	740	13	4875	512	5	8	0.27	0.64
Pooled data	Froese & Pauly 2000	C	U	-0.73	927	900	17	12500	488	4	13	0.17	0.35
<i>L. buccanella</i>													
S Florida	Ault <i>et al.</i> 1998	L	U	-2.896	730	459	9	2400	393	2	7	0.084	0.23
SE Cuba	Espinoza <i>et al.</i> 1984	O	U	-3.16	643	620	30	4140	351	5	25	0.1	0.46
SE Cuba	Espinoza & Pozo 1982	U	M	-2.64	635	613	9	1326	319	4	5	0.1	0.65
SE Cuba	Espinoza & Pozo 1982	U	F	-2.08	632	610	9	1306	388	6.5	2.5	0.11	0.65
SE Cuba	Espinoza & Pozo 1982	U	U	-2.05	601	579	9	1125	330	4.5	4.5	0.12	0.68
SE Cuba	Espinoza & Pozo 1982	O	M	-4.04	699	675	9	1764	348	6	3	0.07	0.61
SE Cuba	Espinoza & Pozo 1982	O	F	-3.37	681	658	9	1632	416	8	1	0.08	0.62
SE Cuba	Espinoza & Pozo 1982	O	U	-3.52	667	644	9	1535	363	6	3	0.08	0.63

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Jamaica	Munro, 74In:Pauly 1980	O	M	-0.19	600	532	4	3200	278	4	0	0.7	0.68
Jamaica	Munro, 74In:Pauly 1980	O	F	-0.404	530	532	9	1890	256	1.5	7.5	0.35	1.83
NE Costa Rica	Tabash & Sierra 1996		U	-0.387	620	598	9	2150	340	2	7	0.35	0.48
Pooled data	Froese & Pauly 2000	C	U	-0.39	620	750	8	1499	340	2	6	0.35	0.57
<i>L. campechanus</i>													
Gulf of Mexico	Collins, et al. 1996		F	-0.1	941	1000	53	12415	350	2	51	0.162	0.19
Gulf of Mexico	Nelson et al. 1985	O	U	-0.1	925	898	10	11817	487	5	5	0.14	0.47
Gulf of Mexico	Nelson & Manooch 1982	O	U	-0.1	941	914	13	12415	494	4	9	0.17	0.46
W Florida	Nelson & Manooch 1982	O	U	-0.1	941	914	11	12415	494	4	7	0.17	0.19
E Florida	Nelson & Manooch 1982	O	U	-0.01	970	942	12	14232	508	4.5	7.5	0.155	0.19
Carolinas	Nelson & Manooch 1982	O	U	-0.01	970	942	16	14232	508	4.5	11.5	0.165	0.18
SE USA	Nelson & Manooch 1982	O	U	0	975	947	16	13801	510	5	11	0.16	0.31
Alabama	Fischer et al. 2002	O	M	0.63	908	891	34	11163	439	4	30	0.21	0.47
Alabama	Fischer et al. 2002	O	F	0.63	908	941	34	11163	439	4	30	0.21	0.47
Alabama	Szedlmayer & Shipp, 94	O	U	-0.812	1025	988	42	14374	534	4	38	0.15	0.43
Louisiana	Nelson & Manooch 1982	O	U	0.1	950	922	13	11700	498	4	9	0.175	0.2

(Table continued)

Species & Location	Reference	Method	Sex	t₀	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Louisiana	Fischer et al. 2002	O	M	0.73	896	938	37	10753	434	3.5	33.5	0.24	0.48
Louisiana	Fischer et al. 2002	O	F	0.73	896	934	37	10753	540	4.5	32.5	0.24	0.48
Louisiana	Wilson & Nieland 2001	O	M	-0.48	904	946	53	11013	437	3	50	0.19	0.47
Louisiana	Wilson & Nieland 2001	O	F	-0.63	977	1039	53	13888	586	5	48	0.16	0.45
Louisiana	Wilson & Nieland 2001	O	B	-0.54	935	1039	53	12174	491	4	49	0.18	0.46
Texas	Fischer et al. 2002	O	M	-2.92	1050	867	45	17224	500	6	39	0.07	0.43
Texas	Fischer et al. 2002	O	F	-2.92	1050	816	45	17224	628	10	35	0.07	0.43
S Florida	Ault et al. 1998	L	U	-0.01	975	955	16	12991	510	2	14	0.162	0.19
<i>L. carponotatus</i>													
GBR	Newman et al. 2000	O	M	-0.031	357	400	18	1227	208	2	16	0.371	0.88
GBR	Newman et al. 2000	O	F	0.001	295	354	17	777	189	2	15	0.45	1.01
GBR	Newman et al. 2000	O	B	-0.016	325	400	20	1227	190	2	18	0.45	0.2
Papua New Guinea	Munro & Williams 1985	O	U	-0.447	582	561	10	3730	321	2	8	0.31	0.76
Pooled data	Froese & Pauly 2000	C	U	-0.43	357	400	8	1227	207	2	6	0.37	0.77
<i>L. cyanopterus</i>													
S Florida	Ault et al. 1998	L	U	-0.3	1200	910	20	34900	615	2	18	0.16	0.15

(Table continued)

Species & Location	Reference	Method	Sex	t₀	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Cuba	Baisre & Paez 1981	O	U	-0.979	1033	1004	24	5480	536	5	19	0.125	0.46
Pooled data	Froese & Pauly 2000	C	U	-0.863	1633	1600	24	57000	811	1	23	0.125	0.33
<i>L. decussatus</i>													
In captivity	DeGraaf 1977	A	U	-0.879	315	300	16	1083	185	4	12	0.19	0.92
Pooled data	Froese & Pauly 2000	C	U	-0.879	315	300	16	1083	185	4	12	0.19	0.98
<i>L. erythropterus</i>													
GBR	McPherson & Squirre 1990	O	M	0.21	625	624	7	3480	342	2	5	0.41	0.73
GBR	McPherson & Squirre 1990	O	F	0.21	625	584	7	3480	342	2	5	0.44	0.73
GBR	Newman et al. 2000	O	U	0.1768	625	584	32	3480	342	2	30	0.39	0.15
N Australia	Milton et al. 1994	R	U	-0.447	656	633	6	3999	357	2	4	0.3	0.63
NW Australia	Ju et al. 1988	V	M	-0.714	726	600	7	5349	360	2.5	4.5	0.21	0.58
NW Australia	Ju et al. 1988	V	F	-0.714	726	630	7	5349	443	4	3	0.21	0.58
<i>L. fulviflamma</i>													
New Caledonia	Loubens 1980a & b	O	M	-0.553	303	300	23	490	215	3.5	19.5	0.3	0.96
New Caledonia	Loubens 1980a & b	O	F	-0.553	303	331	22	490	200	3	19	0.3	0.96
Pooled data	Froese & Pauly 2000	C	U	-0.55	303	350	10	483	179	2	8	0.3	0.66

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
<i>L. gibbus</i>													
Palau	Kitalong & Dalzell 1994		U	-0.373	429	411	8	1300	244	2	6	0.4	0.9
Papua New Guinea	Munro & Williams 1985	O	U	-0.472	476	457	10	1790	268	2	8	0.31	0.87
New Caledonia	Loubens 1980	O	U	-0.89	458	440	18	1735	259	4	14	0.17	0.71
Pooled data	Froese & Pauly 2000	C	U	-0.37	433	500	7	1751	246	2	5	0.4	0.82
<i>L. griseus</i>													
Florida	Burton 2001	O	M	0.49	697	687	24	4961	347	4	20	0.18	0.55
Florida	Burton 2001	O	F	0.16	768	744	24	6118	467	6	18	0.15	0.51
NE Florida	Burton 2001	O	B	-0.001	716	760	24	5217	387	5	19	0.17	0.43
S Florida	Burton 2001	O	B	-1.33	625	618	15	3463	282	3	12	0.13	0.38
S Florida	Rutherford et al. 1989		U	-0.963	716	692	21	4606	387	4.5	16.5	0.14	0.54
S Florida	Ault et al. 1998	L	U	-0.863	722	556	10	5200	390	2	8	0.136	0.3
S Florida	Crocker, 119962		U	-0.862	550	529	18	1820	305	4	14	0.167	0.66
E Florida	Manooch & Matheson 1983	O	U	-0.316	890	873	21	10743	470	7	14	0.101	0.22
SE Cuba	Baez Hidalgo et al. 1980 & 1982	O	F	-0.616	538	551	7	2000	341	3.5	3.5	0.24	0.73
SE Cuba	Baez Hidalgo et al. 1980 & 1982	O	M	-0.616	538	551	7	2000	257	2	5	0.24	0.73

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Cuba	Claro 1983	O	U	-1.065	575	554	9	2450	318	2	7	0.23	0.7
SW Cuba	Salahange 1984	O	U	-1.84	528	498	20	1830	294	3.5	16.5	0.15	0.74
SW Cuba	Perez & Rubio 1986	L	U	-0.624	629	607	14	3070	344	3	11	0.22	0.65
Pooled data	Froese & Pauly 2000	C	U	-1.29	890	890	29	11297	470	6	23	0.1	0.22
<i>L. guttatus</i>													
W Mexico, Colima	Cruz-Romero et al. 1996		U	-0.682	762	737	16	4577	409	3	13	0.19	0.39
Pooled data	Froese & Pauly 2000	C	U	-0.667	826	800	16	1310	440	3	13	0.19	0.49
<i>L. jocu</i>													
S Florida	Ault et al. 1998	L	U	-2	854	790	9	10200	453	2	7	0.1	0.33
Jamaica	Thompson & Munro 1983	O	F	-1.01	787	762	22	9100	342	5	18	0.13	0.3
Cuba	Claro et al. 1994a	O	U	-2	903	876	30	12900	476	5.5	24.5	0.1	0.5
Pooled data	Froese & Pauly 2000	C	U	-1.28	902	1280	29	20000	476	6	23	0.1	0.24
<i>L. johnii</i>													
Andaman Sea	Druzhinin 1970	S	M	-1.084	948	921	9	16600	304	2	7	0.116	0.5
Andaman Sea	Druzhinin 1970	S	F	-1.084	948	921	8	16600	294	2	6	0.116	0.5
Indonesia	Badrudin 1985		U	-0.345	724	700	8	6450	391	2	6	0.37	0.62

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Philippines	Pinto 1986	L	U	-1.06	667	644	23	5050	363	5	18	0.13	0.63
N Australia	Marriot & Cappo 2000		U	-0.507	826	800	12	9557	440	2.5	9.5	0.25	0.54
N Australia	Marriot & Cappo 2000		U	-1.167	884	857	28	11703	467	6	22	0.11	0.51
Pooled data	Froese & Pauly 2000	C	U	-0.61	998	970	14	10500	521	3	11	0.2	0.4
<i>L. kasmira</i>													
Hawaii	Morales-Nin & Ralston 1990	O	U	-1.37	340	345	10	676	198	2	8	0.29	0.93
Hawaii	Morales-Nin & Ralston 1990	O	U	-0.37	429	400	6	1399	225	2	5	0.33	0.45
Hawaii	Morales-Nin & Ralston 1990	L	U	-0.454	281	268	8	369	167	2	6	0.37	1.06
Hawaii	Morales-Nin & Ralston 1990	L	U	-0.492	289	275	9	404	171	2	7	0.34	1.04
Hawaii	Morales-Nin 1989	O	U	-0.599	337	322	11	730	197	3	8	0.27	0.93
New Caledonia	Loubens 1980	O	U	-0.457	248	283	8	295	149	2	6	0.38	1.11
American Samoa	Ralston & Williams 1988a	O	U	-1.35	305	291	8	329	180	1	7	0.38	0.91
American Samoa, deep water	Ralston & Williams 1988a	O	U	-0.75	408	391	14	827	233	3	11	0.21	0.74
N Mariana	Ralston & Williams 1988b	O	U	-0.75	412	395	14	1250	235	3	11	0.21	0.74
Pooled data	Froese & Pauly 2000	C	U	-0.73	424	400	14	1237	242	3	11	0.21	0.46
<i>L. lutjanus</i>													

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Gulf of Aden	Druzhinin & Filatova 1981		U	-0.154	340	325	3	590	198	1	2	1	0.96
Philippines	Corpuz et al. 1985		U	-0.225	252	240	4	271	151	1	3	0.75	1.32
E Malaysia	Ambak et al. 1985		U	-0.345	251	239	6	200	151	1.5	4.5	0.49	1.26
Indo-Pacific	Allen 1985		U	-0.611	315	300	11	470	120	1	10	0.27	0.92
Pooled data	Froese & Pauly 2000	C	U	-0.22	256	350	4	271	154	1	3	0.75	1.52
<i>L. mahogoni</i>													
S Florida	Ault et al. 1998	L	U	-1.728	618	418	10	3200	339	2	8	0.097	0.3
<i>L. malabaricus</i>													
Vanuatu	Brouard & Grandperrin 1984	O	U	-0.382	1028	1000	10	13600	535	2	8	0.31	0.42
GBR, Australia	Newman et al. 2000	O	U	0.2398	728	704	20	5571	392	3	19	0.287	0.13
GBR, Australia	McPherson & Squirre 1992	O	M	-0.13	987	959	7	16700	473	3.5	3.5	0.18	0.45
GBR, Australia	McPherson & Squirre 1992	O	F	-0.13	838	812	7	10400	507	4	3	0.23	0.5
GBR, Australia	McPherson et al. 1985	O	M	-0.641	993	965	16	10100	475	3	13	0.19	0.44
GBR, Australia	McPherson et al. 1985	O	F	-0.474	1054	1025	12	12100	630	3	9	0.25	0.43
NW Australia	Chen et al. 1984		M	-0.085	861	816	10	11300	211	2	8	0.252	0.32
Australia	Edwards 1985	O	U	0.418	866	840	10	7373	459	5	5	0.168	0.53

(Table continued)

Species & Location	Reference	Method	Sex	t₀	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
NW Australia	Chen et al. 1984		F	-0.085	861	816	10	11300	211	2	8	0.252	0.32
NW Australia	Lai & Liu 1974	V	U	-1.339	937	910	8	14500	492	4.5	3.5	0.126	0.49
Arafura Sea	Lai & Liu 1974	V	U	-1.291	964	936	8	15400	505	5	3	0.12	0.48
N Australia	Milton et al. 1994		U	-0.6	725	700	9	5504	391	3	6	0.22	0.59
S China	Lai & Liu 1974	V	U	-0.886	968	940	11	12787	507	4	7	0.14	0.49
S China, Taiwan	Han-lin & Hsi-Chiang 1974		U	-0.842	969	941	20	12826	507	4	16	0.147	0.49
Kuwait	Mathews & Samuel 1985		U	-1.847	917	890	46	10920	483	9	37	0.07	0.41
Kuwait	Lee & Al-Baz 1989		U	-0.76	689	667	8	5960	473	2.5	5.5	0.36	0.5
E Africa	Druzhinin 1970	S	M	-0.312	627	605	7	3604	211	2	5	0.43	0.66
E Africa	Druzhinin 1970	S	F	-0.312	627	605	7	3604	211	2	5	0.43	0.66
NW Australia	Newman 2002	O	M	-0.33	711	831	31	4680	353	3.5	27.5	0.18	0.112
NW Australia	Newman 2002	O	F	-0.09	586	639	26	2720	361	3.5	22.5	0.26	0.112
NW Australia	Newman 2002	O	B	-0.09	645	831	31	3914	352	3	28	0.22	0.112
Fishbase estimate	Froese & Pauly 2000	C	U	-0.82	969	1000	19	12826	508	4	15	0.15	0.32
<i>L. monostigma</i>													
<i>Papua New Guinea</i>	Munro & Williams 1985	O	U	-0.64	574	553	14	2980	317	3	11	0.22	0.76

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Pooled data	Froese & Pauly 2000	C	U	-0.64	584	600	13	3244	322	3	10	0.22	0.5
<i>L. notatus</i>													
Gulf of Aden	Druzhinin & Filatova 1981	S	U	-0.2	381	365	4	1254	219	1	3	0.75	0.82
Pooled data	Froese & Pauly 2000	C	U	-0.222	263	250	4	904	157	1	3	0.75	1.11
<i>L. peru</i>													
W Mexico, Guerrero	Santamaria & Chavez 1999		B	-0.23	870	1100	21	9400	250	3	18	0.26	0.38
W Mexico, Michoacan	Ruiz et al. 1985	L	U	0.725	815	789	7	8805	434	4.5	2.5	0.2	0.49
SW Mexico, Michoacan, Guerrero, Oaxaca	Aguilar-Salazar 1986	S	U	1.48	826	798	27	8925	440	8	19	0.11	0.48
S Baja Peninsula, Mexico	Castro 1981	S, L	U	-0.54	667	644	8	7206	363	3	5	0.23	0.56
NW Costa Rica	Gutierrez-Vargas 1990	L	U	0.035	833	807	12	9000	443	0.5	11.5	1.46	1.33
Baja Peninsula, Mexico	Rocha-Olivares 1998	O	M	0.14	973	992	31	10840	275	3	28	0.11	0.22
Baja Peninsula, Mexico	Rocha-Olivares 1998	O	F	-0.316	973	992	26	10840	288	3	23	0.11	0.22
W Mexico, Colima	Cruz-Romero et al. 1996		M	-0.84	783	758	19	5536	269	2	17	0.156	0.33
W Mexico, Colima	Cruz-Romero et al. 1996		F	-0.84	783	758	19	5536	281	2	17	0.156	0.33
<i>L. purpureus</i>													
Brazil	Menezes & Gesteria 1974	S	F	-1.304	989	961	30	11989	517	6	24	0.096	0.35

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Brazil	Alves 1971, Gesteira & Ivo 1973	S	M	0	1005	977	26	13668	400	5	21	0.117	0.28
Brazil	Alves 1971, Gesteira & Ivo 1973	S	F	-2.587	851	825	23	8690	420	5	18	0.13	0.28
Brazil	Lima 1965	O	U	0	977	950	26	13800	511	6	20	0.117	0.4
Brazil	Ximenes & Fonteles-Filho 1988		U	-1.233	929	902	29	10804	489	6	23	0.103	0.41
Brazil	Fonteles-Filho 1970		U	-1.2	967	939	30	11665	506	6.5	33.5	0.096	0.49
N Brazil	Ivo & Gesteira 1974		U	-1.312	967	940	30	11664	506	6	34	0.096	0.37
Trinidad & Tobago	Manickchand-Heileman & Phillip 1996		M	-0.984	877	851	20	8690	270	5	15	0.13	0.28
Trinidad & Tobago	Manickchand-Heileman & Phillip 1996		F	-0.984	877	851	20	8690	390	5	15	0.13	0.28
Pooled data	Froese & Pauly 2000	C	U	-0.99	851	1000	22	8313	452	5	17	0.13	0.25
<i>L. quinquelineatus</i>													
GBR, Australia	Newman et al. 1996a	O	M	-0.695	227	247	30	150	128	2.5	27.5	0.26	0.154
GBR, Australia	Newman et al. 1996a	O	F	-1.119	216	238	31	127	140	5	26	0.166	0.154
GBR, Australia	Newman et al. 1996a	O	B	-0.592	219	247	31	133	133	2.5	28.5	0.306	0.154
Rib reef, GBR	Newman et al. 1996b	O	B	-1.658	227	245	31	148	103	4	27	0.112	1.36
John Brewer reef, GBR	Newman et al. 1996b	O	B	-0.579	216	244	25	127	132	2	23	0.314	1.4
Lodestone reef, GBR	Newman et al. 1996b	O	B	-1.108	210	244	25	116	129	1	24	0.466	0.153

(Table continued)

Species & Location	Reference	Method	Sex	t₀	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Davies reef, GBR	Newman et al. 1996b	O	B	-2.313	225	237	22	143	137	1	21	0.305	1.37
Myrmidon reef, GBR	Newman et al. 1996b	O	B	-1.082	220	232	16	135	134	4	12	0.17	0.335
Kelso reef, GBR	Newman et al. 1996b	O	B	-0.828	233	247	30	161	141	2	28	0.218	1.33
Pooled reef data, GBR	Newman et al. 1996b	O	B	-2.587	219	247	31	133	133	0.5	30.5	0.306	1.39
New Caledonia	Loubens 1980a & b	O	M	-0.495	205	224	22	177	133	2.5	19.5	0.366	1.46
New Caledonia	Loubens 1980a & b	O	F	-0.495	205	231	20	177	134	2.5	19.5	0.366	1.46
Pooled data	Froese & Pauly 2000	C	U	-1.66	397	380	32	982	228	8	24	0.09	0.26
<i>L. rivulatus</i>													
Papua, New Guinea	Munro & Williams 1985	O	U	-0.608	694	671	14	4310	376	3	11	0.22	0.67
Pooled data	Froese & Pauly 2000	C	U	-0.58	800	800	13	4968	427	3	10	0.22	0.46
<i>L. russelli</i>													
N Australia	Sheaves 1995	O	U	-0.826	484	465	17	1995	272	4	13	0.18	0.72
Pooled data	Froese & Pauly 2000	C	U	-0.83	520	500	17	2517	290	4	13	0.17	0.39
<i>L. sanguineus</i>													
Arafura Sea	Lai & Liu, 1979	V	U	-1.291	999	971	8	13731	521	5	3	0.119	0.47
NW Australia	Lai & Liu 1979	V	U	-1.339	971	943	8	12576	508	4.5	3.5	0.126	0.48

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
S China, Gulf of Tonkin	Lai & Liu 1974	V	U	-0.819	960	932	11	14100	503	4	7	0.142	0.49
S China, N Sunda	Lai & Liu 1974	V	U	-0.67	1000	972	10	13773	522	4	6	0.148	0.48
Djibouti	Sanders & Morgan 1989		U	-0.542	887	860	13	9509	469	3	10	0.23	0.4
Djibouti	Kedidi & .Bouhleb 1985		U	-0.528	890	863	13	9590	470	3	10	0.236	0.34
Pooled data	Froese & Pauly 2000	C	U	-0.45	1028	1000	13	15000	535	3	10	0.23	0.44
<i>L. sebae</i>													
N Australia	Milton et al. 1994	R	U	-1.808	1773	1739	9	118000	873	9	0	0.06	0.31
Yemen	Druzhinin & Filatova 1981	S	U	-1.015	851	825	11	12900	452	4	7	0.157	0.54
GBR, Australia	Newman et al. 2000	O	U	-0.92	826	800	22	11416	440	4.5	17.5	0.14	0.294
GBR, Australia	McPherson & Squirre 1990	O	M	-0.32	1017	989	8	16100	486	4	4	0.15	0.44
GBR, Australia	McPherson & Squirre 1990	O	F	-0.32	912	885	8	10300	549	5	3	0.18	0.47
GBR, Australia	McPherson et al. 1985	O	M	-0.858	1088	1059	21	15900	516	4	17	0.14	0.42
GBR, Australia	McPherson et al. 1985	O	F	-0.601	861	835	14	7540	520	4	10	0.21	0.49
NW Australia	Yeh et al. 1986		U	-1.09	811	786	10	7950	432	5	5	0.13	0.54
NW Australia	Newman & Dunk 2002	O	M	-0.595	655	759	30	5611	328	4	26	0.151	0.113
NW Australia	Newman & Dunk 2002	O	F	0.065	503	609	34	2496	313	4	30	0.271	0.113

(Table continued)

Species & Location	Reference	Method	Sex	t₀	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
NW Australia	Newman & Dunk 2002	O	B	0.056	548	759	34	3243	304	3.5	30.5	0.233	0.113
Arafura Sea	Liu & Yeh 1991	O	U	-0.378	877	851	11	13719	464	4	7	0.166	0.51
Arafura Sea	Liu & Yeh 1991	O	U	-0.403	832	806	11	11683	442	4	7	0.18	0.53
Seychelles	Mees 1992	L	M	-0.317	939	897	8	16883	452	1.5	6.5	0.38	0.65
Seychelles	Mees 1992	L	F	-0.461	876	816	11	13669	529	3	8	0.27	0.53
Seychelles	Mees 1992	L	U	-1.37	969	897	19	18604	507	3	16	0.157	0.361
Seychelles	Mees 1992	L	U	-0.39	992	964	10	19986	518	2	8	0.307	0.47
Seychelles	Lablache & Carrara 1988		U	-0.531	960	932	13	15200	490	2.5	10.5	0.23	0.48
Seychelles	Moussac 1998		U	-0.546	1022	994	14	15500	532	3	11	0.22	0.46
New Caledonia	Loubens 1980	O	U	-1.45	857	831	35	13810	454	7	28	0.09	0.52
Pooled data	Froese & Pauly 2000	C	U	-0.69	947	1210	16	19730	497	3	13	0.18	0.36
<i>L. stellatus</i>													
In captivity	Hamamoto et al. 1992		M	-0.708	571	550	15	1963	266	2.5	12.5	0.2	0.61
In captivity	Hamamoto et al. 1992		F	-0.708	571	550	15	1963	207	1.5	13.5	0.2	0.61
Pooled data	Froese & Pauly 2000	C	U	-0.708	571	550	15	1963	316	3	12	0.2	0.44
<i>L. synagris</i>													

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Alabama	Szedlmayer & Shipp 1994	O	U	-0.376	504	549	10	2125	282	2	8	0.38	0.73
S Florida	Manooch & Mason 1984	O	U	-1.49	501	512	10	2310	281	4.5	5.5	0.134	0.27
S Florida	Ault et al. 1998	L	U	-1.728	618	418	10	3200	339	2	8	0.097	0.3
NW Cuba	Rubio 1986b	O	U	-1.05	488	469	12	1500	274	2	10	0.25	0.79
Cuba	Rodriguez-Pino 1962	O	M	-0.323	313	299	6	1121	92	0.5	5.5	0.5	0.74
Cuba	Rodriguez-Pino 1962	O	F	-0.9	380	410	9	1121	92	0	9	0.35	0.74
Cuba	Rodriguez-Pino 1962	O	B	-1.343	480	461	27	2012	220	2	25	0.113	0.8
Cuba	Claro & Reshetnikov 1981	O	U	-0.5	516	496	15	1830	288	3.5	11.5	0.2	0.44
Cuba	Claro & Lapin 1971	O	U	-0.349	417	400	7	1240	238	1.5	5.5	0.43	0.88
Cuba	Reshetnikov & Claro 1976	O	M	-0.377	315	300	7	558	130	2	5	0.43	1.08
Cuba	Reshetnikov & Claro 1976	O	F	-0.356	386	369	7	992	130	2	5	0.43	0.94
SW Cuba	Claro 1982	O	M	-0.336	478	600	7	1827	196	2	5	0.43	0.8
SW Cuba	Claro 1982	O	F	-0.336	478	600	7	1827	207	2	5	0.43	0.8
SW Cuba	Artiles 1985	O	U	-0.17	491	472	12	1530	276	3	9	0.26	0.79
SW Cuba	Olaechea & Quintana 1970	O	U	-0.52	382	366	11	723	220	2.5	8.5	0.28	0.94
SW Cuba	Buesa & Olaechea 1970	O	U	-0.03	442	424	7	1120	251	2.5	4.5	0.35	0.87

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
SW Cuba	Salahange 1981	O	U	-1.72	430	412	20	1030	245	4	16	0.15	0.87
SW Cuba	Rubio et al. 1985	O	U	-1.83	436	418	19	1070	248	4	15	0.16	0.86
SW Cuba	Rubio 1986	O	U	0.3	472	453	10	1360	266	3	7	0.29	0.81
NE Colombia	Erhardt 1977		F	-0.659	438	420	19	1423	274	1	18	0.23	0.53
Bermuda	Luckhurst et al. 2000	O	M	-1.95	360	413	19	813	255	1	18	0.395	0.84
Bermuda	Luckhurst et al. 2000	O	F	-1.95	360	413	19	813	266	1	18	0.395	0.84
NW Trinidad	Manickchand-Dass 1987	O	M	-0.55	708	430	4	5566	250	1	3	0.22	0.47
NW Trinidad	Manickchand-Dass 1987	O	F	-0.68	603	460	4	3536	310	2	2	0.2	0.43
Jamaica	Thompson & Munro 1983	O	M	-0.648	465	446	19	1689	199	1	18	0.23	0.81
Jamaica	Thompson & Munro 1983	O	F	-0.648	465	446	19	1689	191	1	18	0.23	0.81
Jamaica	Aiken 2001	O	M	-0.001	348	348	14	739	240	4.5	9.5	0.25	0.99
Jamaica	Aiken 2001	O	F	-3.97	586	467	14	3253	291	5	9	0.076	0.69
Puerto Rico	Acosta & Appeldorn 1992 (ELEFAN I)	L	U	-0.459	490	471	13	1209	275	3	10	0.23	0.53
Puerto Rico	Acosta & Appeldorn 1992 (Wetheral)	L	U	-0.63	516	496	13	2271	288	3	10	0.23	0.71
Yucatan	Mexicano-Cintora & Arreguin-Sanchez 1989	L	U	-0.528	465	410	11	1195	262	2.5	8.5	0.28	0.77
Yucatan	Torres-Lara 1984	L	U	-0.622	410	393	12	1177	234	3	9	0.25	0.85

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Yucatan	Torres-Lara 1987	L	U	-0.622	410	393	12	1177	234	3	9	0.25	0.85
Yucatan	Torres-Lara & Chavez 1987	L	U	-1.82	446	428	12	1066	253	1.5	10.5	0.247	0.51
Yucatan	Torres-Lara & Salas-Marquez 1990	S	U	-0.6	388	371	12	1008	223	2.5	8.5	0.26	0.77
Campeche	Rivera-Arriaga et al. 1996	L	U	-0.616	352	336	12	765	204	3	9	0.26	0.95
N Brazil	Alegría & Ferreira de Menezes 1970	O	U	-0.19	505	485	13	1800	283	3.5	9.5	0.23	0.78
Brazil	Gesteira & Ivo, 73	O	F	-0.557	805	780	10	8044	310	2	8	0.23	0.53
Pooled data	Froese & Pauly 2000	C	U	-0.64	478	600	12	2313	269	3	9	0.23	0.54
<i>L. vitta</i>													
Malaysia	Ambak et al. 1985	L	U	-0.594	425	407	12	1160	242	2.5	9.5	0.256	0.37
Philippines	Corpuz et al. 1985	L	U	-0.213	398	381	4	1010	228	1	3	0.7	0.92
GBR, Australia	Newman et al 2000	O	M	-0.075	252	283	9	211	140	1	8	0.98	1.19
GBR, Australia	Newman et al. 2000	O	F	-0.102	250	279	12	206	161	1	11	0.818	1.19
GBR, Australia	Newman et al. 2000	O	B	-0.179	253	283	12	302	152	1	11	0.853	0.34
N.W. Australia	Davis & West 1992	U	M	-0.56	436	418	7	1036	228	3	4	0.22	0.85
N.W. Australia	Davis & West 1992	U	F	-0.23	336	321	6	463	213	2.5	3.5	0.37	1.02
New Caledonia	Loubens 1980	O	M	-0.498	331	366	12	655	176	2	10	0.32	0.9

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
New Caledonia	Loubens 1980	O	F	-0.561	280	310	12	372	176	2	10	0.3	1.02
<i>L. vivanus</i>													
S Florida	Ault et al. 1998	L	U	-2.309	781	512	9	9300	418	3	6	0.09	0.23
US Virgin Islands	Sylvester et al. 1980	L	F	-0.22	1254	686	6	8320	284	0.5	5.5	0.5	0.38
SE Cuba	Pozo & Espinoza 1982	O	U	-2.08	812	600	30	8200	433	5.5	24.5	0.1	0.54
NE Cuba	Pozo et al. 1983 & 1984.	O	M	-2.64	782	757	33	7837	419	6	27	0.09	0.56
NE Cuba	Pozo et al. 1983 & 1984.	O	F	-2.64	782	757	33	7837	515	5	28	0.09	0.56
Costa Rica	Tabash & Sierra 1996		U	-0.425	620	598	9	3405	340	2	7	0.32	0.47
Venezuela	Gomez et al. 1996		M	-1.317	816	790	9	8320	565	6	3	0.1	0.19
Venezuela	Gomez et al. 1996		F	-1.336	775	750	9	7500	540	6	3	0.1	0.19
Pooled data	Froese & Pauly 2000	C	U	-1.32	812	830	29	9167	433	6	23	0.1	0.21
<i>Ocyurus chrysurus</i>													
S Florida	Ault et al. 1998	L	U	-0.712	455	433	14	1300	257	2	12	0.21	0.21
S Florida	Johnson 1983	O	F	-0.355	560	539	14	2397	275	4	13	0.28	0.66
Yucatan, Mexico	Mexicano-Cíntora & Arreguín-Sánchez 1989b	S	U	-0.893	570	549	19	1715	315	4	15	0.16	0.67

(Table continued)

Species & Location	Reference	Method	Sex	t₀	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Yucatan, Mexico	Cantarell 1982	S	U	-1.393	667	644	30	2952	363	6.5	23.5	0.1	0.6
Jamaica	Thompson & Munro 1983	L	M	-0.529	711	685	12	2531	320	2	10	0.25	0.62
Jamaica	Thompson & Munro 1983	L	F	-0.521	748	698	12	3600	365	2	10	0.25	0.62
NW Cuba	Claro 1983b	O	M	-0.272	595	573	4	1497	302	2	2	0.33	0.68
NW Cuba	Claro 1983b	O	F	-0.272	595	573	4	1497	314	2	2	0.33	0.68
NW Cuba	Piedra 1965	V	M	-1.19	619	597	12	3370	163	0	12	0.26	0.2
Cuba	Piedra 1969	V	U	-0.74	596	574	8	1810	328	4.5	3.5	0.15	0.2
SW Cuba	Claro 1983b	O	M	-0.851	850	824	5	4757	302	2	3	0.16	0.53
SW Cuba	Claro 1983b	O	F	-0.851	850	824	5	4757	314	2	3	0.16	0.53
SE Cuba	Carrillo de Albornoz 1999	O	U	-0.65	780	755	8	3156	418	4.5	3.5	0.15	0.56
SE Cuba	Carrillo de Albornoz & Ramiro 1988	O	U	-1.79	872	846	30	4530	462	6	24	0.1	0.51
SE Cuba	Perez & Rubio 1986	L	U	-0.495	516	496	10	1030	288	2.5	7.5	0.29	0.75
USVI & PR	Manooch & Drennon 1987	O	U	-0.955	626	760	17	2400	275	4	13	0.14	0.2
Pooled data	Froese & Pauly 2000	C	U	-0.81	794	863	18	6356	425	4	14	0.16	0.35

***Rhomboplites
aurorubens***

(Table continued)

Species & Location	Reference	Method	Sex	t₀	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Carolinas	Grimes 1976	S,O	F	0.128	627	627	10	4169	186	2	8	0.198	0.43
SE USA, N Carolina - Florida	Potts et al. 1998	O	U	-0.238	650	600	14	3599	354	5	9	0.144	0.42
SE USA, N Carolina - Florida	Cuellar et al. 1996	O	M	-0.549	463	444	11	1329	200	1.5	9.5	0.27	0.53
SE USA, N Carolina - Florida	Cuellar et al. 1996	O	F	-0.48	509	489	10	1760	185	2	8	0.3	0.5
SAB	Zhao et al. 1997	O	M	-0.899	333	318	12	509	140	1	11	0.27	0.68
SAB	Zhao et al. 1997	O	F	-0.899	333	318	12	509	151	2	10	0.27	0.68
S Florida	Ault et al. 1998	L	U	0.111	614	542	10	2800	337	4	6	0.206	0.23
Trinidad & Tobago	Manickchand-Heileman & Phillip 1999	O	U	-0.17	532	512	12	2006	296	6	6	0.13	0.73
NW Gulf of Mexico	Nelson 1988	O	M	-0.3	557	516	14	2288	284	3	11	0.22	0.67
NW Gulf of Mexico	Nelson 1988	O	F	-0.3	557	566	14	2288	344	2	12	0.22	0.67
Gulf of Mexico	Schirripa 1992	O	U	-0.94	535	515	15	2031	298	3.5	11.5	0.2	0.69
Pooled data	Froese & Pauly 2000	C	U	-0.69	630	600	14	4368	345	3	11	0.2	0.36
Paradicichthyinae													
<i>Symphorus nematophorus</i>													
Papua New Guinea	Munro & Williams 1985	O	U	-0.539	910	883	13	16500	480	2.5	10.5	0.23	0.47
Pooled data	Froese & Pauly 2000	C	U	-0.53	974	1188	13	15724	510	3	10	0.23	0.43

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Etelinae													
<i>Aphareus rutilans</i>													
N Marianas	Ralston & Williams 1988b	O	U	-0.36	1446	1414	18	23754	727	4	14	0.16	0.29
Pooled data	Froese & Pauly 2000	C	U	-0.725	1130	1100	18	18563	583	3.5	14.5	0.16	0.36
<i>Aprion virescens</i>													
Hawaii	Everson et al. 1989		F	-0.613	962	934	15	8048	509	5	10	0.2	0.43
Seychelles & Mauritius	Pilling et al. 2000	O	U	-1.123	895	990	27	7487	530	6	21	0.13	0.42
Seychelles	Mees 1992	L	M	-0.404	1077	1048	10	9010	642	2.5	7.5	0.29	0.547
Seychelles	Mees 1992	L	F	-0.831	1224	1193	21	13100	642	4.5	16.5	0.14	0.327
Seychelles	Mees 1992	L	U	-0.688	962	934	10	10296	642	3	7	0.29	0.496
Seychelles	Mees 1992	L	U	-0.442	1179	1149	12	12650	605	2.5	9.5	0.26	0.41
Seychelles	Van der Knapp et al. 1991		U	-0.353	884	857	9	5082	467	2	7	0.348	0.51
New Caledonia	Loubens 1980	O	U	-0.411	818	879	26	4680	436	2	24	0.31	0.46
Pooled data	Froese & Pauly 2000	C	U	-0.4	1080	1120	10	18140	560	2	8	0.29	0.48
<i>Etelis carbunculus</i>													

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Hawaii	Everson 1984		F	-0.571	732	708	13	6835	324	2	11	0.23	0.38
Hawaii	Smith & Kostlan 1991	O	U	-0.803	782	762	13	6320	419	4	9	0.16	0.36
NW Hawaii	Grigg & Tanoue 1984	L	U	-0.6	639	617	8	4470	318	1	7	0.36	0.56
Tonga	Langi & Langi 1987	L	U	-0.771	691	1140	17	25000	570	3	14	0.17	1.55
Tonga	Sua 1990	L	U	-0.354	1360	1328	10	33000	688	2	8	0.31	0.28
Vanuatu	Brouard & Grandperrin 1984	O	U	-1.792	1024	800	43	14100	279	3	40	0.07	0.08
Vanuatu	Smith & Kostlan,1991	O	U	-0.875	1383	1383	14	34700	698	4.5	9.5	0.129	0.28
Vanuatu	Carlot 1990	L	U	-0.509	1320	1289	14	30000	670	2.5	11.5	0.22	0.29
French Polynesia	Smith & Kostlan,1991	O	U	-1.066	740	740	14	5380	398	5	9	0.126	0.21
N Marianas	Smith & Kostlan 1991	O	U	-0.23	588	588	14	2700	324	2.5	11.5	0.29	0.52
N Marianas	Ralston & Williams 1988b	O	U	-1.06	436	418	9	1104	248	1.5	7.5	0.35	0.63
Pooled data	Froese & Pauly 2000	C	U	-0.51	1320	1383	13	39000	670	3	10	0.22	0.34
<i>E. coruscans</i>													
Hawaii	Williams & Lowe, 97	O	U	1.6	1070	1041	10	16311	555	4	6	0.27	0.4
Tonga	Langi & Langi 1987	L	U	-0.741	976	960	14	12410	496	4	10	0.17	0.38
Vanuatu, NHO	Brouard & Grandperrin 1984	O	U	-1.037	724	700	23	7990	565	4	19	0.128	0.12

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
N Marianas	Ralston & Williams 1988b	O	U	-1.19	1267	1236	24	18600	645	4.5	19.5	0.123	0.36
Pooled data	Froese & Pauly 2000	C	U	-0.836	1231	1200	22	18072	629	4.5	17.5	0.139	0.31
<i>E. oculatus</i>													
Saint Lucia	Murray & Moore 1992	L	U	-0.41	1020	930	10	23300	531	2	8	0.29	0.33
Saint Lucia	Murray et al. 1992	L	U	-0.189	1030	1002	5	23900	536	1	4	0.61	0.33
Pooled data	Froese & Pauly 2000	C	U	-0.19	1030	1000	5	2674	536	1	4	0.61	0.76
<i>Pristipomoides auricilla</i>													
N Marianas	Ralston & Williams 1988b	O	U	-0.88	431	413	8	1050	245	1.5	6.5	0.357	0.62
Tonga	Langi & Langi 1987	L	U	-0.45	426	408	8	1487	243	2	6	0.335	0.81
Pooled data	Froese & Pauly 2000	C	U	-0.43	437	450	8	1607	248	2	6	0.35	0.63
<i>P. filamentosus</i>													
NW Hawaii	Grigg & Tanoue 1984		U	0.02	971	763	10	12550	487	2	8	0.31	0.42
NW Hawaii	Uchiyama & Tagami 1984	O	U	-0.376	1087	1058	10	14300	563	2	8	0.31	0.38
Hawaii	Kikkawa 1984	M	F	-0.684	1193	1163	18	22000	511	2.5	15.5	0.17	0.327
Hawaii	Ralston 1980	O	U	-0.84	901	874	18	9284	475	3.5	14.5	0.164	0.44
Hawaii	Ralston & Miyamoto 1981	O	U	-0.611	809	784	14	7546	431	3	11	0.21	0.47

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Hawaii	Ralston & Miyamoto 1983	O	U	-1.67	873	847	18	5137	462	3.5	14.5	0.146	0.25
Hawaii	Moffitt & Parrish 1996	O	U	-0.617	780	755	14	6814	418	3	11	0.21	0.49
Seychelles	Mees 1992	O	M	-0.865	816	790	20	5737	399	3.5	16.5	0.15	0.53
Seychelles	Mees 1992	O	F	-1.117	746	722	25	4495	454	6.5	18.5	0.12	0.57
Seychelles	Mees 1993	L	M	-0.4	961	869	10	12192	582	3	7	0.3	0.534
Seychelles	Mees 1993	L	F	-0.453	869	869	11	6790	582	4	7	0.275	0.534
Seychelles	Mees 1993	L	U	-0.44	915	894	10	7780	582	4	7	0.287	0.534
Seychelles	Hardman-Mountford et al. 1998	O	M	-0.16	961	858	9	12192	425	1.5	7.5	0.33	0.6
Seychelles	Hardman-Mountford et al. 1998	O	F	0.06	871	776	8	9287	425	2	6	0.36	0.6
Seychelles	Mees & Rousseau 1997	L	U	-0.525	849	823	13	8639	451	3	10	0.24	0.458
Seychelles & Mauritius	Pilling et al. 2000	O	U	-1.246	698	674	27	5008	378	6	21	0.11	0.527
Vanuatu	Brouard & Grandperrin 1984	O	U	-0.46	672	649	10	3140	365	2	8	0.29	0.53
Tonga	Langi & Langi 1987	L	U	-0.59	673	750	13	4531	386	2	11	0.228	0.57
N Marianas	Ralston & Williams 1988b	O	U	-0.54	649	626	10	3230	354	2	8	0.289	0.52
Pooled data	Froese & Pauly 2000	C	U	-0.34	874	1000	8	12835	463	2	6	0.36	0.58

P. flavipinnis

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Vanuatu	Brouard & Grandperrin 1984	O	U	-0.376	622	600	8	3210	341	2	6	0.36	0.83
Tonga	Langi & Langi 1987		U	-0.745	575	570	16	1895	288	3	13	0.19	0.47
N Marianas	Ralston & Williams 1988b	O	U	-1.01	562	541	11	1990	311	2	9	0.268	0.53
Pooled data	Froese & Pauly 2000	C	U	-0.37	647	624	8	3904	353	2	6	0.36	0.59
<i>P. multidentis</i>													
Australia	Edwards 1985	S	U	-0.073	749	725	14	4339	403	4	10	0.219	0.31
NW Australia	Newman & Dunk 2003	O	M	-0.36	664	749	30	3351	332	3.5	26.5	0.187	0.12
NW Australia	Newman & Dunk 2003	O	F	0.0018	673	783	27	3486	311	3.5	23.5	0.187	0.12
NW Australia	Newman & Dunk 2003	O	B	-0.173	668	783	30	3401	363	4	26	0.1873	0.12
S China	Min et al. 1977	M	U	-0.631	721	697	14	3700	346	3	11	0.21	0.59
Vanuatu	Brouard et al. 1983	O	U	-0.377	681	658	9	3606	370	2	7	0.35	0.46
Vanuatu	Brouard & Grandperrin 1984	O	U	-0.467	726	702	11	4348	392	2.5	8.5	0.28	0.42
Papua New Guinea	Ralston & Williams 1988b	O	U	-0.693	747	723	16	4732	402	3	13	0.19	0.63
Pooled data	Froese & Pauly 2000	C	U	-0.6	747	900	13	4732	402	3	10	0.22	0.45
<i>P. sieboldii</i>													
Guam	Langi & Langi 1987	L	F	-0.387	622	600	9	5090	332	2	7	0.35	0.45

(Table continued)

Species & Location	Reference	Method	Sex	t₀	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Hawaii	Williams & Lowe 1997	O	U	-0.91	514	494	7	1667	287	6	1	0.115	0.68
Hawaii	Williams & Lowe 1997	O	U	0.36	601	579	7	2774	330	3	4	0.326	0.61
N Marianas	Ralston & Williams 1988b	O	U	-0.409	504	484	9	1560	282	2	7	0.35	0.57
Pooled data	Froese & Pauly 2000	C	U	-0.41	499	790	8	8400	280	2	6	0.35	0.61
<i>P. typus</i>													
S China	Min et al. 1977	O	F	-0.508	776	751	11	5717	339	2	9	0.254	0.52
Australia	Edwards 1985	S	U	-0.515	624	570	11	2573	342	3	9	0.254	0.66
Pooled data	Froese & Pauly 2000	C	U	-0.55	636	700	12	3320	348	3	9	0.25	0.52
<i>P. zonatus</i>													
Tonga	Langi & Langi 1987	L	U	-0.605	470	451	12	1413	287	3	9	0.245	0.63
N Marianas	Ralston & Williams 1988b	O	U	-0.89	507	487	13	1770	284	2.5	10.5	0.23	0.48
NW Hawaii	Uchiyama & Tagami 1984	O	U	-0.127	497	478	3	1660	279	0.5	2.5	1.09	0.67
Pooled data	Froese & Pauly 2000	C	U	-0.12	518	500	3	2890	289	1	2	1.1	1.53
Apsilinae													
<i>Apsilus dentatus</i>													
S Florida	Ault et al. 1998	L	U	-1.728	618	418	10	3200	339	2	8	0.097	0.3

(Table continued)

Species & Location	Reference	Method	Sex	t_0	L_{inf}	L_{max}	t_{max}	W_{inf}	L_m	t_m	RLS	K	M
Jamaica	Munro 1974	O	M	-0.199	670	608	5	2927	477	1.5	3.5	0.65	1.9
Jamaica	Munro 1974	O	F	-0.449	645	586	10	2617	434	3.5	6.5	0.3	0.83
Pooled data	Froese & Pauly 2000	C	U	-0.2	638	650	4	4092	450	1	3	0.65	0.89

t_0 = age at length zero, L_{inf} = asymptotic length, L_{max} = maximum length, t_{max} = longevity, W_{inf} = asymptotic weight, L_m = length at maturity, t_m = age at maturity, RLS = reproductive life span, K = growth rate and M = mortality rate. Location: N = north, S = south, E = east, W = west, GBR = Great Barrier Reef, SAB = South Atlantic Bight, USVI = U. S. Virgin Islands, PR = Puerto Rico. Methods: O = whole or sectioned otoliths, S = scales, V = vertebrae, U = urohyals, L = length frequency analysis, R = Radiometric analysis, A = Aquarium observation, M = maturity study, C = combined. Sex: U = unsexed, B = both sexes, M = male and F = female.

between maximum length and length at maturity exists. Froese and Binohlan (2000) utilized these findings to create an empirical equation to estimate length at maturity from maximum or asymptotic length. Finally, for snappers in particular Grimes (1987) estimated a value of 51% for populations associated with islands and for deep-water species (Etelinae and Apsilinae), and 43% for shallow-water species on continental coasts. The expanded data set showed that this proportion was 55% for the subfamily Lutjaninae, 49.7% for Paradicichthyinae, 54% for Etelinae and 66% for Apsilinae (Figures 2.4 and 2.9).

The results also suggest that species of snappers reach maturity at about the same age regardless of the number of years they live or the maximum size they reach. This is related to the high correlation between longevity and reproductive life span (since the difference between longevity and reproductive life span is the age at maturity), and the low correlation between age at maturity and longevity or any of the variables measuring size. Results from the PCA also support this hypothesis because large and small species had variable life spans regardless of the size. One fact that should be considered is that inclusion of older studies in the data base lowered the maximum age estimate of some species (e.g., *L. campechanus*) while recent studies for other species (e.g., *L. quinquelineatus* or *L. adetii*) showed steady long life spans (> 30 years) regardless of the size. Recent studies with small (Newman 1996a & b) and large species (Wilson and Nieland 2001) show that snappers of any size have long life spans, indicating that species with apparently low life spans (e.g., *L. sanguineus*) may actually have a longer life span. Studies that included sectioned otolith readings repeatedly produced longer life spans than studies with other methods and have proven to be the most reliable for age determination (Newman 1996a & b, Cappo *et al.* 2000, Wilson and Nieland 2001). When the longevity of a species with a supposedly short life span is re-estimated using the growth rate and the equation by Froese and

Pauly (2000), its estimated life span usually increases considerably. For example the mean estimated longevity from the literature of 10.9 years for *L. sanguineus* changes to 17.1 years and up to 25 years for a particular population from the Arafura Sea following this procedure. A logical assumption is that the species or populations that have suspiciously low life spans (< 20 years) require new age and growth estimates based on sectioned otolith readings, especially when they belong to the same genus.

Comparisons of growth parameters and longevities in among lutjanid species are difficult because age estimates are based on different methods and the growth rate is dependent on an accurate estimation of longevity (Newman 1995). The mean age of species of the genus *Lutjanus* when using sectioned otoliths is 21.5 years, which is nearly double the age estimate of 11.5 years from studies using scales (Druzhinin and Filatova 1980), and the difference is even greater with other techniques. If using vertebrae, the mean age becomes 8.7 years (Lai & Liu 1979, Edwards 1985, Liu & Yeh 1991), 6.8 years with whole otoliths (McPherson and Squire 1992), and just 5.8 years when using length frequency analysis (Ambak 1987). Aiken (2001) compared two different ageing techniques and found that the estimates of longevity for *L. synagris* was 14 years when using sectioned otoliths but only 6 years using whole otoliths.

Higher estimates of longevity and their respective low natural mortality rates suggest that snappers are more vulnerable to over-fishing than other species with shorter life spans and higher natural mortalities (Newman, *et al.* 2000); however, some scientists also suggest that longevities of more than 20 years actually benefit a species by ensuring a relatively long reproductive span and minimizing the risk that prolonged periods of unfavorable environmental conditions will lead to the loss of a stock (King and McFarlane 2003).

In this study smaller species had considerably higher mortality rates, which also affect the longevity of these species (Pauly 1980). Ralston (1987) indicates that mortality and growth rates are highly dependent on each other and that growth rate is a good predictor of mortality rate. He noted that natural mortality rates (M) are approximately double the growth rate (K), he also noted that Pauly's equation to estimate natural mortality has been widely accepted although it tends to overestimate its value.

Snappers have relatively long life spans, low growth rates, and low mortality rates and can be characterized as periodic strategists (Winemiller and Rose 1992). Other information regarding their reproductive biology, also helps characterizing them as periodic life-history strategists. For example, the small egg size and high fecundity are characteristic of periodic strategists. Synchronous episodes of spawning are common among periodic strategists (Winemiller and Rose 1992), and there are numerous spawning aggregations reported for snappers. The occurrence of spawning aggregations could be more wide spread among species of snappers than previously thought. Domeier *et al.* (1996) suggested two different spawning strategies for inshore snappers (subfamilies Lutjaninae and Paradicichthyinae) saying that medium sized, schooling species do not form spawning aggregations, while large and solitary species do migrate and form aggregations during the spawning season. However, this hypothesis would exclude species such as yellow-fin snapper (*O. chrysurus*) and lane snapper (*L. synagris*) and this is not the case because there are numerous reports of these species migrating during the spawning season. Bell and Colin (1986) and Domeier and Colin (1997), also documented mass spawning aggregations of about 1000 individuals of the closely related species, *Cesio teres* and *Pterocaesio diagramma*, species similar in size or smaller than lane and yellow-fin snappers. Finally, several species of snappers attain large sizes and reach maturity at around 50 % of their

maximum observed length (even more as results indicated in the present study). These are characteristics of periodic strategists that tend to delay maturation in order to attain a large size sufficient for production of large clutches (Winemiller and Rose 1992).

The present study analyzed through several methods the sources of life-history variation among species of snappers. Ten variables were selected (age at length zero, asymptotic length, maximum length, longevity, asymptotic weight, length at maturity, age at maturity, reproductive life span, growth rate and mortality rate) and the results indicated that the principal source of variation is size measured either by length (asymptotic, maximum or the correlated length at maturity), or by weight (asymptotic). The second source of variation is longevity which is highly correlated to reproductive life span; however, age studies for several species appear to have underestimated the real values and there is a tendency to find new estimations that show an increase which doubles or triples earlier estimates. Longevity was not correlated to size attained and therefore is considered independent, small species showed long life spans and vice versa.

As a result of the high correlation between longevity and reproductive life span, and the low correlation between longevity and age at maturity, it appears that species of snappers mature at a relatively constant age, regardless of the number of years that a species lives. Snappers reach maturity at about 3.5 years. Asymptotic length was correlated to length at maturity and snappers reach maturity when they are slightly over 50% of their maximum length. All these characteristics categorize the snappers as periodic strategists and other reproductive biology traits, including high fecundity, small egg size, delayed maturity and synchronized spawning, corroborate this view.

CHAPTER 3

COMPARISON OF SOME DISTRIBUTIONAL FACTORS AMONG SNAPPERS

Introduction

The family Lutjanidae is confined in general to tropical and subtropical marine waters, although three species of the genus *Lutjanus* from the Indo-West Pacific inhabit fresh water and the juveniles of several species in this genus around the world frequent brackish estuaries and lower parts of freshwater streams. There are 103 species in the family Lutjanidae and it is divided in four subfamilies. The subfamily Lutjaninae has 73 species, the subfamily Paradicichthyinae has two species, the subfamily Etelinae has 18 species, and the subfamily Apsilinae has 10 species. The family occurs in the eastern Pacific, Indo-West Pacific, eastern Atlantic and western Atlantic. Although Allen (1985) reports that no species occurs in more than one of these geographical areas, there are reports for species of the subfamily Lutjaninae (*L. apodus*, *L. griseus* and *O. chrysurus*) occurring on both sides of the Atlantic (Druzhinin 1970, Lloris and Rucabado 1990).

In addition to their natural distribution, species of snappers have been introduced to new regions to enhance sport fisheries (Baltz 1991). For example, *L. kasmira* was introduced to Hawaii from the Society Islands to supplement the limited populations of indigenous shallow-water snappers, and *L. jocu* was introduced to Bermuda for similar reasons (Hoese and Moore 1998).

Most lutjanids (subfamilies Lutjaninae and Paradicichthyinae) live in shallow to intermediate depths (<100 m), but the majority of the species on the subfamily Etelinae and some members of the Apsilinae are confined to deeper water (100 to 500 m). Most lutjanids are solitary in habit and exhibit territorial behavior (Allen 1985). Szedlmayer

and Shipp (1994) reported in a mark and recapture study of red snapper (*L. campechanus*) that 74% (n = 37) of the individuals tagged were recaptured within 2 km of their release site even after being at large for periods up to 1.5 years. The greatest movement they recorded was 32 km. Ingram and Patterson (2001) also found similar results with red snapper wherein 58% were recaptured at the site of release and 80% were recaptured within 20 km after being at large for up to 1.5 years.

The juveniles of the genus *Lutjanus* display different behaviors regarding their vertical distribution. The juveniles of some species are usually found on shallow estuaries, especially at the edges of them, while the juveniles of other species are found almost exclusively in coastal waters at depths of about 20 to 40 meters, within a few kilometers of the coast. On the continental coast of the Gulf of California during the spring and summer months of 1994 and 1995, juveniles of three out of seven species of *Lutjanus* present in the area (*L. argentiventris*, *L. colorado* and *L. novemfasciatus*) were found in estuaries, while the juveniles of the spotted rose snapper (*L. guttatus*) were located at some distance from the coast (1 – 2 km) and at a depth between 20 – 40 meters. The individuals observed from bottom trawl collections measured 95 – 150 mm TL (Martinez-Andrade, pers. obs.). The species found in estuaries were usually in mixed species assemblages of individuals of similar size and occupying different areas of the estuary depending on their size. For a few days in the summer of 1994, I observed large numbers of post-settled (< 20 mm TL) yellow snappers (*L. argentiventris*) at the edge of a tranquil bay inlet, swimming at the surface in clear water less than 1 meter deep. The substrate was bare coarse sand and the water temperature was 23 °C; on the other side of the same bay I frequently found larger individuals (70 – 160 mm TL) of yellow snapper

and dog snapper (*L. novemfasciatus*). These individuals were near the mouth of an estuary with no influence of fresh water. They were scattered at the edges where mangrove vegetation was present, the water depth was 0.5 – 1.5 m, the substrate was sand with little or no vegetation, apart from the mangroves, and the water temperature was 23 °C. Finally, a mixed aggregation of sub-adults (250 – 300 mm TL) of all three species was found in another estuary near the mouth. Water depth was around 2 m, mangroves were present and the substrate was mud which probably contributed to the turbidity of the water (Martinez-Andrade 1997).

Several authors have noted these two basic types of habitat selection in juvenile snappers. For example, for the Indo-West Pacific, the mangrove red snapper (*L. argentimaculatus*) is the most widely distributed lutjanid in estuaries throughout the region (Blaber 2000). In the Morrumbene Estuary, Mozambique, East Africa, four species are present (*L. argentimaculatus*, *L. fulviflamma*, *L. fulvus* and *L. sanguineus*) in open-water channels with intertidal mudbanks lined by mangroves (Blaber 2000). Juveniles of Russell's snapper (*L. russelli*) 35 – 124 mm TL, and mangrove red snapper (*L. argentimaculatus*) 59 – 405 mm TL, are present in Embley Estuary, Northern Australia, over seagrass areas, Russell's snapper also occurs in Ranong Estuary, Western Thailand (Blaber 2000).

In the eastern Pacific, juveniles of the Pacific red snapper (*L. peru*) and spotted rose snapper are restricted to depths between 20 and 40 meters on the coasts of Jalisco and Colima, Mexico (Saucedo-Lozano *et al.* 1998, Saucedo-Lozano and Chiappa Carrara 2000). For the Pacific red snapper they found 641 individuals ranging in size from 37 – 219 mm TL, captured with bottom trawl from May 1995 to March 1996; for the spotted

rose snapper they found 249 individuals with sizes from 66 – 341 mm TL. In another analysis of the same three species of snappers I studied (*L. argentiventris*, *L. colorado* and *L. novemfasciatus*), Lyons and Schneider (1990) found similar distributions in the fish fauna of the Rio Claro Estuary, Costa Rica, over a period of eight years. Thomson *et al.* (2000) report that the mullet snapper (*L. aratus*) is also found in estuaries along the coasts of the Gulf of California in addition to the species reported before for the eastern Pacific (*L. argentiventris*, *L. colorado* and *L. novemfasciatus*); they also reported juveniles of barred snapper (*Hoplopagrus guntheri*) as being common in coastal waters without specifying a particular depth.

For the western Atlantic, Blaber (2000) reports that dog snapper (*L. jocu*) and grey snapper (*L. griseus*) use the Tortuguero Estuary, Costa Rica, as a nursery; Yanez-Arancibia (1985) also mentions the presence of juveniles of grey snapper in the Terminos Lagoon, Mexico. Nagelkerken *et al.* (2000) reported the presence of grey snapper, yellow-fin snapper (*Ocyurus chrysurus*) and schoolmaster snapper (*L. apodus*) in an estuarine system in Curaçao, Netherlands Antilles. Cuellar *et al.* (1996), after several trawl surveys on the southeastern coast of U.S.A., from 1973 to 1992, found juveniles of vermilion, red, mutton, lane and Caribbean red snappers (*Rhomboplites aurorubens*, *Lutjanus campechanus*, *L. analis*, *L. synagris* and *L. purpureus* respectively) in addition to juveniles of wenchman (*Pristipomoides aquilonaris*), as small as 20 – 30 mm TL. Depths for juveniles were not specified but samples were taken from 14 – 92 m for vermilion snapper, 7 – 68 m for red snapper, 7 – 28 m for mutton snapper, 5 – 16 m for lane snapper and 64 – 179 m for the wenchman. In another study of lane snapper (*L. synagris*) on the Campeche banks, Mexico, Rivera-Arriaga *et al.* (1996) found juveniles

in depths ranging from 20 - 30 meters. The adults spawn offshore, in water depths over 40 meters, and the larvae are transported to shallow coastal waters where they initially settle and later move to deeper waters as they grow.

Finally, for the eastern Atlantic, Baran (1995) lists four species (*L. agennes*, *L. dentatus*, *L. endecacanthus* and *L. goreensis*) out of five of the genus *Lutjanus* present in the Fatale Estuary, Guinea, Western Africa. There is no specification whether the species found here are juveniles or not; however, this is likely because at least for the African red snapper (*L. agennes*), large adults have been recorded spawning in surface waters far from the coast (> 80 Km) (see Chapter 2).

Identifying the particular habitat types where species locate at various stages throughout their life cycles (Livingston 1988) and the areas where they spawn is important for the management of individual fisheries. This information is also important when considering the placement of marine protected areas, and the potential impact of activities such as fishing, dredging, or anchoring on these areas (Sadovy 1996). The objectives of the present chapter are to explore the spatial patterns observed in different species of snappers during ontogeny and also in relation to their breeding site selection.

Methodology

This chapter summarizes two different data sources: a literature survey and my own field observations on the Pacific coast of Mexico. The literature search for information on distribution of snappers focused on ecological variables, including vertical distribution, latitudinal range, habitat type selection (characterized by substrate type) and spawning seasonality. Most of the information was obtained from Allen (1985) and Froese and Pauly (2000). The methodology and results sections of published

information was reviewed in terms of fishing gear selected, depth sampled, species found and sizes obtained. If the size of the individuals collected for a particular species was mentioned, judgment as to whether to consider individuals as adults or juveniles was based on the mean length at maturity reported for that particular species (Table 2.4, Chapter 2). The information was analyzed graphically and through correlation analyses. These data are summarized in a table identifying species by breeding site selection. In addition, a graphical model of the distribution of snappers during ontogeny was prepared. The distribution of juveniles in the genus *Lutjanus* received special attention due to personal observations in estuaries and coastal waters off the city of Guaymas, Sonora, Mexico.

Information on vertical distribution (minimum and maximum depths), latitudinal distribution (north, south and latitudinal range) and substrate selection was available for 82 species of snappers (Allen 1985, Froese and Pauly 2000). Additionally, information on the timing of peak spawning activity was available for 36 species.

Results

Snappers cover a wide range of depths, from near the surface to depths over 500 m. Based on the published information obtained for the minimum and maximum depth at which the adult snappers are found, there are marked differences in vertical distribution among subfamilies (Table 3.1 and 3.2). The subfamilies Lutjaninae and Paradicichthyinae inhabit the continental shelf almost exclusively, while the species in the subfamilies Etelinae and Apsilinae are restricted to the continental slope (Figure 3.1). These differences are apparent in the means for the maximum depths reported for species in each subfamily. For individuals of the subfamily Lutjaninae, the mean is 87 m with a

maximum of 400 m for the lane snapper (*L. synagris*) and a minimum of 20 meters for the Indo-West Pacific species *L. coeruleolineatus* and *L. ehrenbergii*. For the subfamily Paradicichthyinae, the mean was 67.5 meters with a maximum of 75 meters for *Symphorus nematophorus*, and a minimum of 60 meters for *Symphorichthys spilurus*. For the subfamily Etelinae, the mean was 284 meters with a maximum of 550 meters for *Pristipomoides macrophthalmus*, and a minimum of 70 meters for *Aphareus furcatus*. And finally, for the subfamily Apsilinae, the mean was 236 meters with a maximum of 460 meters for *Parapristipomoides squamimaxillaris*, and a minimum of 100 meters for *Paracaesio caeruleus*.

Their latitudinal distribution in the northern hemisphere extends from the Equator to 43° N and in the southern hemisphere it extends from the Equator to 37° S. Some snappers span across the Equator up to 70° of latitude (equivalent to almost 7,800 km). In general the species often have broad distributions including both hemispheres. Nevertheless, some species are restricted to the northern hemisphere (*L. campechanus*, *Apsilus dentatus*, *A. fuscus*, *Pristipomoides macrophthalmus*), while some others are restricted to the southern hemisphere (*L. adetii* and *L. notatus*) and relatively few have localized distributions (*L. adetii*, *L. ambiguous*, *L. coeruleolineatus*, *L. dodecanthoides*, *L. notatus*, *L. stellatus*, *Paracaesio caeruleus*, *Parapristipomoides squamimaxillaris*, *Pristipomoides freemani* and *P. macrophthalmus*).

Discussion

The maximum depth distributions among species in the four subfamilies showed marked differences in depth selection (Figure 3.1). Species of the subfamilies Lutjaninae and Paradicichthyinae inhabit relatively shallow waters (usually on the continental shelf),

Table 3.1 Asymptotic length, vertical and latitudinal distribution, range, habitat selection and reproductive peak months for most species of snappers.

Species	L inf	Min D	Max D	N	S	Range	Subst.	Spawning
Lutjaninae								
<i>H. guntheri</i>	947	1	50	32 N	5 N	37	1	
<i>L. adetii</i>	324	1	125	9 S	37 S	28	2	Nov-Jan
<i>L. apodus</i>	696	0.4	25	42 N	5 S	47	2,3,4,5,6	Apr-Jun
<i>L. argentimaculatus</i>	989	1	100	31 N	32 S	63	1	Apr-Oct
<i>L. bengalensis</i>	315	10	25	30 N	10 S	40	2	
<i>L. biguttatus</i>	211	5	25	22 N	13 S	35	2	
<i>L. bitaeniatus</i>	315	40	65	2 N	15 S	17	1	
<i>L. bohar</i>	732	10	93	30 N	32 S	62	1, 2	Oct-Dec
<i>L. bouton</i>	315	15	50	34 N	20 S	54	2	Jan-Dec
<i>L. buccanella</i>	638	9.15	220	36 N	5 S	41	2, 3	Apr
<i>L. campechanus</i>	955	10	190	43 N	18 N	25	1	May-Jul, Nov
<i>L. carponotatus</i>	383	2	40	23 N	25 S	48	2	
<i>L. coeruleolineatus</i>	417	10	20	26 N	12 N	14	2	
<i>L. cyanopterus</i>	1289	1	40	36 N	2 S	38	1	
<i>L. decussatus</i>	315	5	30	30 N	18 S	48	2	
<i>L. dodecakanthoides</i>	315	1	30	20 N	6 S	26	2	
<i>L. ehrenbergii</i>	327	5	20	28 N	30 S	58	2	
<i>L. erythropterus</i>	664	1	100	34 N	27 S	61	1	Sep-Feb
<i>L. fulviflamma</i>	303	3	45	30 N	35 S	65	2	
<i>L. fulvus</i>	418	2	40	34 N	8 S	42.2	1, 2	
<i>L. gibbus</i>	449	6	68	33 N	28 S	61	2	
<i>L. griseus</i>	670	0.4	180	43 N	23 S	66	2, 5, 6	Jun-Aug
<i>L. guilcheri</i>	622	1	70	20 N	20 S	40	1	
<i>L. jocu</i>	862	5	25	43 N	6 S		2	Mar
<i>L. johnii</i>	856	1	80	30 N	20 S	50	2	Sep
<i>L. kasmira</i>	347	1	65	35 N	35 S	70	1, 2	Nov-Mar
<i>L. lemniscatus</i>	673	1	80	21 N	25 S	46	1	
<i>L. lunulatus</i>	366	10	30	25 N	16 S	41	2	
<i>L. lutjanus</i>	283	1	90	34 N	20 S	54	1, 2	Jan-Jun, Nov
<i>L. madras</i>	315	5	90	21 N	10 S	31	1, 2	

(Table continued)

Species	L inf	Min D	Max D	N	S	Range	Subst.	Spawning
<i>L. mahogoni</i>	618	0.4	25	36 N	9 N	27	2	Aug
<i>L. malabaricus</i>	843	12	100	34 N	34 S	68	1, 2	Oct-Dec
<i>L. mizenkoi</i>	315	100	150	3 N	15 S	18	1	
<i>L. monostigma</i>	579	5	30	30 N	25 S	55	2	Feb, Nov
<i>L. notatus</i>	322	10	40	11 S	29 S	18	2	
<i>L. novemfasciatus</i>	1734	11	70	25 N	16 S	41		
<i>L. peru</i>	836	12	160	23 N	20 S	43	1	
<i>L. purpureus</i>	929	2	128	34 N	35 S	69	1	Apr-Sep
<i>L. quinquelineatus</i>	232	1	100	34 N	30 S	64	2	Nov-Feb
<i>L. rivulatus</i>	758	1	80	34 N	35 S	69	1, 2	
<i>L. russelli</i>	502	1	100	30 N	28 S	58	1, 2	
<i>L. sanguineus</i>	962	10	100	34 N	34 S	68	1, 2	Oct
<i>L. sebae</i>	910	10	30	20 N	25 S	45	1, 2	Aug-Feb
<i>L. synagris</i>	465	5	400	36 N	25 S	61	1, 2	Mar, Sep
<i>L. timorensis</i>	520	20	130	20 N	20 S	40	1, 2	
<i>L. vitta</i>	329	10	45	34 N	23 S	57	2, 5	Sep-Feb, Apr
<i>L. vivanus</i>	826	73.2	320	36 N	12 S	48	1	Apr-Sep
<i>M. niger</i>	775	5	75	30 N	15 S	45	2	
<i>M. macularis</i>	622	5	90	30 N	28 S	58	2	
<i>O. chrysurus</i>	671	10	70	43 N	25 S	68	2	Jan-Feb, Apr, Aug-Sep
<i>P. pinjalo</i>	826	1	60	30 N	19 S	49	1	
<i>R. aurorubens</i>	528	37	128	36 N	25 S	61	1	Jun-Nov
Paradicichthyinae								
<i>S. nematophorus</i>	932	1	75	32 N	25 S	57	2	
<i>S. spilurus</i>	622	5	60	30 N	25 S	55	2, 3	
Etelinae								
<i>A. furca</i>	906	6	70	34 N	28 S	62	2	
<i>A. rutilans</i>	1288	1	100	34 N	28 S	62	1, 3, 4	Nov-Dec
<i>A. virescens</i>	1009	1	100	34 N	30 S	64	1, 2	Nov-Jan
<i>E. carbunculus</i>	918	90	300	34 N	25 S	59	1	Nov
<i>E. coruscans</i>	1054	100	300	34 N	22 S		1	Sep-Oct
<i>E. oculatus</i>	1027	135	450	35 N	14 S	49	1	
<i>E. radiosus</i>	826	90	200	34 N	25 S	59	1	

(Table continued)

Species	L inf	Min D	Max D	N	S	Range	Subst.	Spawning
<i>P. aquilonaris</i>	581	64	366	36 N	15 S	51	1	
<i>P. argyrogrammicus</i>	417	70	300	34 N	15 S	49	1	
<i>P. auricilla</i>	431	90	360	35 N	22 S	57	1	
<i>P. filamentosus</i>	858	90	360	34 N	23 S	57	1	Mar
<i>P. flavipinnis</i>	602	90	360	30 N	25 S	55	1	Dec-Feb
<i>P. macrophthalmus</i>	520	229	549	25 N	9 N	16	1	
<i>P. multidens</i>	708	40	245	32 N	36 S	68	1	Dec-Jan
<i>P. sieboldii</i>	548	180	360	34 N	32 S	66	1	
<i>P. typus</i>	679	40	100	31 N	28 S	59	1	Feb-Jun
<i>P. zonatus</i>	498	70	300	34 N	28 S	62	1	
<i>Randallichthys filamentosus</i>	520	150	300	28 N	23 S	51	1	
Apsilinae								
<i>A. dentatus</i>	643	120	180	27 N	11 N	16	1	Feb, Apr, Oct, Nov
<i>A. fuscus</i>	775	30	300	20 N	25 S	45	1	
<i>L. carnolabrum</i>	520	90	300	31 N	15 S	46	1	
<i>P. caeruleus</i>	520		100	35 N	30 N		1	
<i>P. gonzalesi</i>	438	140	250	20 N	19 S	39	1	
<i>P. kusakarii</i>	622	100	200	30 N	23 S	53	1	
<i>P. sordida</i>	499	100	200	30 N	19 S	49	1	
<i>P. stonei</i>	816	200	320	31 N	19 S	50	1	
<i>P. xanthura</i>	520	20	150	34 N	32 S	66	1	
<i>P. squamimaxillaris</i>	417	130	460	25 N	28 S	53	1	

L inf = asymptotic length in mm, Min D = minimum depth in meters, Max D = maximum depth in meters, N = northern distribution on either hemisphere in degrees of latitude, S = southern distribution on either hemisphere in degrees of latitude, Range = latitudinal range in degrees of latitude, Subst. = Substrate selection: 1 = rock, 2 = coral, 3 = sand, 4 = mud, 5 = seagrass, 6 = mangrove, Spawning = spawning season peak months.

while species of the Apsilinae and Etelinae subfamilies are deep-water snappers (continental slope). For several species of snappers in the subfamily Lutjaninae there is a consistent pattern of depth distribution where the adult individuals of medium and large species move to deeper waters as they increase in size. Davis and West (1993) believe

Table 3.2 Mean asymptotic length, minimum depth, maximum depth, and latitudinal range by subfamily

Subfamily	L_{inf}	Min D	Max D	Range
Lutjaninae	604 ± 300 (52)	9.7 ± 17.6 (52)	87 ± 72.6 (52)	47.8 ± 15.4 (51)
Paradicichthyinae	777 ± 219 (2)	3 ± 2.8 (2)	67.5 ± 10.6 (2)	56 ± 1.4 (2)
Etelinae	744 ± 251 (18)	85.3 ± 60.5 (18)	284 ± 129 (18)	55.6 ± 11.7 (17)
Apsilinae	577 ± 134.7 (10)	103 ± 55 (9)	246 ± 103 (10)	46.3 ± 13.6 (9)

Mean ± S.D. (N), L_{inf} = asymptotic length in mm TL, Min D = minimum depth in meters, Max D = maximum depth in meters, Range = latitudinal range in degrees of latitude.

that this behavior could be due to the requirement of larger species for more space and nutritional resources as they grow. Under this assumption the smaller species remain closer to the coast and are usually found in schools of variable numbers and mixed with other species. One way to examine this pattern of larger individuals found in deeper waters is to look at the sites where commercial fishermen obtain their catches. In Mexico, for example, the commercial catch of snappers is obtained at depths around 120 m and the weight per individual is usually between 4 and 6 kg (Ruiz Dura 1992).

During the spawning season the same medium and larger species form large aggregations and migrate towards off-shore areas where they spawn near the surface (Chapter 2). Sadovy (1996) supports this theory, suggesting that the larger species of reef fishes are the ones that generally migrate and form spawning aggregations because they are capable of moving greater distances during the spawning season. They must migrate to assemble in numbers since normally they live more dispersed and would otherwise have difficulty in finding mates. Depth apparently also plays an important role because most of the descriptions of spawning aggregations note that the aggregations occur where a steep drop-off is present (Chapter 2). Aggregations at some of these spawning sites have been documented over several decades and are used sequentially by various species of snappers and groupers at different times. For example, some areas around the Virgin

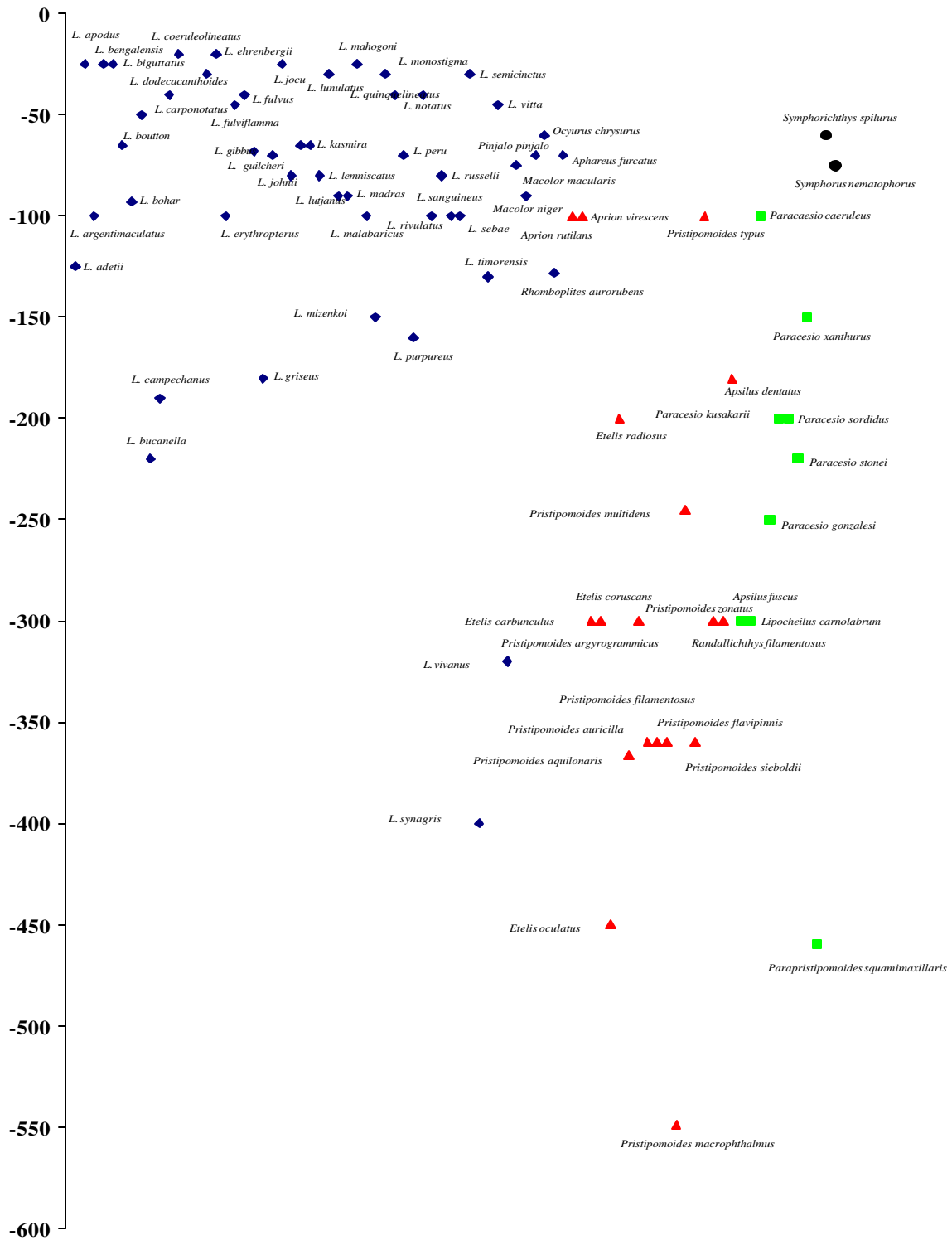


Figure 3.1 Maximum depth distribution (meters) for adults of most species of snappers in the four subfamilies, (Lutjaninae (diamonds), Etelinae (triangles), Apsilinae (squares) and Paradicichthyinae (circles)).

Islands are used by several species of groupers and also by the lane snapper (*L. synagris*) (Sadovy 1996).

Since pelagic larval durations provide information on potential dispersal distances (Boehlert 1996) there is little doubt that spawning takes place in offshore waters. Lindeman *et al.* (2001) studied the pelagic larval durations (PLD) for grunts, snappers and groupers and found that the mean larval duration for snappers is 30 days. This is considerably longer than the 14 days average larval duration found for the closely related grunt family (genera *Haemulon* and *Anisotremus*). Groupers (Serranidae) in contrast have the longest larval duration with an average of 40 days (genera *Myteroperca* and *Epinephelus*). All three families show very little variation among species. The larger species of groupers are well known for their highly social spawning and often protogynous behavior. And some species migrate distances of 110 km or more to aggregation sites. Snappers have been reported to migrate up to 80 km to spawn in aggregations (Chapter 2), and grunts in contrast travel short distances, remaining within inshore waters (Sadovy 1996).

Snapper eggs and/or newly hatched larvae are transported by surface currents to in-shore waters while they remain as part of the zooplankton. After larvae arrive in coastal waters, there is a marked difference in the habitat selected depending on the species. The juveniles of some species of the genus *Lutjanus* are found in estuaries while juveniles of other species, including also the genus *Lutjanus*, are found in coastal waters at depths ranging generally from 20 – 40 meters. Most of the species of snappers reported either in estuaries or in deeper coastal waters had a minimum size around 20 mm, indicating that they just recently settled. Snappers typically settle when they reach

10 – 18 mm TL and grow at an average rate of 0.81 mm/day. Grunts (Haemulidae) in comparison, settle at a considerably shorter length (6.5 – 9 mm TL) and grow slower (0.47 mm/day) (Lindeman *et al.* 2001). These facts suggest that the selection of their respective areas occurs before settlement. Based on these minimum sizes reported and my own observations, where not a single individual of the species I found in coastal areas (*L. guttatus*) was found inside estuaries over an extended period of sampling, I think that settlement site selection is non-random. Supporting this hypothesis Leis *et al.* (1996) concluded in one study in northern Australia, that the late pelagic stages of coral reef fishes (including one species of the genus *Lutjanus*) are strong swimmers, and easily capable of horizontal and vertical movement and apparently able to detect and orientate to settlement habitats (reefs in this case) more than one kilometer away. Leis *et al.* (1996) also concluded that a taxonomic component is evident in most of the behaviors displayed by the different species and fish families studied. Boehlert (1996) supports the hypothesis that pre-settlement larval behavior plays an important role in detection of settlement habitat. He indicates that it is possible that current flow and topography interactions may result in physical perturbations, which may extend some distance from the settling habitat and provide cues for the larvae. The enhanced swimming abilities of pre-settlement larvae may facilitate movement to selected habitats once these cues are detected.

Another fact that may influence the settlement of different species of snappers is the vertical positioning of pelagic larvae (Lindeman *et al.* 2001). During the day they move to depths between 20 and 40 meters while at night they are found at 0 to 20 meters.

This movement occurs either in offshore or inshore waters. In comparison, the larvae of grunts always remain near the bottom and are found only inshore (Lindeman *et al.* 2001).

There is no question about the relevance of estuaries as nursery areas, providing shelter and food to numerous species of fishes and invertebrates (Blaber 2000). Snapper species of snappers which utilize estuaries as nursery habitat show little movement within the estuary when compared to other families. Sheaves (1993, 1996, 2001) used mark and recapture to study the movement patterns of several species within an estuary in northeastern Australia. He found that the juveniles of groupers (*Epinephelus coloides* and *E. malabaricus*) and the snapper *L. russelli* showed the least movement, usually being recaptured within 40 meters of their release site. Porgies (Sparidae) in contrast, showed the greatest movement, being recaptured hundreds of meters from their release site. In addition to relatively strong site tenacity within the estuary, there is a strong influence on maturation (Sheaves 1995). *L. russelli* and *L. argentimaculatus* remain sexually immature while in the estuary, even when individuals of *L. argentimaculatus* reach 541 mm FL and 8 years of age. Similar results were found for the gray snapper (*L. griseus*) in southern Florida. Rutherford *et al.* (1989a, b), concluded that grey snapper do not reach maturity until they leave the nursery area.

Many snapper species, where the juveniles are found in estuaries, demonstrate a clear dependency on these environments, and can be considered estuarine-dependent. In contrast, other snappers do not utilize estuaries as nursery areas and can be considered estuarine-independent (Table 3.3).

These findings indicate that the species of snappers belonging to the subfamily Lutjaninae exhibit two different patterns regarding their distribution. Small species (up

Table 3.3 Partial listing of estuarine-dependent and estuarine-independent species of snappers.

Estuarine -dependent species	Estuarine -independent species
<i>Lutjanus agennes</i>	<i>Hoplopagrus guntheri</i>
<i>L. apodus</i>	<i>L. analis</i>
<i>L. aratus</i>	<i>L. campechanus</i>
<i>L. argentimaculatus</i>	<i>L. guttatus</i>
<i>L. argentiventris</i>	<i>L. peru</i>
<i>L. colorado</i>	<i>L. purpureus</i>
<i>L. dentatus</i>	<i>L. quinquelineatus</i>
<i>L. endecacanthus</i>	<i>L. synagris</i>
<i>L. fulviflamma</i>	<i>Pristipomoides aquilonaris</i>
<i>L. fulvus</i>	<i>Rhomboplites aurorubens</i>
<i>L. goreensis</i>	
<i>L. griseus</i>	
<i>L. novemfasciatus</i>	
<i>L. russelli</i>	
<i>L. sanguineus</i>	
<i>Ocyurus chrysurus</i>	

to 350 mm TL) remain in coastal waters throughout their entire life cycle and most likely do not migrate offshore for spawning. Medium to large species (over 350 mm TL) move to deeper waters (> 40 m) as they grow and during the spawning season migrate offshore to spawn in surface waters, from where the eggs and larvae are transported to coastal

waters (Fig. 3.2). The juveniles of some species are found in estuaries, while other species (specially medium and large snappers) appear on coastal waters at an approximate depth of 20 – 40 meters. Diaz-Ruiz *et al.* (1996) documented a similar pattern for *Ocyurus chrysurus* and *L. griseus*, but also identified an alternative pattern for *L. analis* where the juveniles and pre-adults occur in relatively deep water (~ 15 meters) and then migrate to coastal lagoons to spawn as adults. However, the evidence is equivocal since actual spawning was not observed and the juveniles occur in deeper water, it is probable that large individuals of *L. analis* were pre-adults which later moved to deeper waters and migrated during the spawning season as reported by several authors (see Chapter 2).

Larval abundances of species from the Etelinae and Apsilinae are recorded from offshore waters only (Leis 1987). Thus spawning probably takes place offshore, but whether or not adults undergo spawning migrations is unknown. Nevertheless, the presence of small juveniles and sub-adults in coastal waters suggests that larvae are transported by superficial currents and settle somewhere on the continental shelf rather than on the slope in adult habitat. They later move to deeper waters as they grow in a similar manner to that of large species of Lutjaninae snappers.

In conclusion, size is a factor in the distribution patterns of snapper species and varies across the family and within subfamilies. There is a marked difference in the vertical distribution of the adult populations depending on the subfamily. Lutjaninae and Paradicichthyinae species are in general distributed on the continental shelf at depths less than 200 meters, while species of the Etelinae and Apsilinae inhabit deeper waters principally over the continental slope out to depths of 550 meters. In the subfamily

Lutjaninae, the small species (up to 350 mm TL) remain in coastal waters throughout their entire life cycle and most likely do not migrate offshore during the spawning season.

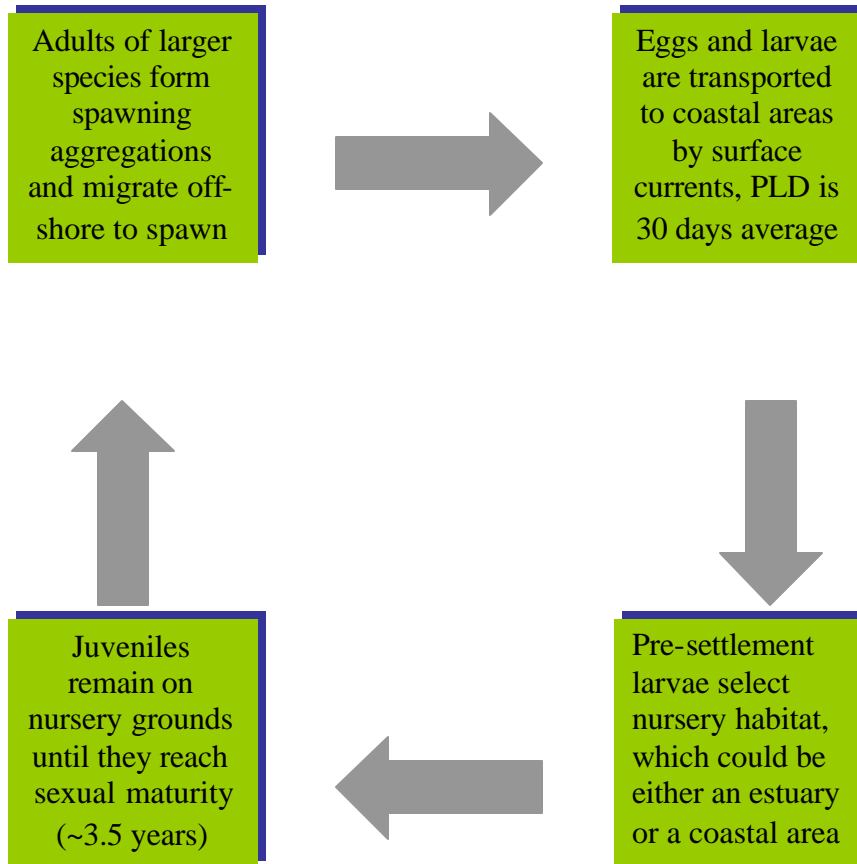


Figure 3.2 Suggested life cycle for medium to large species of snappers (PLD = Pelagic Larval Duration).

In contrast, medium to large species (over 350 mm TL) move to deeper waters as they grow and during the spawning season migrate offshore to spawn in surface waters. From there the eggs and larvae are transported to coastal waters. Juveniles of several species of snappers are found in estuaries regardless of the maximum size they attain, while the

juveniles of medium and large snappers within the subfamily Lutjaninae appear in coastal waters at approximate depths of 20 – 40 meters; selection for either habitat is presumed to occur before settlement. Within the family Lutjanidae there appear to be several distributional patterns, but my review has also pointed out the need for additional information on the vertical distribution of snappers during ontogeny in general and on the nursery habitat selection of other species not included here.

CHAPTER 4

COMPARISON OF FEEDING HABITS AMONG SNAPPERS

Introduction

The study of feeding habits is important because fish growth depends on the quality and quantity of food that is eaten. Most studies of food habits identify the species of food in the contents of the alimentary canal and their respective weights or volumes. The question of how fish select their food was first addressed during the late 1960's (McArthur and Pianka 1966, Emlen 1966) and led to the development of the optimal foraging theory which attempts to explain how an individual chooses between alternative sources of food by weighing the benefits and costs of capturing one possible prey over another. This theory, although not precise, has influenced studies of fish feeding ecology for the last 20 years (Gerking 1994).

Fishes grow throughout their lives and this phenomenon is a major element in their life history that influences how optimal foraging theory applies to them. As fishes grow they should make adjustments in their foraging strategy reflected as changes in food quantity, size or other characteristics. The larval stage in fishes is less well developed than the young of other vertebrates, and its food intake with regard to size and variety is limited when compared to that of adults; therefore, one optimal foraging strategy is not a consistent feature throughout the life of a fish species, but it needs to be adjusted during ontogeny (Livingston 1988, Gerking 1994). Migratory coastal fishes in particular undergo diverse ontogenetic trophic transformations with a progression of distinct nutritional stages within species and an evident resource partitioning among species in different habitat types (Livingston 1988).

Snappers are active predators, often characterized as opportunistic carnivores that feed mainly at night on a variety of items. Although fishes are dominant in the diet of most snapper

species, other important prey include crustaceans (mainly crabs and shrimp), gastropods, cephalopods, and planktonic organisms, particularly pelagic urochordates. The larger, deep-bodied snappers generally feed on fishes and large invertebrates (especially stomatopods and lobsters) on or near the surface of reefs; they are usually equipped with large canine teeth adapted for seizing and holding their prey (Allen 1985).

Plankton is generally important in the juvenile and adult diets of species of the subfamilies Etelinae and Apsilinae, especially in the genera *Pristipomoides* and *Paracesio*. It is also important in some species of the subfamily Lutjaninae (*Ocyurus chrysurus*, *Pinjalo pinjalo*, *P. lewisi* and *Rhomboplites aurorubens*). These snappers tend to have a relatively slender, fusiform body shape, a forked caudal fin and weaker dentition with fewer enlarged canines in the jaws (Parrish 1987).

Snappers occur and feed from the surface to depths of over 500 meters; however, the adults of several species are restricted to feeding in water deeper than 100 m deep. Diets of the mainly deepwater species are poorly known because of the remote locations they inhabit and the loss of gut contents by regurgitation due to the expansion of the swimming bladder when a fish is brought to the surface (Parrish 1987).

The objectives of this Chapter are to acquire and standardize information regarding the feeding habits of snappers, describe the feeding habits among species of snappers, compare the feeding habits of species among and within subfamilies, and identify sources of variation on major components reported in diets of this family.

Methodology

An extensive literature search for information regarding the feeding habits of snappers was conducted. Only sources of information identifying prey items to at least the genus level

and indicating the percent by volume or weight of those items were incorporated in this review. Some of the publications available analyzed the diets of juveniles and sub-adults; in these cases, the size range of the individuals was noted as well. After an initial literature search, ten different prey categories were selected to sort the information found. These categories were the most abundant and distinctive prey items for snappers, and all the items reported in the literature were reassigned to one of these categories. The reassignment was based on the taxonomic status of the prey species (family, order, class, etc.), its size and mobility (plankton, nekton), life stage (adult or larvae), and location within the water column (benthic or pelagic). The prey items included in each of the selected categories are the following:

Fish (FISH) included identified or unidentified species of teleost fishes at any ontogenetic stage, or partial remains of them.

Pelagic small crustaceans (PESC) included mainly members from the class Copepoda, the orders Euphausiacea and Mysidacea, and larvae of other crustaceans with a pelagic stage.

Decapoda (DECA) included juvenile or adult shrimps, crabs and lobsters. It was selected to shed some light on the impact of snappers on species that have a high commercial value. Nevertheless, non-commercial species such as brachyurans, anomuran, portunid and calappid crabs were reported frequently and included here.

Other benthic crustaceans (OBEC) included species of the classes Amphipoda, Stomatopoda and Isopoda, the order Tanaidacea and other unidentified crustaceans.

Cephalopods (CEPH) included species of squid and octopus.

Other mollusks (OTMO) include pelagic gastropods (pteropods and heteropods) mainly, and some benthic mollusks such as bivalves.

Annelida (ANNE) included mostly worms belonging to the class Polychaeta.

Pelagic urochordates (PEUR) included the class Thaliacea (salps), a prey item particularly common among lutjanids.

Benthic urochordates (BEUR) included organisms of the class Asidiacea (tunicates).

Other (OTHE) included mainly eggs, plants and debris.

A database of ten prey category variables expressed as percent by volume, and their respective snapper stock was created. Additional information for each stock included the species name, reference author, geographic location, and any other available information related to the conditions of the study, such as size range of the individuals, season when the study was conducted, substrate type from where individuals were collected, etc. Comparisons of the feeding habits in species within the subfamilies Lutjaninae and Etelinae were prepared using the mean value of the populations for each species. An additional comparison of the feeding habits in snappers of the subfamilies Lutjaninae and Etelinae, and grunts of the family Haemulidae was conducted in a similar way.

Principal Component Analysis

A Principal Component Analysis (PCA) of ten prey category variables was performed to explore variance patterns among 30 species of snappers in the subfamilies Lutjaninae and Etelinae. The PCA was conducted using the Factor Procedure in SAS and Varimax rotation of the first four factors to facilitate the interpretation of each separate component (SAS Institute 1996). The PCA was configured to resolve ten non-correlated prey category variables into four orthogonal factors to facilitate interpretation and comparisons among species and subfamilies. The input data included prey category variables in 113 snapper stocks without missing data. Thus data on 113 stocks representing 30 species of snappers were used to estimate variable loadings and generate principal component scores for each species. The mean value of the

variables for each species was obtained from the populations through the Means Procedure in SAS and the species were plotted as centroids in 3-dimensional prey category space (SAS Institute 1996). The interpretation was based on eigenvalues of the correlation matrix = 1.0 and rotated factor loadings = 0.50 (Grossman 1991). Other analyses performed were descriptive statistics, correlation and graphic analyzes.

Results

The results of the literature search (Table 4.1) yielded information on feeding habits of 30 species and 113 stocks in the subfamilies Lutjaninae and Etelinae. No quantitative information was available for species of the subfamilies Paradicichthyinae or Apsilinae. Additionally, information on feeding habits of species in the closely related family Haemulidae (grunts) were added for comparison.

Fish was an important category reported in the diets for both subfamilies. For snappers inhabiting intermediate depths (Lutjaninae), small pelagic fishes such as clupeids and engraulids were the most common species, although juvenile anguilliform fishes were also common and usually abundant in their diets. Crabs and shrimps (decapods) were the most important item in the diet of snappers in the subfamily Lutjaninae, but not for the subfamily Etelinae. The mean values of the categories found in the diets for 30 species of the subfamilies Lutjaninae and Etelinae are expressed in percent by volume (Table 4.2). In the subfamily Lutjaninae the main prey items (Figure 4.1) are decapods (44.16 % by volume), followed by teleost fishes (29 %), other benthic crustaceans (11.04 %), small pelagic crustaceans (5.45 %) and cephalopods (3.86 %). For the subfamily Etelinae the main prey items (Figure 4.2) are teleost fishes (34.23 %), pelagic urochordates (24.07), small pelagic crustaceans (20.64 %), benthic mollusks (8.79 %), decapods (5.69 %), cephalopods (2.28 %) and other benthic crustaceans (2.05 %). The feeding

habits of these two families are significantly different based on the statistical analysis (Table 4.2), the interpretation of these results indicate that the species of the subfamily Lutjaninae are primarily benthic feeders since over 55 % of their diet is composed of benthic crustaceans mainly decapods or other groups such as the stomatopods in the category of other benthic crustaceans. In addition to the benthic crustaceans, the second major category for this subfamily, fish, frequently included juveniles of anguilliform fishes which are also associated with the substrate. Species of the subfamily Etelinae feed in the water column instead of on or near the bottom. This is reflected in the pelagic items in their diets, small crustaceans and urochordates which make 44.71 % of the diet. These items also indicated the increased dependency on zooplankton and the particular habit of preying on the urochordates, commonly called salps. A simple correlation analysis performed on the ten categories of prey items from the diets of snappers was unable to detect any significant pair-wise correlations between variables (Table 4.3).

One distinctive example of food partitioning was found when comparing the species of snappers from the subfamily Lutjaninae with species of the closely related grunts (Figure 4.3). Grunts usually inhabit the same areas, and are similar in size to many species of snappers; however, after analyzing their diets it is apparent that fish was practically absent and that they rely heavily on other benthic crustaceans, which contributed to about 43 % of their diets.

In the Principal Component Analysis, the first four components had eigenvalues greater than 1.0 and explained over 61 % of the variability in feeding habits among species of the subfamilies Lutjaninae and Etelinae (Table 4.4). The first component (PC1) explained 20.7 % of the variability and loaded heavily (greater than 0.50) and positively for other mollusks, pelagic urochordates, and small pelagic crustaceans; it also loaded heavily but negatively for decapods.

The second principal component (PC2) explained 15.1 % of variability and loaded positively for fish and negatively for decapods. The third principal component (PC3) explained 14.4 % of the variability and loaded positively for other items and annelids. The fourth principal component (PC4) explained 11 % of the variability and loaded positively for other benthic crustaceans.

When the centroids for all 30 species of snappers are plotted in 3-dimensional prey space (Fig. 4.4), three easily distinguished groups of snappers were arranged on the PC1 axis. The first group consists of three species of the genus *Pristipomoides* (*P. auricilla*, *P. filamentosus* and *P. sieboldi*) from the subfamily Etelinae, the second group has another species of *Pristipomoides* (*P. zonatus*) and three species from the subfamily Lutjaninae (*Lutjanus argentimaculatus*, *L. peru* and *Rhomboplites aurorubens*); the last group consists of all 23 remaining species including four from the subfamily Etelinae (*Aphareus furcatus*, *Aprion virescens*, *Etelis carbunculus* and *E. coruscans*) and 19 from the subfamily Lutjaninae (18 of the genus *Lutjanus* and *Ocyurus chrysurus*). Variation along the second axis did not show any clear groupings of species, but placed *L. argentimaculatus* (Lutjaninae) in one end and *Etelis carbunculus* (Etelinae) on the other. The third axis grouped five species in one end, four from the subfamily Lutjaninae (*Lutjanus rivulatus*, *L. gibbus*, *L. synagris* and *Rhomboplites aurorubens*) and one from the subfamily Etelinae (*Pristipomoides auricilla*); on the other end it placed 13 species, nine from the subfamily Lutjaninae (all genus *Lutjanus*) and four from the subfamily Etelinae (*Etelis carbunculus*, *E. coruscans*, *P. filamentosus* and *P. zonatus*).

Discussion

Only information on the subfamilies Lutjaninae and Etelinae was found; however, these two subfamilies include most of the species in the family Lutjanidae and are fairly representative of the in-shore dwelling species (Lutjaninae) and the deep-water species (Etelinae). The available

Table 4.1 Feeding habits found for most species of snappers and some grunts at different populations and ontogenic stages.

Subfamily, species & location	FISH	PESC	DECA	OBEC	CEPH	OTMO	ANNE	PEUR	BEUR	OTHE
Lutjaninae										
<i>L. analis</i>										
Colombia (Arevalo 1996)	41.94	4.28	43.99	0	0	0	0	0	0	9.79
Cuba (Sierra 1997)	21.8	6.7	59.9	11.6	0	0	0	0	0	0
Cuba, 40-50mmFL, (Sierra 1997)	0	100	0	0	0	0	0	0	0	0
Cuba, 60-79mm (Sierra 1997)	28.9	71.1	0	0	0	0	0	0	0	0
Cuba, 80-99mm (Sierra 1997)	48.5	0	51.5	0	0	0	0	0	0	0
Cuba, 100-119mm (Sierra 1997)	0	0	100	0	0	0	0	0	0	0
Cuba, 120-139mm (Sierra 1997)	0	0	100	0	0	0	0	0	0	0
Cuba, 140-160mm (Sierra 1997)	0	0	100	0	0	0	0	0	0	0
Cuba, 180-300mm (Claro 1981)	31	0	59.4	0.9	0.1	1.8	0	0	0	6.8
Cuba, 180-720mm (Claro 1981)	41.3	0	50.9	1.5	1.3	1.5	0	0	0	3.5
Colombia, 211-460mm (Duarte & Garcia 1999)	46.06	0	31.18	12.21	3.45	1.28	0.6	0	0	5.22
<i>L. apodus</i>										
Mexico, <70 mm (Sanchez 1994)	0	0	65.9	34.1	0	0	0	0	0	4.7
Mexico, 71-80 mm (Sanchez 1994)	14.6	0	69	8	0	0	0	0	0	0
Mexico, 81-90 mm (Sanchez 1994)	22.2	0	62.5	3	0	0	0	0	0	4.5
Mexico, 91-100 mm (Sanchez 1994)	34.7	0	20	45	0	0	0	0	0	0
Mexico, 101-110 mm (Sanchez 1994)	82.6	0	13.2	3.3	0	0	0	0	0	0

(Table continued)

Subfamily, species & location	FISH	PESC	DECA	OBEC	CEPH	OTMO	ANNE	PEUR	BEUR	OTHE
Mexico, > 111 mm (Sanchez 1994)	53.7	0	29.1	10.7	0	0	0	0	0	0
Cuba (Sierra 1997)	0.5	4.8	76.1	14.4	0	0	4.2	0	0	0
Cuba 60-69 mm FL, (Sierra 1997)	3.9	23.7	66.2	0	0	0	6.2	0	0	0
Cuba, 70-79 mm (Sierra 1997)	0	21.6	12.6	0	0	0	40.8	0	0	25
Cuba, 80-89 mm (Sierra 1997)	0	0	100	0	0	0	0	0	0	0
Cuba, 90-99 mm (Sierra 1997)	0	0	100	0	0	0	0	0	0	0
Cuba, 100-109mm (Sierra 1997)	0	0	100	0	0	0	0	0	0	0
Netherlands Antilles, 70-180 mm, seagrass (Nagelkerker et al. 2000)	7	3	68	15	0	0	0	0	0	7
Netherlands Antilles, 120-210 mm, mangrove (Nagelkerker et al. 2000)	26	0	72	0	0	0	0	0	0	2
Netherlands Antilles, 90-220 mm, boulder (Nagelkerker et al. 2000)	33	0	68	0	0	0	0	0	0	0
Puerto Rico, < 70 mm, mangrove, summer 1988 (Rooker 1995)	0	0	44	53	0	0	0	0	0	3
Puerto Rico, < 70mm, mangrove, fall 1988 (Rooker 1995)	0	0	53	47	0	0	0	0	0	0
Puerto Rico, < 70mm, mangrove, winter 1989 (Rooker 1995)	0	0	39	56	0	0	0	0	0	5
Puerto Rico, < 70mm, mangrove, spring 1989 (Rooker 1995)	0	0	52	46	0	0	0	0	0	2
Puerto Rico, > 70mm, mangrove, summer 1988 (Rooker 1995)	74	0	18	0	0	0	0	0	0	8
Puerto Rico, > 70mm, mangrove, Puerto Rico, fall 88 (Rooker 1995)	79	0	6	9	0	0	0	0	0	6

(Table continued)

Subfamily, species & location	FISH	PESC	DECA	OBEC	CEPH	OTMO	ANNE	PEUR	BEUR	OTHE
Puerto Rico, > 70mm, mangrove, winter 1989 (Rooker 1995)	10	0	79	8	0	0	0	0	0	3
Puerto Rico, > 70mm, mangrove, spring 89 (Rooker 1995)	15	0	55	27	0	0	0	0	0	3
Puerto Rico > 70mm, coral reef, , summer 1988 (Rooker 1995)	50	0	44	6	0	0	0	0	0	0
Puerto Rico > 70mm, coral reef, fall 1988 (Rooker 1995)	37	0	59	5	0	0	0	0	0	0
Puerto Rico > 70mm, coral reef, winter 89 (Rooker 1995)	39	0	42	19	0	0	0	0	0	0
Puerto Rico > 70mm, coral reef, spring 89 (Rooker 1995)	77	0	13	2	0	0	0	0	0	8
<i>L. argentimaculatus</i> Embley estuary, N Australia 59-405 mm SL,	4.7	0	74.9	2.5	0	17.8	0	0	0	0.2
<i>L. bohar</i> East Africa Andaman Sea (Druzhinin 1970 & Allen 1985)	62	0	8	24	0	0	0	0	0	6
<i>L. campechanus</i> Gulf of Mexico, juvenile, spring (Bradley & Bryan 1976)	3	0	75	11.7	2	0	0	0	0	8.3
Gulf of Mexico, juvenile, summer (Bradley & Bryan 1976)	20	0	63	10	0	0	0	0	0	7
Gulf of Mexico, juvenile, fall 70-71(Bradley & Bryan 1976)	0	0	83	0	0	0	0	0	0	17
Gulf of Mexico, juvenile, fall 72(Bradley & Bryan 1976)	15.6	0	33.8	0	45	0	0	0	0	5.6

(Table continued)

Subfamily, species & location	FISH	PESC	DECA	OBEC	CEPH	OTMO	ANNE	PEUR	BEUR	OTHE
Gulf of Mexico, juvenile, winter (Bradley & Bryan 1976)	14.4	9.3	54.1	21.1	0	0	0	0	0	1.1
Gulf of Mexico, adult, spring (Bradley & Bryan 1976)	72	0	11	0	2	0	0	0	13	2
Gulf of Mexico, adult, summer (Bradley & Bryan 1976)	55	0	19	4	0	0	0	0	0	22
Gulf of Mexico, adult, fall (Bradley & Bryan 1976)	38	0	44	6	0	0	0	0	6	6
Gulf of Mexico, adult, winter (Bradley & Bryan 1976)	42	0	39	0	4	0	0	0	2	13
Gulf of Mexico, adult, avg (Bradley & Bryan 1976)	51.75	0	28.25	2.5	1.5	0	0	0	5.25	10.75
<i>L. colorado</i>										
Costa Rica (Rojas 1997)V	32.67	0	58.2	3.29	0	1.04	0	0	0	4.8
<i>L. cyanopterus</i>										
Bahamas (Druzhinin 1970 & Allen 1985)E	50	0	50	0	0	0	0	0	0	0
<i>L. gibbus</i>										
Tahiti (Allen 1985 & Randall & Brock, 60)E	30	0	30	10	10	0	0	0	0	20
<i>L. griseus</i>										
Mississippi (Franks & VanderKooy 2000)	44.45	17.52	37.31	0.48	0	0.12	0.12	0	0	0
Netherlands Antilles, 70-760 mm, seagrass, (Nagelkerker <i>et al.</i> 2000)	7	2	68	10	0	0	0	0	0	13
Cuba (Sierra 1997)W	45.4	0.1	52.3	2.2	0	0	0	0	0	0
Cuba, 60-79mmFL (Sierra 1997)	0	8.2	91.8	0	0	0	0	0	0	0
Cuba, 80-99mm (Sierra 1997)	24.8	6.1	69.1	0	0	0	0	0	0	0
Cuba, 100-119mm (Sierra 1997)	63.9	2.4	33.7	0	0	0	0	0	0	0

(Table continued)

Subfamily, species & location	FISH	PESC	DECA	OBEC	CEPH	OTMO	ANNE	PEUR	BEUR	OTHE
Cuba, 120-139mm (Sierra 1997)	53.6	1.3	44.9	0	0	0	0	0	0	0
Cuba, 140-159mm (Sierra 1997)	1.9	0	98.1	0	0	0	0	0	0	0
Cuba, 160-180mm (Sierra 1997)	0	0	100	0	0	0	0	0	0	0
<i>L. guttatus</i> Gulf of Nicoya, Costa Rica, 121-600 mm (Rojas 1997)	7.78	0	51.2	31.7	0	1	1.5	0	0	7.2
<i>L. johnii</i> Andaman Sea (Druzhinin 1970 & Allen 1985)	42.3	0	28.85	28.85	0	0	0	0	0	0
<i>L. kasmira</i> Tahiti (Randall & Brock, 60)	55.5	0	22.25	22.25	0	0	0	0	0	0
<i>L. malabaricus</i> Andaman Sea (Druzhinin 1970 & Allen 1985)	36.7	0	31.65	31.65	0	0	0	0	0	0
<i>L. monostigma</i> East Africa (Druzhinin 1970 & Allen 1985)	66	0	17	17	0	0	0	0	0	0
<i>L. peru</i> Mexico (Saucedo-Lozano et al. 1999)	18.88	44.17	3.1	30.37	0	0.01	0.03	0	0	3.41
<i>L. rivulatus</i> East Africa (Druzhinin 1970 & Allen 1985)E	40	0	10	10	10	0	5	0	0	15
<i>L. russelli</i> Australia 33-158 mm SL, (Salini et al. 1990)	15.3	0	73.4	9.5	0	2.1	0	0	0	0.1
<i>L. synagris</i> Mississippi, 63.7-86.5 mmSL, (Franks & VanderKooy 2000)	17.16	0.81	77.93	4.11	0	0	0	0	0	0
Cuba (Rodriguez, 62 In: Druzhinin 1970)	31.9	0	0	26.6	0	1.4	0	0	0	40.1

(Table continued)

Subfamily, species & location	FISH	PESC	DECA	OBEC	CEPH	OTMO	ANNE	PEUR	BEUR	OTHE
Cuba, 33-132 mm (Sierra 1997)	39	6.4	29.4	8.4	0	0.7	10.2	0	0	5.9
<i>L. vaigiensis</i>										
Tahiti (Randall & Brock, 1960)	42.4	0	43.98	10.32	0	0	0	0	0	0
<i>L. vitta</i>										
Japan, seagrass, Oct 1975 day (Mori 1984)	47.26	0.131	50.88	1.727	0	0	0	0	0	0
Japan, seagrass, Sep 1977a night (Mori 1984)	48.98	2.317	48.65	0.051	0	0	0	0	0	0
Japan, seagrass, Sep 1977b night (Mori 1984)	71.74	0	28.26	0	0	0	0	0	0	0
Japan, seagrass, Oct 1977 night (Mori 1984)	56.18	0.09	43.69	0	0	0	0.037	0	0	0
Japan, avg (Mori 1984)	56.04	0.635	42.87	0.445	0	0	0.009	0	0	0
<i>Ocyurus chrysurus</i>										
Virgin I. & P. Rico	84.5	0	1.2	14.2	0	0	0	0	0	0.1
Florida	84.5	0	0	14.2	0	0	0	0	0	0
Netherlands Antilles, 60-130 mm, seagrass (Nagelkerker <i>et al.</i> 2000)	7	6	23	53	0	1	1	0	0	9
Netherlands Antilles, mangrove (Nagelkerker <i>et al.</i> 2000)	33	3	0	65	0	0	0	0	0	0
Cuba, 30-130 mm (Sierra 1997)	54.7	16.8	23.1	4.3	0	0	0.6	0	0	0.5
<i>Rhomboplites aurorubens</i>										
1-50 mm SL, (Sedberry 1993)	17.1	16.6	31.1	29	0	0.2	2.1	0	0	3.9
51-100 mm SL, (Sedberry & Cuellar 1993)	27.8	4.5	42	19.1	1	0.1	2.8	0	0	2.7
101-150 mm SL, (Sedberry & Cuellar 1993)	32.4	5	19	13.1	24.2	1	2.8	0	0	2.6
>150 mm SL, (Sedberry & Cuellar 1993)	32.7	0.1	7.9	4.1	51.4	0.1	2.2	0	0	1.5

(Table continued)

Subfamily, species & location	FISH	PESC	DECA	OBEC	CEPH	OTMO	ANNE	PEUR	BEUR	OTHE
Carolinas, spring (Grimes 1979)	0.7	22.4	15.9	6.5	38.3	8.1	1.6	0	0	6.5
Carolinas summer (Grimes 1979)	7.6	13.8	6.1	3.9	34.3	23.7	0	0	0	10.6
Carolinas fall (Grimes 1979)	20.5	21.5	6.4	10.8	36.9	1.3	0.3	0	0	2.3
Carolinas winter (Grimes 1979)	0	7.7	68.1	9.4	0	0	0	0	0	14.8
Carolinas offshore(Grimes 1979)	0.7	33.9	10.8	12.1	20.9	11.1	1.2	0	0	9.3
Carolinas inshore (Grimes 1979)	2.6	11.3	25.5	4	50.3	1.1	2.1	0	0	3.1
Carolinas avg (Grimes 1979)	5.35	18.43	22.13	7.78	30.12	7.55	0.87	0	0	7.76
Etelinae										
<i>Aphareus furcatus</i> <i>Aprion virescens</i> Hawaii (Haight <i>et al.</i> 1993)	50	0	25	25	0	0	0	0	0	0
(Druzhinin 1970 & Allen 1985)	96	0.4	0.12	0	0.7	0.01	0	2.7	0	0
	49	17	6	6	7	7	0	0	0	8
<i>Etelis carbunculus</i> Hawaii (Haight <i>et al.</i> 1993)	98.4	1	0.23	0	0.3	0.02	0	0.02	0	0
<i>E. coruscans</i> Hawaii (Haight <i>et al.</i> 1993)	80.6	1	4.46	0	2.9	0	0	11.1	0	0
<i>Pristipomoides auricilla</i> Mariana Archipelago (Seki & Callahan 1988)	11.8	0.7	1.2	3.6	7.4	39	5.4	25	0	5.9
<i>P. filamentosus</i> Hawaii (Haight <i>et al.</i> 1993)	7.24	31.1	0.1	0	0.5	13	0	47.3	0	0.6
Hawaii, day (Haight <i>et al.</i> 1993)	10.1	42.6	0.1	0	0.4	18.1	0	28.2	0	0.5

(Table continued)

Subfamily, species & location	FISH	PESC	DECA	OBEC	CEPH	OTMO	ANNE	PEUR	BEUR	OTHE
Hawaii, night (Haight et al. 1993)	1.7	6.6	0.1	0	0.4	5.9	0	84.8	0	0.7
Hawaii, summer (Haight et al. 1993)	13.8	57.2	0.01	0	0.8	10.2	0	15	0	2.9
Hawaii, winter (Haight et al. 1993)	9.43	29.9	0.02	0	0.3	22.2	0	37.7	0	0.4
Hawaii, spring (Haight et al. 1993)	1.61	9.3	0.7	0	0.4	4.8	0	83.3	0	0.03
Hawaii (Parrish 1989)	5	90	0	0	2	0	0	3	0	0
<i>P. sieboldii</i>										
Hawaii (Haight et al. 1993)	2.1	47.2	1.9	0	1.5	28.9	0.1	16.4	0	1.8
<i>P. zonatus</i>										
Hawaii (Haight et al. 1993)	55.2	0	6.5	0	0	0	0	38.4	0	0
Mariana Archipelago (Seki & Callahan 1988)	41	0	38.4	0.3	0.3	0.3	0.3	16.3	0	3.1
Haemulidae										
<i>Haemulon flavolineatum</i>										
Netherlands Antilles, seagrass (Nagelkerker et al. 2000)	1	4	3	58	0	2	1	0	0	32
Netherlands Antilles, mangrove (Nagelkerker et al. 2000)	0	43	0	15	0	0	18	0	0	24
<i>H. sciurus</i>										
Netherlands Antilles, seagrass (Nagelkerker et al. 2000)	0	11	1	55	0	5	3	0	0	25
Netherlands Antilles, mangrove (Nagelkerker et al. 2000)	0	0	0	43	0	0	0	0	0	57

FISH= Fish, PESC= Pelagic Small Crustaceans, DECA= Decapoda, OBEC= Other Benthic Crustaceans, CEPH= Cephalopods, OTMO= Other Mollusks, ANNE= Annelida, PEUR= Pelagic Urochordates, BEUR= Benthic Urochordates, OTHE= other.

Table 4.2 Mean values of the diet categories for species of the subfamilies Lutjaninae and Etelinae.

Species	FISH	PESC	DECA	OBEC	CEPH	OTMO	ANNE	PEUR	BEUR	OTHE
Lutjaninae										
<i>L. analis</i>	23.6	16.55	54.26	2.38	0.44	0.42	0.05	0	0	2.3
<i>L. apodus</i>	24.41	1.97	52.84	15.24	0	0	1.9	0	0	3.01
<i>L. argentimaculatus</i>	4.7	0	74.9	2.5	0	17.8	0	0	0	0.2
<i>L. bohar</i>	62	0	8	24	0	0	0	0	0	6
<i>L. campechanus</i>	31.18	0.93	45.02	5.53	5.45	0	0	0	2.63	9.28
<i>L. colorado</i>	32.67	0	58.2	3.29	0	1.04	0	0	0	4.8
<i>L. cyanopterus</i>	50	0	50	0	0	0	0	0	0	0
<i>L. gibbus</i>	30	0	30	10	10	0	0	0	0	20
<i>L. griseus</i>	26.78	4.18	66.13	1.41	0	0.01	0.01	0	0	1.44
<i>L. guttatus</i>	7.78	0	51.2	31.7	0	1	1.5	0	0	7.2
<i>L. johnii</i>	42.3	0	28.85	28.85	0	0	0	0	0	0
<i>L. kasmira</i>	55.5	0	22.25	22.25	0	0	0	0	0	0
<i>L. malabaricus</i>	36.7	0	31.65	31.65	0	0	0	0	0	0
<i>L. monostigma</i>	66	0	17	17	0	0	0	0	0	0
<i>L. peru</i>	18.88	44.17	3.1	30.37	0	0.01	0.03	0	0	3.41
<i>L. rivulatus</i>	40	0	10	10	10	0	5	0	0	15
<i>L. russelli</i>	15.3	0	73.4	9.5	0	2.1	0	0	0	0.1
<i>L. synagris</i>	29.35	2.4	35.78	13.04	0	0.7	3.4	0	0	15.33
<i>L. vaigiensis</i>	42.4	0	43.98	10.32	0	0	0	0	0	0
<i>L. vitta</i>	56.04	0.63	42.87	0.44	0	0	0.01	0	0	0
<i>Ocyurus chrysurus</i>	52.74	5.16	9.46	30.14	0	0.2	0.32	0	0	1.92

(Table continued)

Species	FISH	PESC	DECA	OBEC	CEPH	OTMO	ANNE	PEUR	BEUR	OTHE
<i>R. aurorubens</i>	13.4	14.11	23.18	10.89	26.13	4.93	1.45	0	0	5.92
Etelinae										
<i>Aphareus furcatus</i>	50	0	25	25	0	0	0	0	0	0
<i>Aprion virescens</i>	64.67	11.47	6.04	2	7.23	2.34	0	0.9	0	2.67
<i>Etelis carbunculus</i>	98.4	1	0.23	0	0.3	0.02	0	0.02	0	0
<i>E. coruscans</i>	80.6	1	4.46	0	2.9	0	0	11.1	0	0
<i>Pristipomoides auricilla</i>	11.8	0.7	1.2	3.6	7.4	39	5.4	25	0	5.9
<i>P. filamentosus</i>	6.98	38.1	0.15	0	0.69	10.6	0	42.76	0	0.73
<i>P. sieboldii</i>	2.1	47.2	1.9	0	1.5	28.9	0.1	16.4	0	1.8
<i>P. zonatus</i>	48.1	0	22.45	0.15	0.15	0.15	0.15	27.35	0	1.55
Lutjaninae										
Mean	29.00	5.45	44.16	11.04	3.86	0.88	0.91	0	0.276	4.1
Std. Dev.	24.77	14.34	28.65	14.8	11.28	3.37	4.38	0	1.56	6.5
Etelinae (N = 17)										
Mean	34.23	20.64	5.69	2.05	2.28	8.79	0.34	24.07	0	1.40
Std. Dev.	33.64	25.9	10.59	6.13	3.77	11.84	1.3	27.07	0	2.34

FISH= Fish, PESC= Pelagic Small Crustaceans, DECA= Decapoda, OBEC= Other Benthic Crustaceans, CEPH= Cephalopods, OTMO= Other Mollusks, ANNE= Annelida, PEUR= Pelagic Urochordates, BEUR= Benthic Urochordates, OTHE= Other.

Table 4.3 Correlation analysis among prey items found in diets of snappers of the subfamilies Lutjaninae and Etelinae.

	FISH	PESC	DECA	OBEC	CEPH	OTMO	ANNE	PEUR	PEUR	OTHE
FISH	1									
PESC	-0.29	1								
DECA	-0.44	-0.38	1							
OBEC	-0.17	-0.15	-0.10	1						
CEPH	-0.14	0.06	-0.26	-0.08	1					
OTMO	-0.25	0.22	-0.28	-0.10	0.12	1				
ANNE	-0.14	0.08	-0.10	-0.06	0.03	0.01	1			
PEUR	-0.17	0.16	-0.31	-0.18	-0.07	0.33	-0.03	1		
PEUR	0.15	-0.07	-0.14	-0.10	0.14	-0.06	-0.03	-0.04	1	
OTHE	-0.09	-0.06	-0.14	0.06	0.08	0.00	0.34	-0.12	-0.02	1

FISH= Fish, PESC= Pelagic Small Crustaceans, DECA= Decapoda, OBEC= Other Benthic Crustaceans, CEPH= Cephalopods, OTMO= Other Mollusks, ANNE= Annelida, PEUR= Pelagic Urochordates, BEUR= Benthic Urochordates, OTHE= other.

Table 4.4 Loadings, eigenvalues and variance explained by factor from the Principal Component Analysis of the categories in the diets of snappers of the subfamilies Lutjaninae and Etelinae.

Categories	Factor 1	Factor 2	Factor 3	Factor 4
Other mollusks	0.75203	-0.10039	0.09574	-0.07302
Pelagic urochoradtes	0.68333	0.00973	-0.21440	-0.14506
Pelagic small crust.	0.66233	-0.05578	0.10263	0.05373
Decapods	-0.56984	-0.74967	-0.22751	-0.22710
Fish	-0.26762	0.86281	-0.19388	-0.15141
Other	-0.11852	0.06271	0.79643	0.06038
Annelids	0.00368	-0.10309	0.73166	-0.12858
Other benthic crust.	-0.20882	0.04341	0.01905	0.88984
Cephalopods	0.26510	0.01283	0.39227	0.05102
Benthic urochordates	-0.15957	0.38851	0.07946	-0.46150
Eigenvalue	2.07238	1.51225	1.44348	1.09657
Proportion of variation	0.2072	0.1512	0.1443	0.1097
Cumulative variance	0.2072	0.3585	0.5028	0.6125

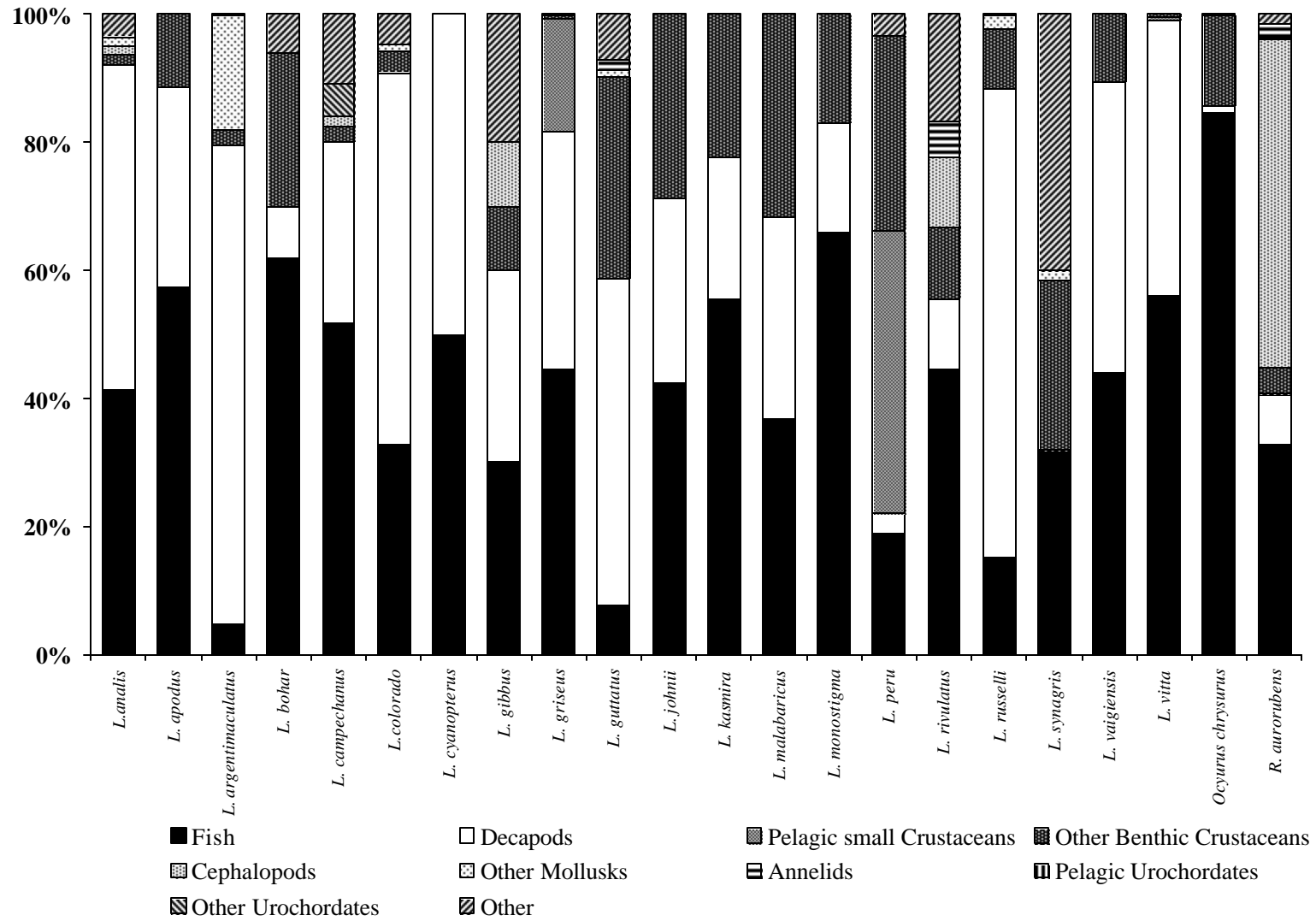


Figure 4.1 Feeding habits in 22 species of the subfamily Lutjanidae

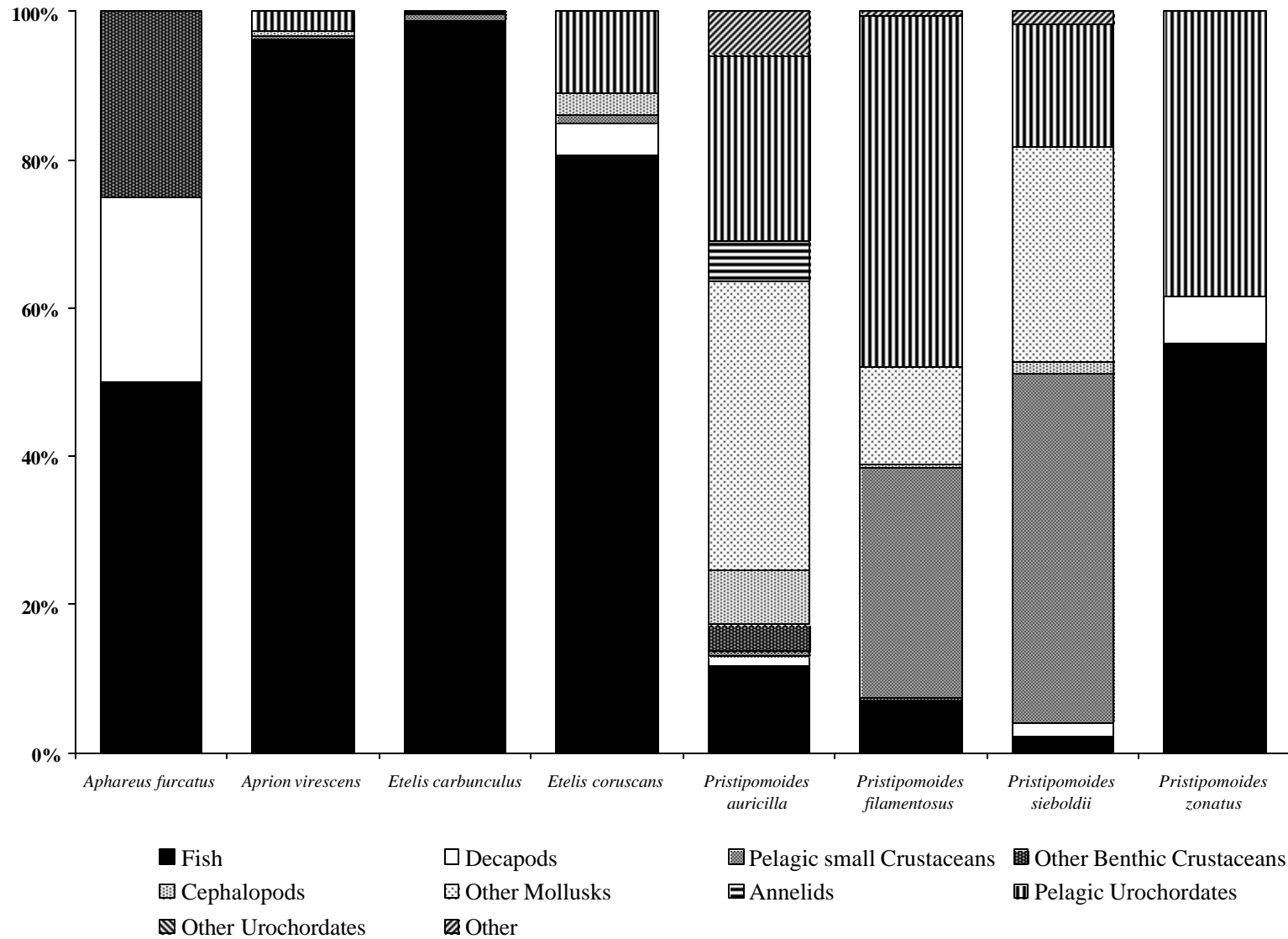


Figure 4.2 Feeding habits in eight species of the subfamily Etelinae.

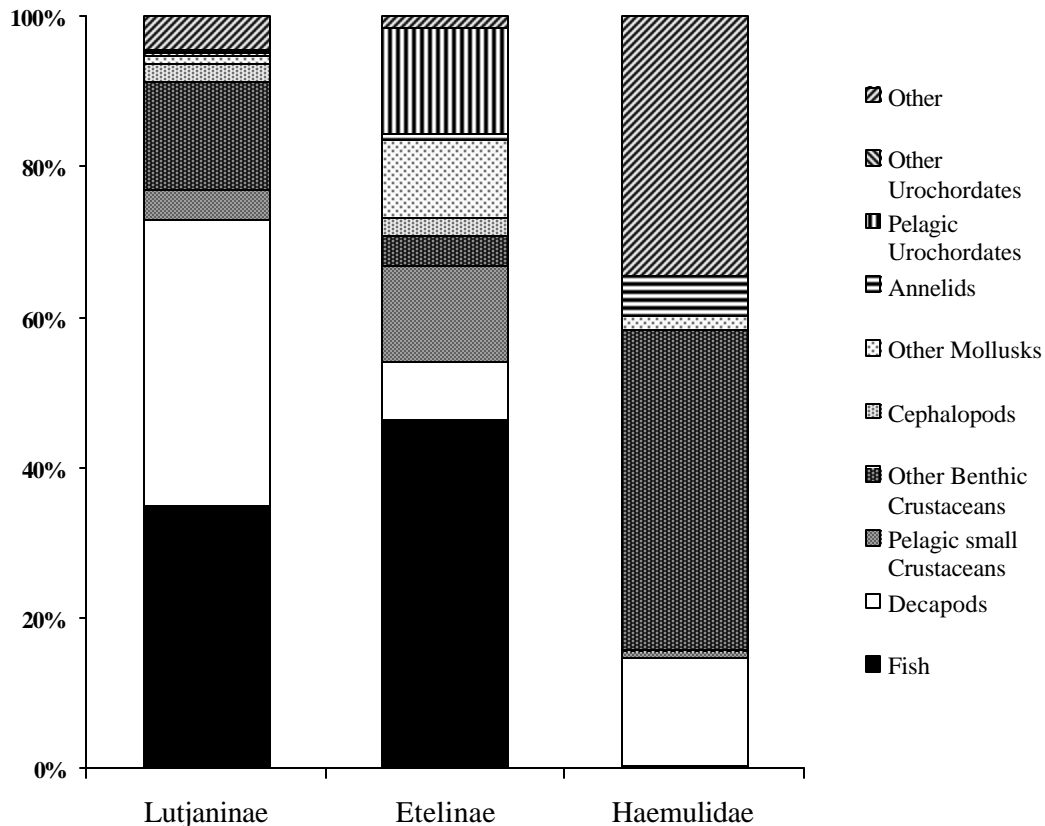


Figure 4.3 Feeding habits in species of the subfamilies Lutjaninae and Etelinae, and the family Haemulidae.

data contribute to an ample description of the spectrum of food items and variability among snappers. Most species of inshore dwelling snappers (subfamily Lutjaninae) rely heavily on fish and crustaceans (decapods specially) for their diets, while deep water species apparently select either an almost exclusively piscivorous diet (genera *Etelinae* and *Aprion*) or a diet based mostly on pelagic invertebrates such as mollusks and urochordates (genus *Pristipomoides*).

Nevertheless, a full appreciation of the feeding ecology of snappers requires additional information on species in the subfamilies Paradicichthyinae and Apsilinae. Most of the results found here agree with what it is known until now about the feeding habits for species of these

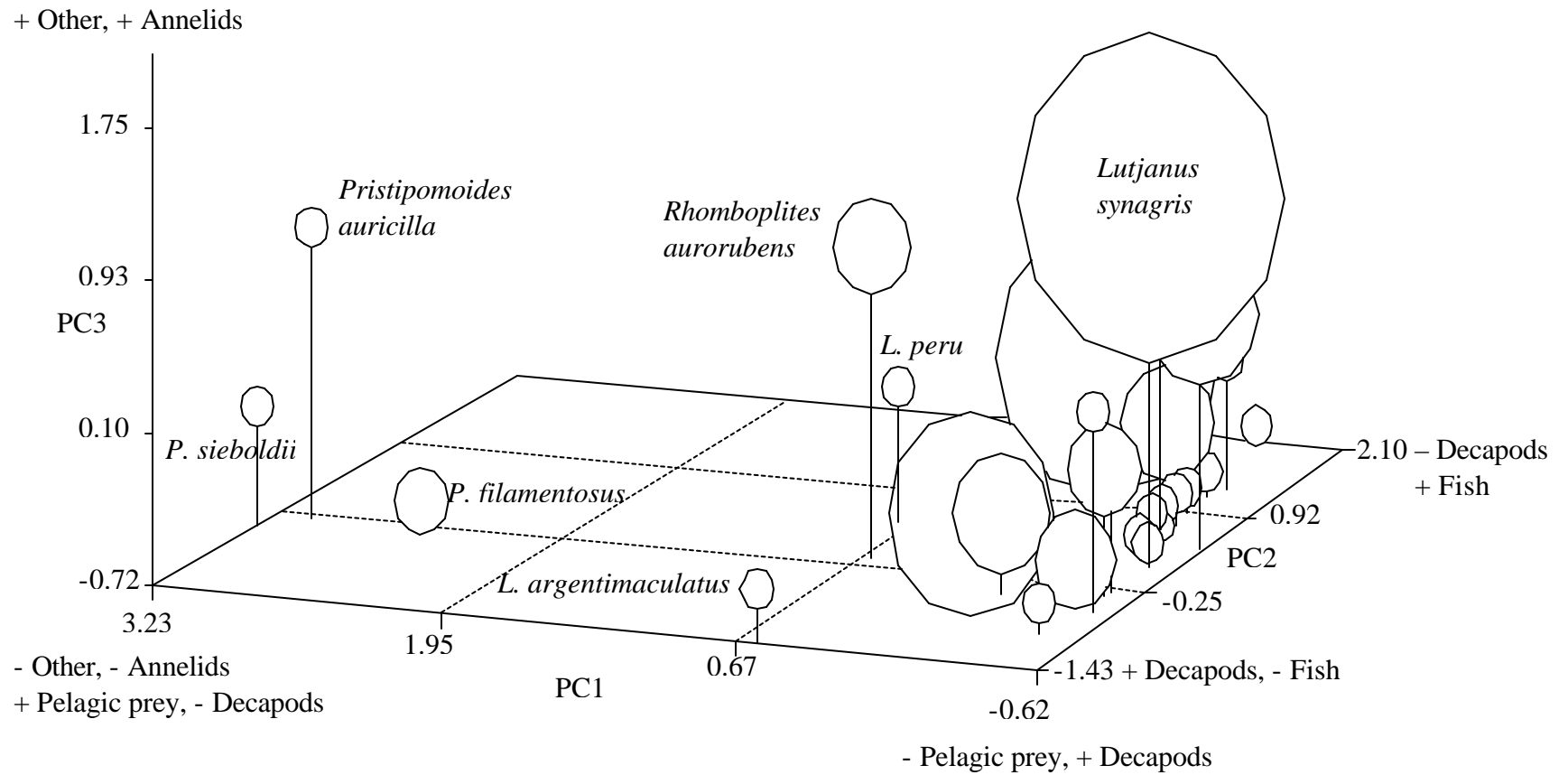


Figure 4.4 Variation in feeding habits among snappers. Species in 3-dimensional prey space

subfamilies. For species in the subfamily Lutjaninae inhabiting intermediate depths, the main component by volume of the diet are small pelagic fishes, such as clupeids and engraulids, and also anguilliforms, followed by crabs as the second largest component and shrimps the third (Parrish 1987). In the present study, crabs and shrimps were combined in a single category (decapods) and for this reason they ranked as the main component of the diet; in addition, fish prey accounted for almost the same percentage as decapods (34.62 % fish vs. 37.82 % decapods), so if the decapod category is subdivided, it is almost certain that fish prey would be the main item followed by different decapods.

Parrish (1987) notes that small pelagic zooplankton is a significant component in the diets of adult vermilion snapper (*Rhomboplites aurorubens*) and yellow-fin snapper (*Ocyurus chrysurus*); however, in a study of two other species, Pacific red snapper (*L. peru*) and mutton snapper (*L. analis*) had higher values of small pelagic crustaceans in their diets than vermilion and yellow-fin snappers (Table 4.2). Although some of the populations analyzed included juveniles, the mean value was considerably higher, indicating that this category plays an important role in adult populations as well. The Pacific red snapper has a more fusiform body type and deeper forked caudal fin than most snappers, characteristics of fish that feed in the water column rather than the bottom (Sedberry and Cuellar 1993). Additionally, Grimes (1979), and Sedberry and Cuellar (1993) found that the feeding habits of vermilion snapper switch during ontogeny from a diet of small pelagic crustaceans as juveniles to an adult diet constituted primarily of small pelagic fishes and cephalopods, especially squid. In the present study cephalopods constituted over 26 % of the diet of vermilion snapper, by far the highest of any other species in either subfamily. My results for yellow-fin snapper also differed from Parrish's

(1987), since only slightly over 5 % of the diet was constituted by zooplankton and the main categories were benthic crustaceans (decapods and other ~ 40 %) and fish (~ 53 %) (Table 4.2).

For the deepwater species of the subfamily Etelinae, pelagic fish is also the main prey category and resembles diets in shallow water species (Parrish 1987). Next in importance are pelagic items, mainly pelagic urochordates and gastropods. Parrish (1987) indicates that the occurrence of these organisms is frequent and that the volume present in stomachs is usually considerable. The results of my study agree, and I found that the category of prey fish was the most important accounting for over 45 % of the volume, followed by the categories of pelagic urochordates and other mollusks (composed primarily of pelagic forms), which constituted almost 24 % of their diets and placed these items as the second and fourth most important categories, respectively. Other categories of small pelagic crustaceans accounted for an additional 12 % of the volume.

In a study with deep-water species of the genus *Pristipomoides*, Seki and Callahan (1988) found little overlap between the diets of *P. auricilla* and *P. zonatus*, except for the presence once again, of pelagic urochordates. The nutritional value of the urochordates was questioned by Parrish (1987); however, Seki and Callahan (1988) indicate that they contain filtered concentrations of phytoplankton and microzooplankton, which elevate their nutritional value.

CHAPTER 5

AN ANALYSIS OF LIFE-HISTORY, DISTRIBUTION AND PREY AMONG SNAPPERS

Introduction

The life-history, distributional and trophic variables analyzed in previous chapters represent separate components of the ecology of snappers; however, these components also interact with each other. For example, as fishes grow larger, larger prey with relatively higher energy content become accessible, which in theory should allow them to grow faster. However, with growth fishes also move into deeper waters, lower in temperature that decrease the metabolic rate and consequently also the food intake, which should have a negative impact on the growth rate. Longhurst and Pauly (1987) indicate in this case, that the decrease in food intake is actually compensated by richer amounts of dissolved oxygen present in deeper waters that reduce the cost of maintenance metabolism permitting the allocation of more energy into growth.

In this chapter a final PCA to compare the effects of all variables analyzed in previous chapters was performed after combining most of the life-history, physical distribution and food habits databases into a single database.

Methodology

Redundant variables from the life-history database were removed, keeping asymptotic length (L_{inf}), longevity (t_{max}), maturity age (t_m), growth rate (K), and mortality rate (M). Latitudinal range (Range) and maximum depth (maxD) were included as distribution variables. The ten variables from the feeding habits database, representing different prey categories in the diets of snappers, were included: teleost fish (FISH), small pelagic crustaceans (PESC), decapods (DECA), other benthic crustaceans

(OBEC), cephalopods (CEPH), other mollusks (OTMO), annelids (ANNE), pelagic urochordates (PEUR), benthic urochordates (BEUR), and other items (OTHE).

Only species occurring in all previous three databases were included in this database. The populations and species from the life-history database were placed first, and then the information on latitudinal range and maximum depth distribution were matched to each species from the first database and was assumed to be the same for all populations within a species. Finally, the items found in the diets of snappers were matched as well to each species. If the number of populations with information on life-history and distribution variables was more than the number of populations with information on feeding habits, then the feeding items were assumed to be the same and were repeated for the remaining populations. If the number of population with life-history and distribution variables was less than the number of populations with information on feeding habits, the mean of the populations with feeding habits was estimated and assigned to the populations of that species with other variables.

Principal Component Analysis

A Principal Component Analysis (PCA) of 18 life-history, physical distribution and prey category variables was performed to explore variance patterns among species of snappers. The PCA compared 27 species of the sub families Lutjaninae and Etelinae. The PCA was conducted using the Factor Procedure in SAS, and the first four factors were rotated using the Varimax option to facilitate the interpretation of each separate component (SAS Institute 1996). The PCA was configured to resolve 18 inter-correlated and non-correlated variables into four orthogonal factors to facilitate interpretation and comparisons among species and subfamilies. Variables in 259 snapper stocks without

missing data were used to estimate variable loadings and generate principal component scores for each species. The mean value of the variables for each species was obtained from the populations through the Means Procedure in SAS and the species were plotted as centroids in 3-dimensional ecological space (SAS Institute 1996). The interpretation was based on axes with eigenvalues more than or equal to 1.0 and rotated factor loadings more than or equal 0.50 (Grossman 1991).

Results

Seven eigenvalues were > 1.0 and the first four explained almost 48 % of the variability in life history, distribution and feeding habits. The first component (PC1) loaded heavily (> 0.5) and positively for growth rate, age at zero length, and mortality rate, and also loaded heavily but negatively for age at maturity and longevity. The second component (PC2) loaded heavily and positively for most of the pelagic components of the diet, other mollusks (mainly pelagic), pelagic urochordates and small pelagic crustaceans; it also loaded heavily but negatively for maximum depth distribution and the fish prey category. The third component loaded heavily and positively for mortality rate and the annelids found in the diets, and loaded negatively for asymptotic length. Finally, the fourth component loaded heavily and positively for latitudinal range and heavily but negatively for benthic urochordates (Table 5.1).

There is a tremendous amount of ecological variation in the family Lutjanidae and only about 40 % is characterized in the first three Principal Components (Table 5.1, Figure 5.1). Four groups of species were distinguished in the 3-dimensional factor space (Figure 5.1). The first group had four medium sized species from both subfamilies, with particularly high growth and mortality rates, short lived, inhabiting relatively shallow

waters and feeding more on fish and less pelagic invertebrates. The second group had most of the species and was located at the center; it had species of diverse sizes, with average life span and growth and mortality rates; the species are occur in shallow waters and feed mainly on fish; most of them are from the subfamily Lutjaninae (*Lutjanus apodus*, *L. johnii*, *L. monostigma*, *L. peru*, *Ocyurus chrysurus*). The third group has only three species, all of the genus *Pristipomoides*, with the same characteristics for life span and growth and mortality rates than the second group, but inhabit deep waters and feed mainly on pelagic invertebrates. The last group has seven medium and large species from the subfamily Lutjaninae with low growth and mortality rates, which inhabit shallow waters and feed mainly on fish and benthic items (e.g., *Lutjanus analis*, *L. argentimaculatus*, *L. campechanus*, *L. cyanopterus*, *L. griseus*).

Discussion

The interpretation of this PCA was more complex than previous PCA's because it involved almost twice the number of input variables and some are correlated while others are completely uncorrelated. However, the results indicate that larger and long-lived species have lower growth and mortality rates, even considering that mortality rate loaded heavily and positively in two components (PC1 and PC3). Higher growth and mortality rates were paired to apparently short-lived species in PC1 and to smaller species in PC3; results from Chapter 2 indicated that small and short-lived species are the ones with higher growth and mortality rates, and support even further the findings of previous chapters. The results regarding feeding habits are also coherent, the second component (PC2) grouped most of the pelagic prey items (pelagic small crustaceans,

pelagic mollusks, and pelagic urochordates), which occur in deep water, and loaded negatively

Table 5.1 Loadings, eigenvalues, and variance explained by factor from the Principal Component Analysis of all ecological variables for snappers.

	Factor 1	Factor 2	Factor 3	Factor 4
Growth rate	0.80583	-0.00551	0.15883	-0.04157
Age at length zero	0.56253	-0.00464	-0.26436	-0.37069
Natural mortality rate	0.51427	-0.04823	0.58179	0.15356
Age at maturity	-0.71376	-0.03133	-0.16572	-0.06003
Longevity	-0.62847	-0.09706	-0.04600	-0.46545
Other mollusks	0.01185	0.74867	-0.02246	0.09654
Pelagic urochordates	0.09127	0.70410	-0.19091	0.04812
Pelagic small crust.	0.13183	0.58119	-0.34597	-0.00325
Maximum depth	-0.02773	-0.62441	-0.41777	0.00720
Fish	0.13869	-0.52829	-0.25516	0.10505
Annelids	0.04430	0.16510	0.52373	0.10817
Asymptotic length	-0.41277	0.05845	-0.66326	-0.27189
Latitudinal range	0.12316	-0.04086	0.03445	0.85871
Benthic urochordates	-0.09406	-0.08605	-0.00629	-0.64798
Decapods	-0.32108	-0.23966	0.44873	-0.16574
Cephalopods	0.11759	0.11741	0.01547	-0.22109
Other	0.05975	0.00071	0.37507	-0.13041
Other benthic crust.	0.00511	-0.43743	-0.11890	0.28710
Eigenvalue	3.11279	2.35453	1.61703	1.54688
Proportion of variation	0.1729	0.1308	0.0898	0.0859
Cumulative variance	0.1729	0.3037	0.3936	0.4795

for maximum depth. The species in this group are in effect of the subfamily Etelinae and agree with other authors' characterizations (Allen 1985, Parrish 1987). Results from Chapter 4 agree with the results of this global PCA because in both analyses there was a clear grouping of similar prey items particularly benthic and pelagic categories. An important implication of these findings is a better understanding of where in the water column particular species are feeding and what their main sources of energy are.

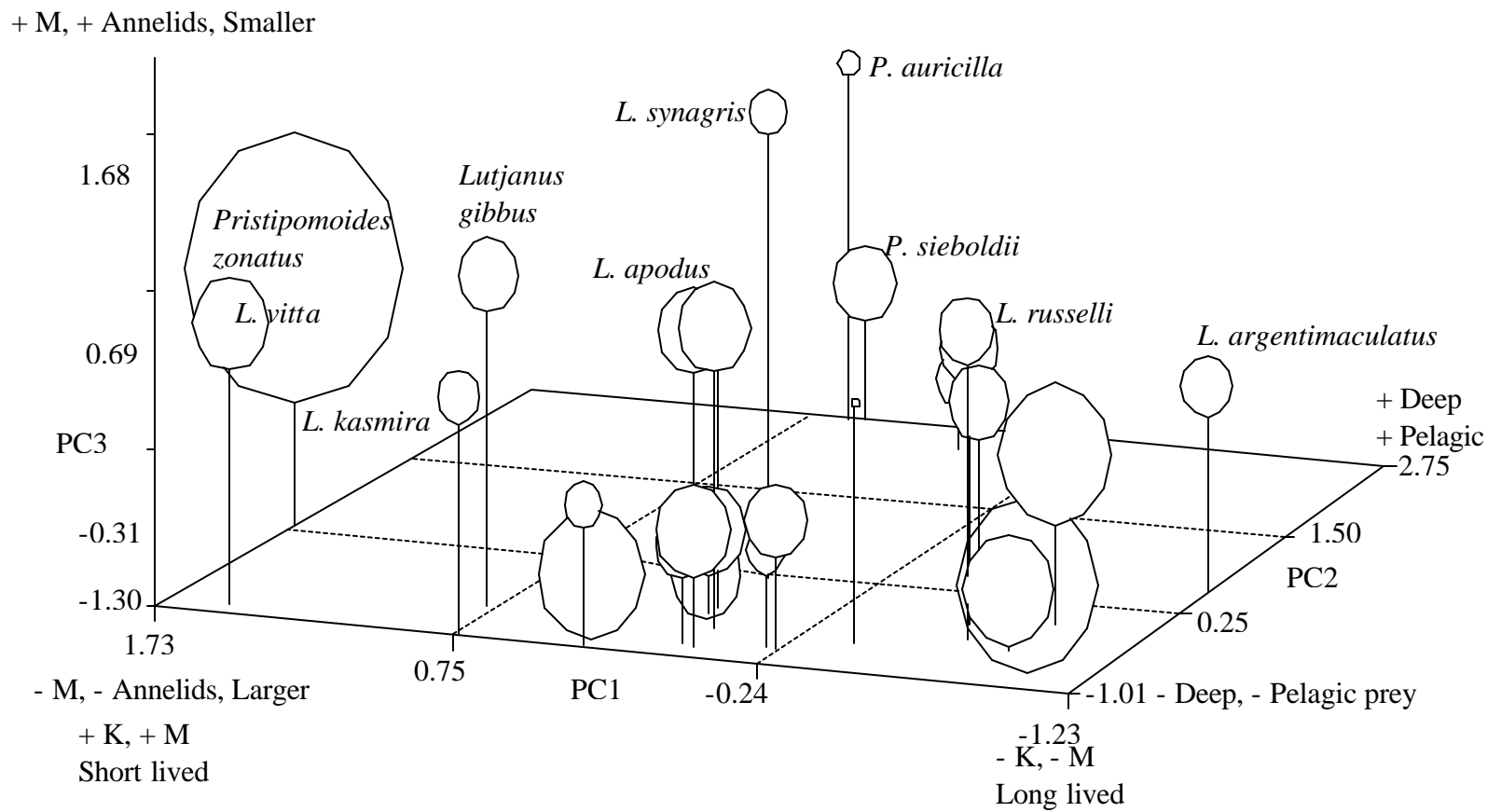


Figure 5.1 Variation of ecological factors among snappers. Species in 3-dimensional ecological space

The centroids of several species from both subfamilies overlapped to some degree, indicating a high degree of ecological similarity between them; however, overlap is not complete indicating a continuous display of strategies that evolved by natural selection to adapt to different environments. Principal Component Analyses were effective and useful in synthesizing large amounts of data that otherwise would be hard to synthesize and interpret. All PCA's returned satisfactory results and this type of analysis is a reliable tool in the understanding of ecological variables.

Removing redundant life-history variables was an important step to better detect patterns of variation in the general ecology of snappers. For example, Reproductive Life Span (RLS) is a variable derived by subtracting age at maturity from longevity. Without the reproductive life span variable in the input data set, PC1 loaded longevity and age at maturity and inversely correlated them with growth rate, natural mortality rate and age at zero length (Table 5.1). These variables were originally distributed over three orthogonal factors in a previous PCA (Table 2.3) indicating a high degree of independence among them; however, the way they were rearranged here does not contradict earlier assumptions but rather synthesizes a larger amount of information. Natural mortality and growth rates are correlated (Ralston 1987) and they are inversely correlated to longevity and age at maturity (Froese and Pauly 2000). The location of the species in 3-dimensional ecological space (Figure 5.1) regarding the life-history axis (PC1) indicated a broad range of variation among snappers, but did not show particular differences between the subfamilies Lutjaninae and Etelinae. PC2 loaded for all three pelagic components of the diets and inversely correlated them with depth and the fish prey category. Depth values were entered in negative numbers so higher values are for less

deep waters and vice versa, thus resulting in a rather positive correlation with the pelagic components of the diet. Location of the species in 3-dimensional ecological space showed that three of the four species of the genus *Pristipomoides* (subfamily Etelinae) had the most distinctive feeding habits and depth distribution, with a diet based mainly on pelagic items and inhabiting deeper waters (Parrish 1987). Finally, the loadings for PC3 in this PCA also supported previous findings regarding the low correlation of size variables with most other life-history variables. In this case, asymptotic length indicates no correlation with growth rate or any of the age variables (age at length zero, age at maturity or longevity); however, natural mortality was inversely correlated. Pauly (1979) noted the inverse relationship between asymptotic length and natural mortality because in general, larger species have fewer potential predators than smaller species. Natural mortality was correlated with variables in PC1 and PC2 further reinforcing the low correlation between asymptotic length and other life-history variables. The location of the species in 3-dimensional ecological space showed also a broad range of variation in this factor among species of snappers that is clearly driven by asymptotic length and there were no clear groups of species or differences among subfamilies. This final principal component analysis (Figure 5.1 and Table 5.1) summarizes a wealth of ecological information on snappers that should be useful to fishery managers who need to make initial management decisions about species or populations that have not been well studied. Somewhat incomplete information on distribution, diet, and life-history variables should help managers identify better studied species of interest in a manner that suggests an initial management approach.

Other implications for the management of snapper fisheries

For years it has been recognized that tropical fisheries often require different management measures than fisheries in temperate zones (Hongskul 1979). Fisheries in temperate zones consist of relatively few exploited populations that have a long history of fisheries research that provides information to experiment with multi-species models. Tropical fisheries, in contrast, have numerous populations with inadequate information to create reliable models to predict the impacts associated with various exploitation schemes (Hongskul 1979).

The life-history variables reviewed in this study have direct applications for the scientific management of the snapper fisheries. For example, the asymptotic length or the highly correlated length at maturity is necessary to determine the maximum possible yield (expressed as optimum harvest length) of a particular species. Growth rate data are essential to determine whether a species is exploitable or not, to describe the population age structure, or to predict growth responses to environmental changes. Good estimations of growth rate rely on adequate age estimates (Brothers 1979). Unfortunately half of the species of snappers lack any kind of growth or age estimate and many of the species that do have age estimates have not used sectioned otolith readings and have not been validated. Mortality rate is another important variable and is basic for fishery analysis using population dynamics models. Smaller species of snappers have considerably higher natural mortality rates and several populations are either unexploited (Newman et al. 1996a, b) or are utilized by local artisanal fishermen usually making low impact on the mortality attributed to fishing activities (F).

My findings indicate that current databases to support policies for the management of many snapper fisheries are highly inadequate. In the U.S. the minimum legal size for red snapper is 16 inches (406 mm TL) when actually the mean length at maturity estimated here is 19.5 inches (494 mm TL) (Table 2.4) and the optimum length to achieve a “maximum possible exploitation” of this species is 24 inches (615 mm TL). This means that many of the individuals caught, especially by sport fishermen, have not been able to reach maturity and consequently have not contributed to the reproductive effort of the population.

The synthesis and diffusion of scientific information to resource managers and the general public plays a vital role in the adequate management of tropical and subtropical fisheries in areas such as the Gulf of Mexico. The number of sport fishermen in the U.S. has increased dramatically over the last few decades and this sector contributes considerably to the total fishing effort of species such as snappers. Making reasonable recommendations about optimum sizes and fishing grounds for individual species based on strong evidence should have a positive feedback, considering that the sport fishing boats normally used offshore are now equipped with relatively sophisticated navigational equipment such as GPS capable of avoiding protected areas.

Shrimp trawlers continue as a major problem for red snapper and many other species of snappers since they constantly target the same grounds where the juveniles are located, and continue to take a toll in the number of individuals that reach maturity and are able to reproduce. Thus the creation of marine protected areas is a promising approach to achieve the well being of several reef species. The adequate placement of these areas depends almost completely in understanding the life cycle and reproductive

biology of the target species. For snappers, vertical distribution during ontogeny and the spawning migrations of several medium and large species are important considerations in deciding where to place a protected area. The use of information on spawning site fidelity and timing by commercial fishermen has proven to be disastrous for many populations of snappers (Claro 1994) because it makes aggregations highly vulnerable to over-harvest; however, this high predictability could also work to locate and enforce closures of important fishing aggregation sites during critical points in the life cycle.

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APPENDIX: Length conversion formulas. Unless otherwise noted all were obtained from Froese and Pauly (2000).

Species	FL to TL	SL to TL
Lutjaninae		
<i>Lutjanus adetii</i>	1.082267 x FL	1.243698 x SL
<i>L. aggenes</i>	1.030797 x FL	1.161224 x SL
<i>L. analis</i>	1.082862 x FL	1.239224 x SL
<i>L. apodus</i>	1.021661 x FL	1.1841 x SL
<i>L. aratus</i>	1.070209 x FL	1.220779 x SL
<i>L. argentimaculatus</i>	1.017699 x FL	1.175869 x SL
<i>L. argentiventris</i>	1.043071 x FL	1.195279 x SL
<i>L. bohar</i>	1.054482 x FL	1.192843 x SL
<i>L. buccanella</i>	1.067416 x FL	1.212766 x SL
<i>L. campechanus</i>	1.026871 x FL	1.191537 x SL
<i>L. carponotatus</i>	1.039146 x FL	1.201646 x SL
<i>L. colorado</i>	1.042048 x FL	1.189979 x SL
<i>L. cyanopterus</i>	1.023132 x FL	1.178279 x SL
<i>L. decussatus</i>	1.04417 x FL	1.17495 x SL
<i>L. dentatus</i>	1.019493 x FL	1.159645 x SL
<i>L. dodecacanthoides</i>	1.046595 x FL	1.184584 x SL
<i>L. ehrenbergii</i>	1.031802 x FL	1.196721 x SL
<i>L. endecacanthus</i>	1.01306 x FL	1.206667 x SL
<i>L. erythropterus</i>	1.0 x FL	1.161585 x SL
<i>L. fulgens</i>	1.033044 x FL	1.171598 x SL
<i>L. fulviflamma</i>	1.162 x FL	1.165992 x SL
<i>L. fulvus</i>	1.043011 x FL	1.212679 x SL
<i>L. fuscescens</i>	1.016981 x FL	1.189845 x SL
<i>L. gibbus</i>	1.076923 x FL	1.187879 x SL
<i>L. goldiei</i>	1.0 x FL	1.211712 x SL
<i>L. goreensis</i>	1.028681 x FL	1.214447 x SL
<i>L. griseus</i>	1.04878 x FL	1.171908 x SL
<i>L. guilcheri</i>	1.034221 x FL	1.167382 x SL
<i>L. guttatus</i>	1.046679 x FL	1.187373 x SL
<i>L. inermis</i>	1.129817 x FL	1.240535 x SL
<i>L. jocu</i>	1.057793 x FL	1.19604 x SL
<i>L. johnii</i>	1.008606 x FL	1.160396 x SL
<i>L. jordani</i>	1.049541 x FL	1.235421 x SL
<i>L. kasmira</i>	1.031858 x FL	1.173038 x SL
<i>L. lutjanus</i>	1.019504 x FL	1.143141 x SL
<i>L. mahogoni</i>	1.049541 x FL	1.204211 x SL
<i>L. malabaricus</i>	1.0 x FL	1.225322 x SL

(Table continued)

Species	FL to TL	SL to TL	
<i>L. monostigma</i>	1.043103 x FL	1.172481 x SL	
<i>L. notatus</i>	1.045455 x FL	1.183128 x SL	
<i>Lutjanus novemfasciatus</i>	1.042991 x FL	1.210412 x SL	
<i>L. peru</i>	1.051331 x FL	1.223451 x SL	
<i>L. purpureus</i>	1.075506 x FL	1.245203 x SL	
<i>L. quinquelineatus</i>	1.05914 x FL	1.184369 x SL	
<i>L. rivulatus</i>	1.029144 x FL	1.160164 x SL	
<i>L. russelli</i>	1.044484 x FL	1.202869 x SL	
<i>L. sanguineus</i>	1.035778 x FL	1.176829 x SL	
<i>L. sebae</i>	1.043088 x FL	1.195473 x SL	
<i>L. semicinctus</i>	1.030142 x FL	1.157371 x SL	
<i>L. stellatus</i>	1.046595 x FL	1.186992 x SL	
<i>L. synagris</i>	1.087 x FL	1.203463 x SL	
<i>Lutjanus timorensis</i>	1.006993 x FL	1.205021 x SL	
<i>L. viridis</i>	1.049904 x FL	1.191721 x SL	
<i>L. vitta</i>	1.034358 x FL	1.174538 x SL	
<i>L. vivanus</i>	1.072222 x FL	1.229299 x SL	
<i>Macolor macularis</i>			
<i>M. niger</i>			
<i>Ocyurus chrysurus</i>	-0.8 + 1.26 x FL		Thompson and Munro 1983
<i>Rhomboplites aurorubens</i>	2.348 x 1.105 FL		Grimes, 78
Etelinae			
<i>Aphareus furca</i>	1.150765 x FL	1.27484 x SL	
<i>A. rutilans</i>	1.175549 x FL	1.318591 x SL	
<i>Aprion virescens</i>	1.133464 x FL	1.24681 x SL	
<i>Etelis carbunculus</i>	1.088847 x FL	1.17551 x SL	
<i>E. coruscans</i>	1.162 x FL	1.223158 x SL	
<i>E. oculatus</i>	-0.986 + 1.159 x FL	n/a	
<i>E. radiosus</i>	1.1341 x FL	1.264957 x SL	
<i>Pristipomoides aquilonaris</i>	1.099792 x FL	1.207763 x SL	
<i>P. auricilla</i>	1.13372 x FL		This study, based on measurement of picture
<i>P. filamentosus</i>	1.12 x FL		This study, based on measurement of picture
<i>P. flavipinnis</i>	1.1470588 x FL		This study, based on measurement of picture

(Table continued)

Species	FL to TL	SL to TL	
<i>P. macrophthalmus</i>	1.23333 x FL		This study, based on measurement of picture
<i>P. multidentis</i>	2.18 + 1.12 x FL		Newman et al., 2002
	1.1164 x FL		This study, based on measurement of picture
<i>P. sieboldii</i>	1.144531 x FL		Based on measurement of picture
<i>P. typus</i>		SL/0.8251852	This study, based on measurement of picture
<i>P. zonatus</i>	1.152 x FL		
Apsilinae			
<i>Apsilus dentatus</i>	1.084735 x FL	1.236056 x SL	
	1.157009 x FL	1.225743 x SL	
Paradicichthyinae			
<i>Symphorus nematophorus</i>	1.0 x FL	1.188017 x SL	

VITA

Fernando Martínez Andrade was born on October 29, 1967, in México City, México. Fernando graduated from the Universidad Autónoma Metropolitana, Unidad Iztapalapa in his hometown, in 1992, with a Bachelor of Science in hydrobiology. His passion for aquatic life pushed him to continue a master's program in ecology, conservation, and natural resources management at the Instituto Tecnológico y de Estudios Superiores de Monterrey, ITESM, in Guaymas, Sonora, México, where he focused on coastal fisheries and marine aquaculture. He obtained a Fulbright Scholarship in 1995 and enrolled in the doctoral program at the Department of Oceanography and Coastal Sciences at Louisiana State University in the fall of 1995, while still working on his master's thesis. He obtained the Master of Science degree from the ITESM in June of 1997 and will earn his Doctor in Philosophy degree from LSU in December of 2003.