ECOLOGY, ABUNDANCE, DIVERSITY, AND DISTRIBUTION OF LARVAL FISHES AND SCHINDLERIIDAE (TELEOSTEI: GOBIOIDEI) AT TWO SITES ON O‘AHU, HAWAI‘I

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ABSTRACT

Light traps were deployed in Hanauma Bay (the Bay) over a 2.5-year period to determine the effect of physical factors on the catch of larval fishes and Schindleriidae. Significantly more larval fishes and *Schindleria* were caught in light traps moored over sand habitat than in those over rubble, coral, or mixed habitats. The currents of the outer reef of the Bay were mapped using drogue analysis, but the recorded pattern (shoreward and westerly) did not explain the catches of larval fishes or *Schindleria*. Other measured physical factors (e.g., wave height, wind speed, temperature, *etc.)* were not statistically correlated with light trap catches; only tidal range had a significant ($p=0.017$) relationship with *Schindleria* catch. The strong swimming abilities of late-stage larvae and adult *Schindleria* can probably overcome small-scale physical factors, specifically currents typical to the Bay. Only 119 fish larvae were caught in 81 samplings, considerably less than reported in other regions. This is probably due to an absence, in Hawai‘i, of the most common species caught in light traps elsewhere.

In Kane‘ohe Bay, paired silent and sound traps were used to determine if sound is an attractant or deterrent for larval fishes and adult *Schindleria.* Sound appeared to be a deterrent for larval shorefishes ($p=0.13$) and *Schindleria* ($p=0.058$), and an attractant for larval reef fishes ($p=0.104$). Shorefishes and *Schindleria* may use sound to avoid predation and reef fish may use sound to recruit to suitable habitat.

Schindleria, with two species in Hawai'i, are progenetic, cryptic fishes and little is known about their ecology. Otolith and histological analyses revealed that both species have extremely high growth rates: *Schindleria pietschmanni* grows an average of 0.72 mm/day and *Schindleria praematura* grows an average of 0.60 mm/day. For both species, females were found to be larger than males ($p=0.007$, $p=0.001$) and in *S. pietschmanni*, temperature was negatively related to growth rate and size ($p=0+$). This genus is abundant in Hawaiian waters (3600+ were caught in my light traps) and may be an important part of the energy budget of a reef, due to sheer number, fast turnover, and high productivity.

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CHAPTER 1:

GENERAL INTRODUCTION

Ichthyology encompasses many diverse subjects and two of the most neglected are larval and cryptic fish ecology. Worldwide, the larval phase of coral reef fishes has been viewed mainly as a "black box" (Leis, 1991), although research in the last 25 years has provided increased knowledge. In Hawai‘i, several studies have described the species diversity and distribution of larval fishes (Leis and Miller, 1976; Lobel and Robinson, 1988; Clarke, 1991) with the majority of research being done in Kane‘ohe Bay (Watson and Leis, 1974; Kobayashi, 1989; Booth 1992), but no Hawaiian study has focused on late-stage larval fishes using light or sound traps, which are both used extensively in this research. Cryptic species make up a large portion of the fish diversity, and possibly the energy budget, of reefs (Munday and Jones, 1998; Greenfield, 2003), but they are largely ignored. One of these species is the lightest vertebrate in the world, *Schindleria pietschmanni* (see Bruun, 1940) and, with its congener *Schindleria praematura,* part of their life history and ecology is examined in this research.

LARVAL BIOLOGY

The Hawaiian archipelago is the most geographically isolated island chain in the world. Because of this feature, Hawai‘i is an important place to study the dynamics of dispersal, especially of larval reef fishes, and to compare local findings to those of the rest of the world. Almost all reef fishes have a distinct phase shift in their early life history--from a pelagic larval stage to a benthic juvenile and adult stage. With this shift come changes in habitat, morphology, size, diet, and behavior (Leis, 1991). Larvae are first planktonic: otolith daily increment analysis suggests that the larval stage can last between 9 and 100+ days, varying among species. Researchers are now observing late pelagic stage fishes actively swimming and delaying metamorphosis (Leis *et al.*, 1996). The term "recruitment" is often used to refer to "settlement," i.e., the movement of a larva from the open ocean to a reef habitat and the subsequent metamorphosis (Sponaugle and Cowen, 1997). Recruitment patterns may account for as much as 90 percent of the spatial variation in certain reef fish abundance (Doherty and Fowler, 1994). Larvae typically have horizontal distributions between 100 meters and five kilometers, or more, away from reefs and a vertical distribution that appears to be photo-controlled--larvae are more closely distributed during the day and widely distributed at night (Leis, 1991). A complex mix of physical, behavioral, morphological, and chemical processes are probably involved in a larva's dangerous transition from a pelagic environment to a benthic one.

POST-SETTLEMENT PROCESSES

Although not a direct focus of this study, density-independent (temporal, physical) factors may be coupled with density-dependent (competition, predation) factors to influence the magnitude of recruitment onto a reef. Booth (1992) found that the major, tested factor affecting the recruitment of the domino damselfish in Kane'ohe Bay was conspecific juvenile density; recruitment was positively related to this density-dependent factor. Booth (1995) concluded that larvae may incur increased survival due to large group size, but growth and time to maturity were negatively influenced. Tupper and Juanes (1999) found recruitment of grunts to be inversely related to piscivore density and, therefore, affected by predation. The first major debate in larval reef fish ecology was the lottery for living space (Sale, 1978) versus the post-settlement processes theory (Robertson, 1995) which ended in the conclusion that recruitment patterns may be different in the Pacific (larvae acquire space if they happen to be in the right place at the right time and therefore, recruitment limitation is the major factor affecting populations) and the Caribbean (larvae compete for space after they settle and therefore, competition and predation are the major factors affecting populations). There are a multitude of factors which may contribute to the successful settlement of larval fishes onto reefs, but the current consensus is that populations are limited by recruitment in years with a low number of recruits and are limited by post-settlement processes in years with a high number of recruits.

MARINE PROTECTED AREAS (MPAS)

Reef fisheries sustain millions of people who, in turn, destroy reef habitat, overexploit reef organisms, degrade water quality through pollution, and threaten biodiversity (Bohnsack and Ault, 1996). The Food and Agriculture Organization (1995) has reported that, worldwide, 70% of all fisheries are not sustainable. Reef fisheries are especially vulnerable because of the array of gear used: dynamite, bleach, cyanide, bottom-set nets, *etc.* Fisheries management can either manage catch or effort (Roberts and Polunin, 1991). Management of catch is a time and cost consuming practice, which includes the implementation of quotas, size limits, gear restrictions, *etc.,* whereas, management of effort restricts the number of fishers or the area where they can fish (Roberts and Polunin, 1991). Marine reserves are areas permanently closed to fishing and have become a common management solution to anthropogenic stress (White, 1988). These "no-take" areas are easier to regulate than other management strategies and may even be beneficial to surrounding fisheries areas (Bohnsack, 1993). One of my study sites, Hanauma Bay, O'ahu, is a year-round Marine Protected Area (MPA).

The use of marine reserves as a management strategy is controversial and their effectiveness is often questioned (Russ, 2002). Studies have found increased abundance of vulnerable species inside a reserve and increased spawning biomass, density, and potential (larger fishes are more than proportionally more fecund; Munro, 1983) (Russ, 1985; Chapman and Kramer, 1999). Migration of fishes from a MPA to a surrounding, fished area has been supported in some cases (Attwood and Bennett, 1994; Russ and Alcala, 1996) and refuted in others (Holland *et al.,* 1993).

MPAs appear to benefit adult fishes and act as a source for larvae, but the assertion of enhanced recruitment is still unproven. This possible effect is hard to study because of the large-scale dynamics, magnitude, and variability of larval dispersal (Leis, 1991). The alternative is that MPAs may act as an overall sink for larvae: remember Tupper and Juanes (1999) found that adult piscivores preyed heavily upon juvenile grunts. Roberts (1995) warned that reserve systems can only be successful if they are networks of areas linking larval supply and settlement areas. The overall effectiveness of a marine reserve on surrounding fisheries depends on a multitude of factors and needs to be examined on a case-by-case basis to determine the target species, fishing pressure, environmental conditions, additional anthropogenic stresses, surrounding reserves, and ecological parameters of the area.

PHYSICAL FACTORS

My second chapter examines the hypothesis that non-biological factors, such as substrate, currents, tides, lunar phase, season, waves, and temperature strongly affect larval ecology, abundance, diversity, and distribution. My research attempts to answer important questions about larval supply, the number of pre-settlement larvae entering an area, specifically Hanauma Bay. Do certain habitats contain more and/or different larvae (and therefore should be included in the planning of a protected area)? Do nearshore current patterns affect the distribution, possibly including retention and accumulation, of larvae within an area? Do certain physical patterns (waves, wind, tides) of an area affect the abundance of larvae? What is the overall larval supply pattern in Hanauma Bay and is it a sink? These questions are important ones for the design and management of MPAs and for the understanding of Hawaiian larval reef fish ecology.

Hypotheses abound concerning the causes of recruitment variability of reef fishes and each case depends upon the scale, location, species selected, and focus of the study.

Survival during the pelagic stage is dependent on several factors including the availability of food and the presence of predators, but settlement must, at some point and to some degree, be dependent on oceanographic transport of larvae (Cowen, 2002). Early, and again recently, research has focused on the physical factors involved in larval recruitment. In Hawai'i, Lobel (1978) found that five coral reef fishes spawn from December to May at dusk between the first quarter and full moon. He concluded that this timing was important for several reasons, including that the annual reproductive peak corresponds to a "shift in ocean current that retains pelagic larvae around the islands and ensures their return to Hawaiian reefs." In 1989, Lobel reiterated his findings with four different reef fishes and suggested that their reproductive peaks (January to July) depend upon mesoscale eddies and ocean currents retaining drifting objects near the islands. These conclusions have been widely criticized for specific aspects of Lobel's study, but not for the idea in general. Sale (1970) also found that ocean gyrals (sic) hold larvae 25-50 km off of Hawaiian shores and sweep past the islands every five-six days. Leber *et al.* (1998), studying the recruitment patterns of cultured, released juveniles in Kahana Bay, O'ahu, Hawai'i, found that release site and the seasonal timing of releases contributed to successful recruitment.

Cowen (2002) provided a thorough review of many of the physical and temporal patterns examined to date. Many different lunar, tidal, seasonal, and monthly patterns of larval abundance have been discussed, but no worldwide consensus has been reached. A predominance of new moon larval recruitment has been found, but it is definitely not the rule. Wind may also contribute to larval recruitment peaks, but Cowen suggested its effect is probably most important in the final settlement push and not in early retention or transport. Tides are important for direct transport of eggs and early-stage larvae away from the reef, and for transport of late-stage larvae towards the reef. Finally, ocean currents are possibly the most important, but the hardest to study, physical factor affecting larval distribution and abundance. Ocean currents are highly variable and constantly changing. Large-scale studies that combine physical and biological oceanography simultaneously are needed to understand the full impact of currents on larval settlement, and these results would still be site and time specific.

Theory about the role of larval biology in the life history of coral reef fishes was built on the principles of open populations. Currents carry fertilized eggs great distances away from their natal reef and the subsequent larvae settle on a non-natal reef. The evolutionary and ecological reasons for this mechanism have been hotly debated (Leis, 1991). Ecological reasons include distancing from predators, expanding territories, and avoiding competition with parents. Evolutionary reasons include distributing the gene pool in case of disturbance, and occupying/adapting to niches in new ecosystems; however, scientists, began to question the validity of a life history strategy that always took offspring away from the habitat to which they were adapted. These questions brought in the latest set of hot topics in larval biology: the investigation of larval retention, accumulation, and natal homing.

Larval retention involves physical factors that maintain larvae near their natal range until they settle; accumulation involves physical factors amassing larvae of different ages (for their whole or partial lives) until they all settle together in time and space; and natal homing involves physical factors and other cues which allow larvae to settle in their natal range after their pelagic stage. Any of these mechanisms may work together or alone. Swearer *et al.* (1999) used otolith microchemistry to test the hypothesis that larvae of the *Thalassoma bifasciatum* in St. Croix, U.S. Virgin Islands were retained near the coast. The researchers found that during the summer recruitment peak of 1997 more than 50% of the larvae never ventured beyond the coastal waters and were therefore, somehow, retained. Jones *et al.* (1999) studied the process of self-recruitment (larvae returning to a natal reef through natal homing, retention, or chance) by staining over 10 million *Pomacentrus ambionensis* eggs with tetracycline, which marks the otoliths. Using light traps, 15 marked individuals were recaptured and, based on the estimate that only .5-2% of the total population of this species on Lizard Island, Great Barrier Reef had been marked, the researchers concluded that between 15 and 60% of juveniles may have been self-recruiting. These two groundbreaking studies, along with genetic analyses, herald the future of larval biology research.

RECRUITMENT CUES

An important topic in larval fish ecology is the investigation of the recruitment cues upon which larval supply and recruitment to an area depend. This is the focus of my third chapter. While many researchers conclude that larval recruitment is mainly a function of physical ocean properties (Lobel, 1989; Blaxter, 1992; Thorrold *et al.*, 1994), others conclude that fine-scale recruitment events may be driven by visual (Kobayashi, 1989; Dufour and Galzin, 1993; Job and Bellwood, 1996), auditory (Stobutzki and Bellwood, 1998; Tolimieri *et al.*, 2000), chemical (Sweatman, 1988), and/or electromagnetic cues. Studies involving visual cues are common, but research on auditory, chemical, and electromagnetic cues are scarce or non-existent.

Chemical: This study does not include chemical cues, but their role in recruitment of larval fishes has been investigated. Sweatman (1988) found that one species of pomacentrid was more likely to recruit to habitats where water was pumped in from coral with resident adults, but two other pomacentrid species were not. All three species of fishes used might have been using chemical cues either to recruit to or to avoid certain habitats. Myrberg and Fuiman (2002), in their review of the sensory systems of coral reef fishes, found no evidence in the literature that various species of larvae were developmentally unable to use olfaction at settlement.

Visual: The research done on visual cues for recruitment has focused on the effect of light, as evidenced by light trap catches and settler counts. Many larvae are photopositive and, therefore, light traps are often used as attraction devices to estimate the larval supply of a particular area. Doherty (1987) first created an integrated marine light trap and, since that time, a wide variety of modified copies have been designed (Thorrold, 1993; Sponaugle and Cowen, 1996). Researchers have attributed the effectiveness of light traps to the ability of larvae to actively orient and locomote vertically and horizontally in the water column (Leis *et al.*, 1996), to possess long-term (up to 194.3 hrs.) swimming capabilities (Stobutzki and Bellwood, 1997), and to respond to visual stimuli (i.e., light, net avoidance) (Dufour and Galzin, 1993; Job and Bellwood, 1996). Light traps are valuable tools because they allow for fine-scale habitat assessment of larval supply, but it must be noted that light traps have limitations; they cannot be used for estimating density and escape is common (Meekan *et al.,* 2000).

Other studies consisted of direct observations of the reaction of larvae and juveniles to light: Dufour and Galzin (1993) fixed a net on the outer reef crest of Moorea Island, French Polynesia and found that fish larvae enter the reef system primarily during moonless dusks and nights (recruitment was four times greater during new moons than during full moons). They concluded that "colonization was closely related to decreasing light intensities." Shenker *et al.* (1993) also found that more larvae settle during dark, moonless nights than during other times of the lunar and 24-hour cycles; however, Kobayashi (1989) found that gobioid larvae in Kane'ohe Bay are found closer to the reef during bright-moon nights and concluded that a lack of visual cues during new moon nights may lead to disorientation. General consensus seems to agree with the former rather than the latter findings (Victor, 1991; Cowen, 2002).

An important question is whether the larvae are morphologically and physiologically ready to respond to light as a settlement cue. Job and Bellwood (1996) studied the ontogenetic change in visual acuity of a larval anenome fish and they found an increase in the lens radius between three- and 10-day post-hatch larvae, which suggested a morphological readiness to use visual cues. Poling and Fuiman (1997) also used a mix of behavioral and morphological studies to examine the physiological ontogeny of larval Atlantic croaker. They found that the importance of the mechanosenory and visual systems changed with ontogeny: larvae >6 mm relied heavily on visual input whereas larvae <6 mm relied equally on visual and neuromast input. In another paper, Poling and Fuiman (1998) concluded that these morphological differences did not correlate with metamorphosis itself, but rather with the environmental conditions of the new habitat. All three of these papers suggest that larvae can morphologically and behaviorally react to visual cues, which may be used to locate the reef.

Auditory: A current theory, especially advanced by Australian field ecologists, is that sound is a major cue used in fish recruitment; this question is addressed in my third chapter: Do larval reef and shorefishes use sound as a recruitment cue? Sound may be the most important stimulus for long distance recruitment of fishes. It is detectable for 100's to 1000's of meters (more than visual, possibly less than olfactory cues) and it is multidirectional (unlike chemical cues). Reef environments are loud and researchers have begun to test the effect of sound in field environments (Stobutzki and Bellwood, 1998; Tolimieri *et al.*, 2000; Leis *et al.,* 2002) and all have concluded that larval fishes do use sound as a recruitment cue. The problem with the conclusions of the field studies lies in the fact that no physiological sound studies exist for larval reef fishes and very few exist for juvenile fishes. Furthermore, those that do exist for juvenile fishes suggest that they are not morphologically ready to interpret sound as a recruitment cue. Further studies are needed of the role of sound in recruitment of reef fish larvae that incorporate the physiological, morphological, and behavioral readiness of the larvae.

OTOLITHS

My fourth chapter, on the ecology of the cryptic genus *Schindleria,* used otolith analyses, which can contribute to the understanding of fish ecology, life history, and population dynamics. Most fishes have three pairs of otoliths, the lapilli, sagittae, and asterici, which are composed of calcium carbonate (Helfman *et al.,* 1997). Otoliths store a record of fish age, growth, and developmental rates (Chambers and Miller, 1995). There exists a direct correlation between fish size and otolith size, so body size can be estimated for any age or developmental stage. Although otolith increments are lain down regardless of environmental conditions, the width of the increments may indicate significant events in the life of the fish (Helfman *et al.,* 1997).

A hundred years of using otoliths for age-based research exists for temperate fishes, but, until recently, little progress has been made for coral reef fishes (Choat and Robertson, 2002; Thorrold and Hare, 2002). Otolith analyses offer the best option for discovering variation in age/growth patterns, rates of reproduction, age structure, length of life, age at settlement, and environmental variation during pelagic larval stage (Choat and Robertson, 2002). Validation, the process of verifying the deposition of increments over a certain time span (daily or annual), is desirable, but many species' otoliths have been validated and only two species have shown no periodicity in increment deposition (Choat and Robertson, 2002).

This chapter was a collaborative effort with Dr. David Shafer and Ross Langston. I collected all the specimens from Hanauma Bay, over 3.5 years, using light traps. These specimens were frozen and later measured, identified to species level, and the otoliths were dissected and mounted from 129 fishes. Dr. Shafer dissected and mounted 67 fishes and I did 62. Langston and I did three plankton tows in Kane'ohe Bay (27 April, 11 May, 15 June 2003) to collect *Schindleria* for sexing because the Hanauma Bay specimens were too degraded for histological analysis. I identified the Kane'ohe Bay specimens to species level and Langston measured and sexed them. I dissected and mounted all 100 otoliths from the Kane'ohe specimens. Dr. Shafer and I both counted the otolith increments and came to a consensus before I analyzed the results. Langston also described batch fecundity and matched the eggs of known *Schindleria* to those found in a worm tube. Except for the histology sections, I wrote the paper.

CHAPTER 2:

PHYSICAL FACTORS IN HANAUMA BAY

Nearshore physical processes, habitat type, and their effect on the abundance, diversity, and distribution of larval fishes and *Schindleria* (Teleostei: Gobioidei) in Hanauma Bay, O'ahu, Hawai'i

Manuscript

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ABSTRACT

The abundance, diversity, and distribution of fish larvae and an abundant progenetic genus, *Schindleria,* have been assessed in relation to the physical processes of nearshore currents, temperature, waves, and tides, as well as lunar, seasonal, and habitat patterns. Permanent anchor lines were placed in four areas of Hanauma Bay (the Bay) and light traps were deployed on 33 nights between 14 December 1999 and 24 July 2002 to test substrate (sand, coral, rubble, and mixed) effect on fish catch. There was a significant difference in the catches of larval fishes (p=0.013) and *Schindleria* (p=0.021) with the trap over sand habitat catching the most, followed by the traps over rubble, coral, and mixed substrates. The sand location probably offered the habitat with the fewest predators and acted as a "waiting room" area before settlement. The nearshore currents were mapped using drogues. All the drogues drifted towards the southwestern (Witches' Brew) side of the Bay, irrespective of the tidal phase. Paired light traps anchored on the Witches' Brew and northeastern (Toilet Bowl) sides were deployed over 10 nights and there was no significant difference in catch for either *Schindleria* or larval fishes. The strong swimming abilities of late-stage larvae can probably overcome the current patterns in the Bay. A data buoy and surf report measurements were used to analyze the relationship between catch and temperature, wave height, wave direction, peak period, average period, wind direction, wind speed, and tidal range. The only significant relationship was a positive relationship between *Schindleria* catch and tidal range (p=0.017) and a negative relationship with sea surface temperature (p=0.075). The only

genera seen as adults in the Bay that were caught in the light traps were *Abudefduf* and *Thalassoma*. The most important result of this study was the paucity of late-stage, photopositive reef fishes caught in my light traps. Only 119 larval fishes were caught in 81 samplings. A "sink" is defined here as an area where predation on larvae by resident adults outweighs the contribution of successful larvae by resident adults to natal and outside areas. This Marine Protected Area (MPA) was probably not a sink (because so few larvae returned, predators in the Bay probably were not eating more than they were producing) for late-stage, photopositive larvae. This research points to the probable low numbers of late-stage, photopositive fish larvae in the Bay during the study period, as compared to other studies done in the western Pacific and the Caribbean.

INTRODUCTION

Hanauma Bay (the Bay) was created in 1967 as the first year-round MPA on O'ahu, Hawai'i. This no-take strategy has created a unique ecosystem for O'ahu: a large population of reproductively mature fishes, but also the number-one tourist beach destination (outside of Waikiki) on O'ahu with over one million visitors a year (Brock and Kam, 2000; DBEDT). Little scientific research has been done in the Bay and none has assessed its larval ecology. Most reef fishes have a distinct life history shift, which is accompanied by a habitat change: from a pelagic larval phase to a benthic juvenile and adult phase (Leis, 1991). Larval supply (the number of larvae entering an area) may be affected by a number of factors including, but not limited to: "hydrographic variables" (Thorrold *et al.*, 1994), lunar cycle (Sponaugle and Cowen, 1996), and habitat complexity

(Friedlander and Parrish, 1998). Factors affecting larval supply are important because, ultimately, recruitment patterns may greatly influence the adult population size of a reef community, especially during times of low recruitment rates (Doherty and Fowler, 1994; Sponaugle and Cowen, 1997).

Arguably the most important question in larval ecology is how larvae recruit to a suitable habitat. A recent consensus concerning factors important for recruitment success includes large- and small-scale physical factors, behavior [e.g., long-term (up to 194.3 hrs.) swimming capabilities (Stobutzki and Bellwood, 1997), recruitment cues], and chance. Hypotheses abound concerning the causes of recruitment of reef fishes and each possibility depends upon the scale, location, species selected, and focus of the study. Survival during the pelagic stage is dependent on several factors including the availability of food and the presence of predators, but settlement must, at some point and to some degree, be dependent on oceanographic transport of larvae (Cowen, 2002). Early, and again recently, research has focused on the physical factors involved in larval recruitment.

This study compares the abundance, diversity, and distribution of fish larvae and adults of the cryptic genus, *Schindleria,* to the physical processes of nearshore currents, temperature, waves, and tides, as well as lunar, seasonal, and habitat patterns. Do certain areas of the Bay harbor more fish larvae than other areas? Do these same areas retain adults of *Schindleria*? Along with spatial variation, is there monthly variation in the species abundance and richness within the Bay? Does a lunar variation of species abundance and richness exist? Does a difference exist in the number of larvae and/or *Schindleria* over coral, rubble, mixed, or sand habitats? Do certain physical factors affect *Schindleria* and larval catches? Do captured larvae species equate to observed adults? Is the Bay a sink for larvae?

MATERIALS AND METHODS

<u>*Study site:*</u> The 100-acre Bay is located on the southeastern shore of Oʻahu (Figure 2.1) and is subjected to strong currents, wave action, surge, and tides. It is located directly off of a fast moving, open-ocean, east-west current, locally called the "Molokaʻi Express."

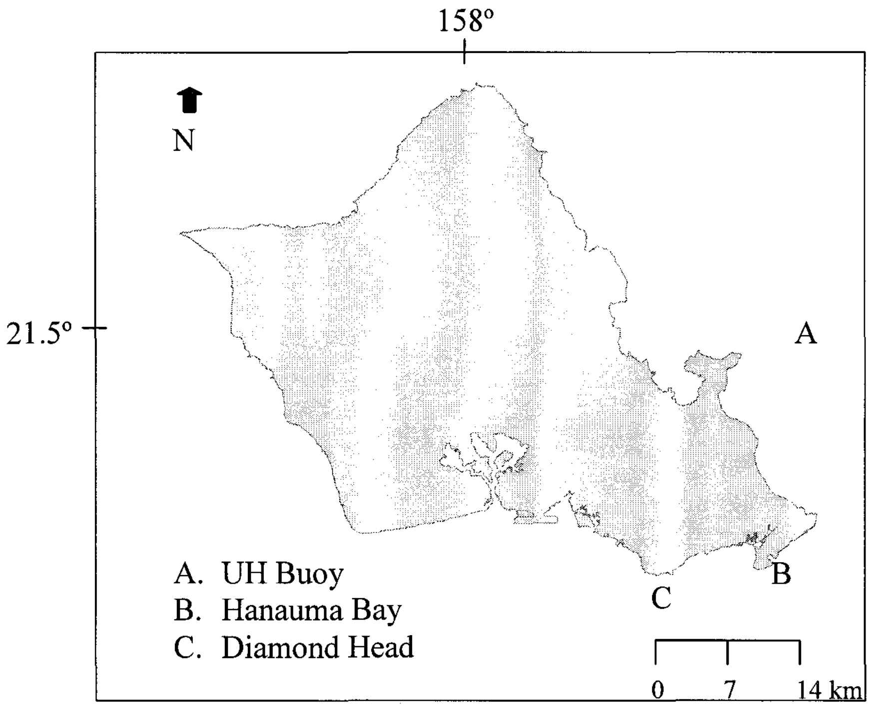


Figure 2.1 Map of Oʻahu, Hawaiʻi showing A) UH Buoy, B) Hanauma Bay, and C) Diamond Head

A calm, protected, tidally-influenced environment exists nearer shore, especially in the inner reef (19.7 acres), which is located inside of the reef crest (Brock and Kam, 2000).

Schindleria: The ecology of *Schindleria pietschmanni* [the lightest vertebrate in the world (Bruun, 1940)] and *Schindleria praematura* is almost unknown. The genus is progenetic (Kon and Yoshino, 2002a) and abundant in Hawaiian waters (Gosline and Brock, 1960; Watson and Leis, 1974).

Collection: Many larvae (and the genus *Schindleria*) are photopositive and, therefore, light traps are often used as attraction devices to estimate the larval supply of a particular area (Doherty, 1987; Thorrold, 1993). Researchers have attributed the effectiveness of light traps to the ability of larvae to actively orient and locomote vertically and horizontally in the water column (Leis *et al.*, 1996), and to respond to visual cues (Dufour and Galzin, 1993; Job and Bellwood, 1996). Light traps are valuable tools because they allow for fine-scale habitat assessment of late-stage, photopositive larval supply, but it must be noted that light traps have limitations; they cannot be used for estimating density and escape is common (Meekan *et al.,* 2000).

Light traps [design by D. Kobayashi, National Marine Fisheries (NMFS) Honolulu Laboratory, with my own modifications; based on the earlier design of Floyd *et al.*, 1984] were fitted with a 6W florescent bulb, a 6V lantern battery, and a collection bucket (Figure 2.2). The fishes were collected from the traps, fixed in 5% formalin (ultimately stored in 55% isopropynol), and identified to the lowest taxon level possible

(Bruce Mundy, NMFS Honolulu Laboratory, unpublished notes; Miller *et al.,* 1979; Watson *et al.,* 1984; Okiyama, 1988; Leis and Trnski, 1989; Watson, 1989; Randall, 1998; Greenfield, 2001). Exceptions were *Schindleria* caught for otolith work; these fishes were placed in fresh water and frozen. Effort in the catch per unit effort (CPUE) analyses was measured as the catch of each trap per night.

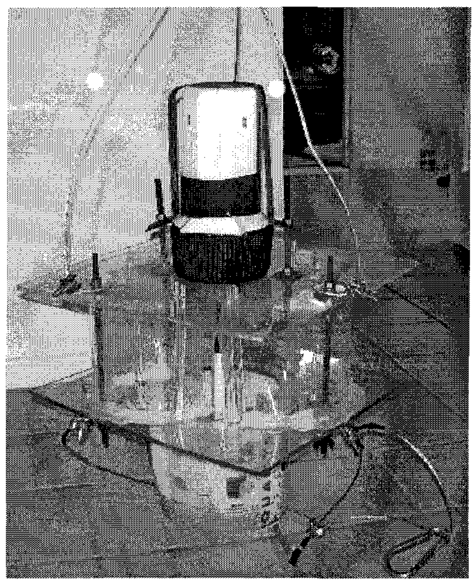


Figure 2.2 Light trap fitted with 6W florescent bulb, 6V lantern battery, collection bucket, and attachment cables.

Substrate: Four locations were made permanent sampling sites by placing 30 kg anchors and stainless steel cable at the specified locations: a sand channel in approximately 15 m of water, an extensive rubble habitat in 14 m of water, a coral habitat in 4 m of water, and a mixed coral, rubble, and sand habitat in 15 m of water (Figure 2.3). These locations were all in the central or western side of the Bay and were therefore subjected to similar currents within the Bay (see below), but the traps in deeper water were closer to the mouth of the Bay and, therefore, to open-ocean currents. Using scuba, and carabineers, the light traps were moored within 3-5 m of the surface. The light traps were deployed 0-4 nights a month, between 14 December 1999 and 24 July 2002, during various phases of the moon. This design allows for direct substrate comparisons as well as cumulative comparisons based on lunar phase, season, tide, and temperature.

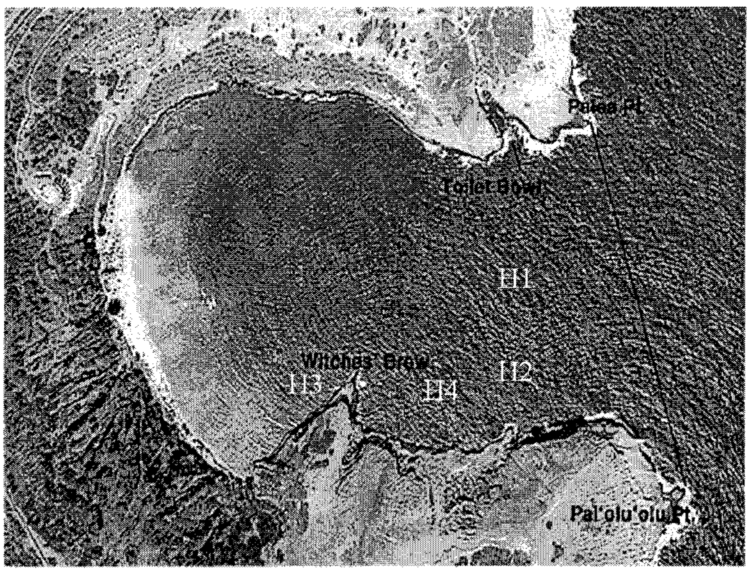


Figure 2.3 Hanauma Bay, showing permanent trap locations: H1 (sand), H2 (mixed), H3 (coral), and H4 (rubble).

Currents: In the 1960s, P.F. Fan and J. Southworth (unpublished data) measured the current velocity and patterns of the inner reef of the Bay. They found that, during a falling tide and tradewind conditions, water entered the inner reef area steadily across the reef/boulder boundary. Water traveled parallel to shore at 2.5 to 5 cm/sec, and then exited the inner reef area at the far sides of the Bay, close to the ledges (up to 50 cm/sec) and through the cable channel in the middle of the Bay (up to 25 cm/sec).

The currents in the outer reef portion of the Bay were mapped using six drogues constructed of 1 m x 1 m x 0.5 m PVC piping with tarp tie-wrapped within the frame (Figure 2.4). Each drogue was individually marked with a different color flag (blue, pink, red, orange, green, light green, yellow or combination) and weighted at the bottom with an 8oz fishing weight. Volunteers armed with watches, binoculars, and compasses stationed four sites around the periphery of the Bay. Each person recorded the time (every 10 minutes) and the angle of each drogue, along with the angles of the other volunteers. Divers swam to different areas of the Bay and released the drogues. When a drogue was harassed by a visitor (rare) or caught up on the reef (common), it was freed and redeployed. Using Adobe Photoshop, the paths of the drogues were plotted onto a map of the Bay using the averaged intercepts of angle/time measurements and the angles of the observers from each other. This experiment was conducted during an incoming tide (11 November 2000), an outgoing tide (31 May 2001) and a mixed tide (1 December 2001), all on calm days.

The average velocity of the drogues for each sampling was computed. The X, Y coordinates from the mapping results were used. A rough estimate of the width of the Bay (using two Division of Aquatic Resources maps) was used to attain the conversion, in meters, of each X and Y unit on Adobe Photoshop (each unit equaled 130 m). The distance formula, SQRT[(change in X)^2 + (change in Y)^2], was used and then divided by the appropriate elapsed time to calculate the velocity (cm/sec) of each drogue.

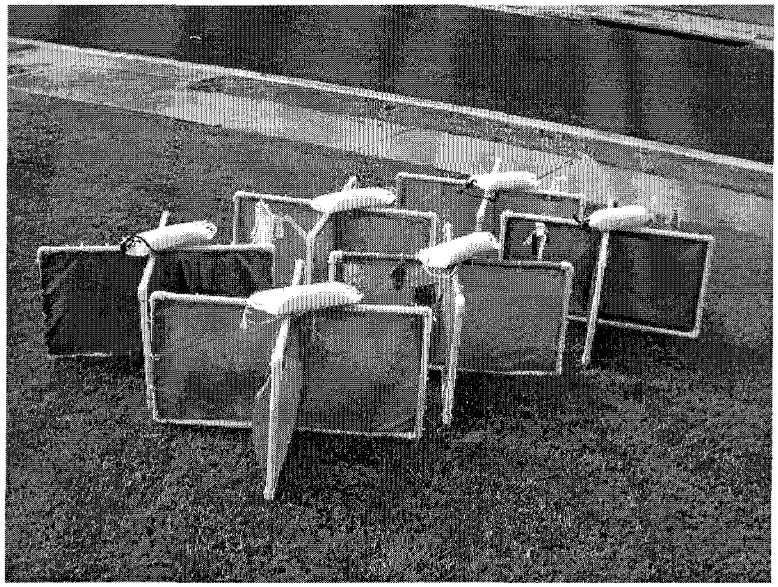


Figure 2.4 Six drogues constructed of 1m x 1m x 0.5m PVC piping with tarp tie-wrapped within the frame. Each drogue was individually marked with a different color flag (blue, pink, red, orange, green, light green, yellow, or combination) and weighted at the bottom with an 8oz fishing weight.

The results from the drogue studies were used to place paired light traps in varying rubble and coral habitats on each side of the Bay (e.g., rubble habitat on the Toilet Bowl side vs. rubble habitat on the Witches' Brew side). This sampling lasted from 1 October 2001 until 31 July 2002 and no permanent locations were established so that most of the rubble and coral habitats on each side of the Bay were assessed to determine the nearshore current effect on larval distribution, abundance, and diversity.

Buoy: Physical oceanographic factors are highly variable and the assessed measurements were those available. The Department of Oceanography at the University of Hawai'i at Mānoa deployed a Datawell Waverider buoy (Station ID #98; N 21 ° 24.900 W 157° 40.700) off the Mokapu peninsula (east coast of O'ahu; Figure 2.1) on 9 August 2000. This buoy measured Hs (wave height in meters), Tp (peak period in seconds), Dp (mean wave direction in degrees), Ta (average period in seconds), and sea surface temperature in Celsius degrees. The buoy recorded these data every 30 minutes and these measurements were averaged over each night of sampling. This buoy provides information on wind waves incident from the east, as well as energetic winter swell from the north; because the Bay is sheltered from waves from the north, only data from measured wave directions between 78 and 154 degrees were used. In the analysis of the effects of oceanographic factors, the fixed location in the middle of the sand channel was used as the source for my fish catch data so that no substrate bias would exist (except for the temperature, and the tidal data below, analyses in which substrate type was used as a covariate). Daily south shore tidal range data (in mm) from the University of Hawai'i at Mānoa Sea Level Center were also analyzed; because my traps were left out overnight, the ranges of the two calendar dates were averaged. These data were compared for correlation between the physical processes and the abundance of larval fishes and *Schindleria.*

Surf report: Because the University of Hawai'i buoy was located on the east coast of O'ahu and the Bay is located on the southeast coast of O'ahu, surf report data (compiled by Pat Caldwell, NOAA, National Coastal Data Development Center) from Diamond Head (south coast of O'ahu; Figure 2.1) were also obtained for analysis of summer energy originating from southern hemisphere storms. These data included wave height (m), wind speed (beaufort), wind direction (degrees), and south shore wave direction (degrees).

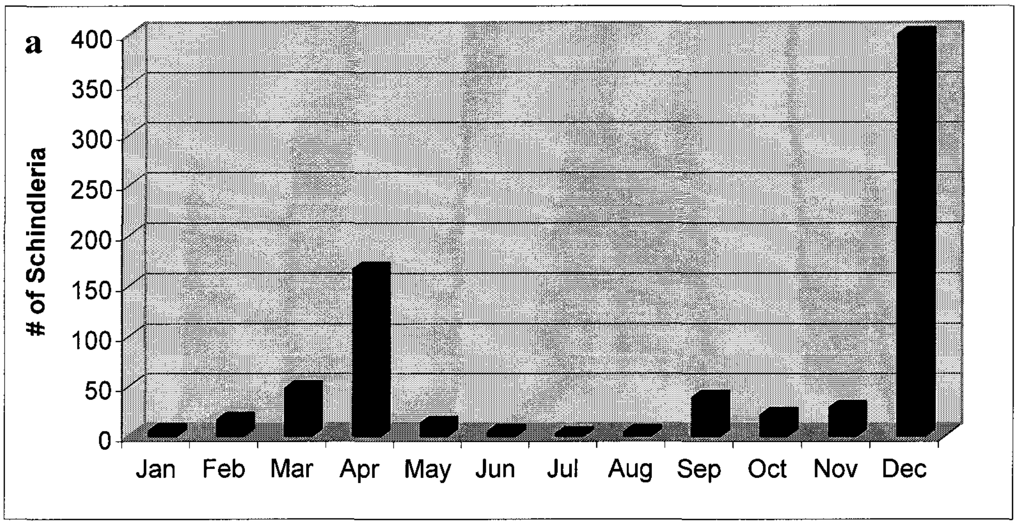
RESULTS

Species: The light traps were known to be functioning on reported nights because the researcher had to call the caretaker of the Bay each night to report how many traps were deployed (due to the threat of poaching); the caretaker reported how many lights he observed and unseen lights were inevitably flooded (approximately 30). In 81 samplings over 44 nights between 14 December 1999 and 31 July 2002, 3638 adult *Schindleria* and 119 larval reef fishes were caught. 31.8% of the *Schindleria* were caught in a single catch and 39.5% of the larval reef fishes were caught in a single, although different night, catch. Many of the *Schindleria* specimens were degraded, and all had perished, upon retrieval, so species-level identification was not possible for most specimens; however, of a sample of 129 light trap-caught specimens, only one was identified as *S. praematura* and 128 were identified as *S. pietschmanni,* so less than 1% of the catch was *S. praematura.* The larval reef fishes were identified to 18 known and 2 unknown families (Table 2.1).

Lunar/monthly: There is no significant monthly or lunar correlation with *Schindleria* catch data, although there is a graphical dip (Figure 2.5 a-b) in CPUE numbers during the summer months and closer to the full moon (with the exception of one catch on day 16).

Table 2.1 Larval fishes caught in Hanauma Bay were identified to species level for 75 specimens, to generic level for 35 specimens, and to family level for 4 specimens. Five specimens were too damaged to be identified to family.

CATCH	SPECIES
46	*Atherinomorus insularum*
20	*Spratelloides delicatulus*
15	*Asterropteryx semipunctatus*
8	*Apogon* sp.
6	*Abudefduf* sp.
5	*Enneapterygius atriceps*
5	unknown
3	*Entomacrodus* sp.
2	*Eviota* sp.
1	*Apogon erythrinus*
1	*Bathygobius cotticeps*
1	Creediidae
1	*Decapterus macarellus*
1	*Psenes cyanophrys*
1	*Pseudamiops diaphanes*
1	*Scorpaenopis* or *Sebastapistes* sp.
1	*Thalassoma* sp.
1	unidentified eel
1	unidentified goby



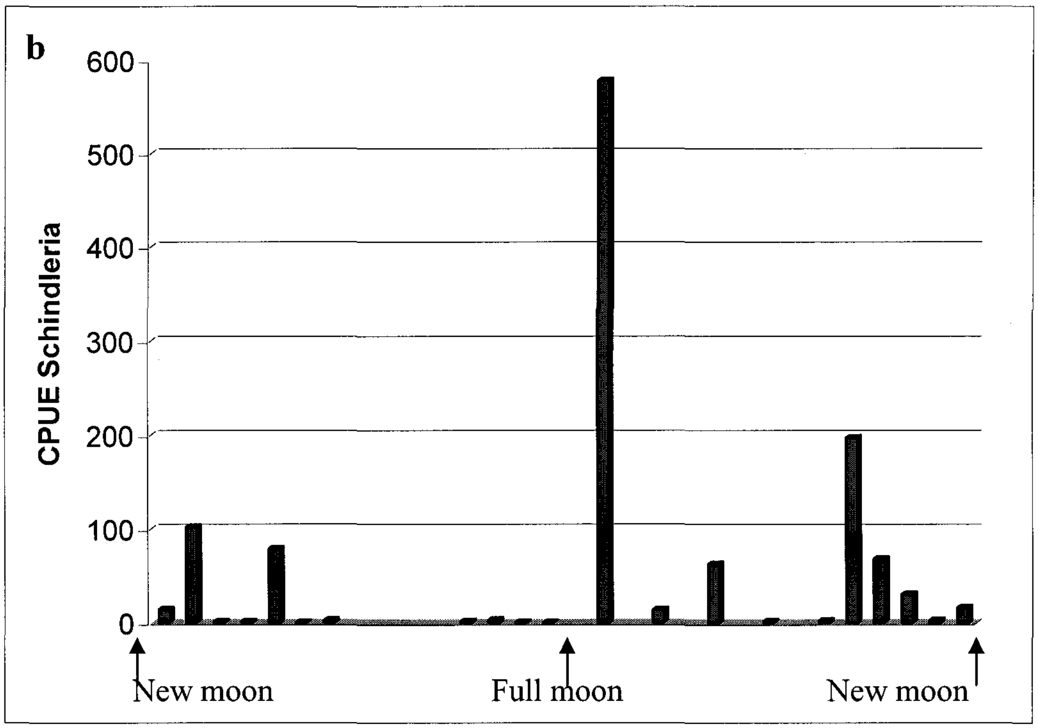


Figure 2.5 a) CPUE for monthly catch for *Schindleria* in Hanauma Bay (n=1,9,8,7,7,3,11,10,6,6,11,1 for each month sequentially). The summer months had lower catches. **b)** CPUE for lunar catch for *Schindleria* as measured by days after the new moon (day 0) (n=2, 10, 2, 6, 5, 4, 5, 0, 0, 0, 0, 3, 5, 3, 2, 0, 2, 0, 5, 0, 4, 0, 4, 0, 1, 2, 2, 1, 4, 7 for each day sequentially). With the single large catch on day 16 as the exception, catches were lower around the full moon (days 10-17).

Similarly, there is no significant monthly or lunar correlation with larval reef fish catch. The presence of several extremely large catches and frequent no-catch samples caused non-normal data, but patterns, or lack thereof, were still evident.

Substrate: Twenty-eight light trap collections were taken at H1, seven at H2, 11 at H3, and 13 at H4. Using a General Linear Model with trap as a fixed effect and date as a random effect, and log-transformed raw catch data for both *Schindleria* and reef fish larvae, significant differences between catches were found. In the *Schindleria* analysis, trap (p=0.021) and date (p=0.02) both were significant at the Δ=0.05 level with the H1

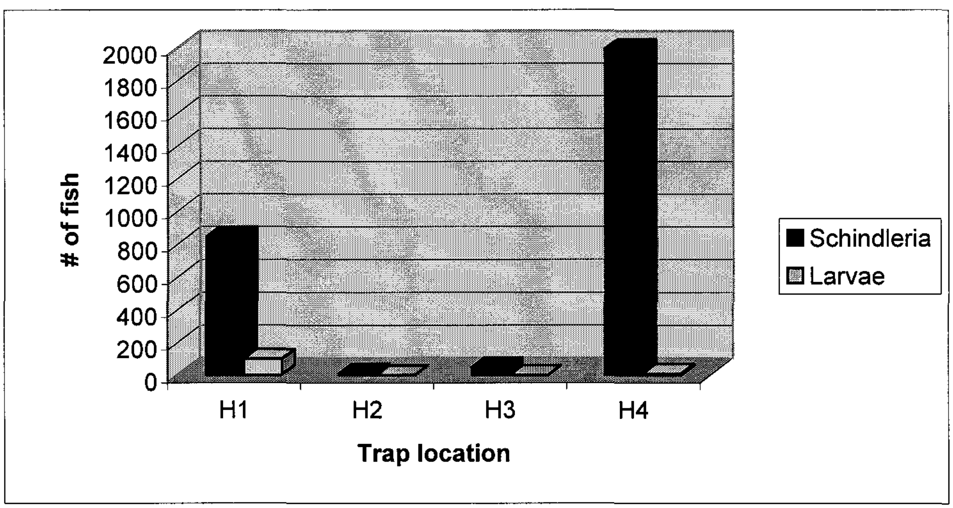


Figure 2.6 Raw data for catches of *Schindleria* and larval fishes by substrate type. When the data were log-transformed to account for non-normality of fish catches (large pulses and many zeros), there were significant differences in substrate effect for *Schindleria* (H1>H4>H3>H2) and larval fishes (H1>H4>H2>H3). Note: a single large pulse at the H4 station caused H4 to have higher raw catch, but when the data were transformed to account for outliers, this result was modified and H1 had higher overall catch for *Schindleria.*

position having the greatest catches, followed by H4, H3 and H2 with the lowest catches. In the reef fish larvae analysis, trap ($p=0.013$) was significant with H1>H4>H2>H3, but the date was not significant ($p=0.105$) at the $\Delta=0.05$ level. (Figure 2.6)

Currents: The overall current patterns in the Bay were mapped for incoming, outgoing, and mixed tides (Figure 2.7 a-c) during tradewind and calm wave conditions. On 10 November 2000, the average velocity for all the drogues was 3.4 cm/sec with a range of 1.7-5.8 cm/sec. On 31 May 2001, the
average velocity for all the drogues was 3.1 cm/sec with a range of 0.1-6.5 cm/sec. On 1 December 2001, the average velocity for all drogues was 2.7 cm/sec with a range of 0.8-5.1 cm/sec. The drogues placed towards the outer boundary of the Bay tended to have higher average velocities compared to those in shallower water. Water moved towards Witches' Brew during all tidal phases

Using the assessed currents patterns, paired light traps were successfully placed on the Witches' Brew side and on the Toilet Bowl side on ten occasions. There was no significant difference between the catches of *Schindleria* or larval fishes on the Toilet Bowl side or Witches' Brew side.

Buoy: There were 12 samplings when both the buoy and the trap were functional and the buoy measured wave direction at a degree (78-154), which would affect the Bay. Using the unbiased data from H1, none of the physical factors were significant for either

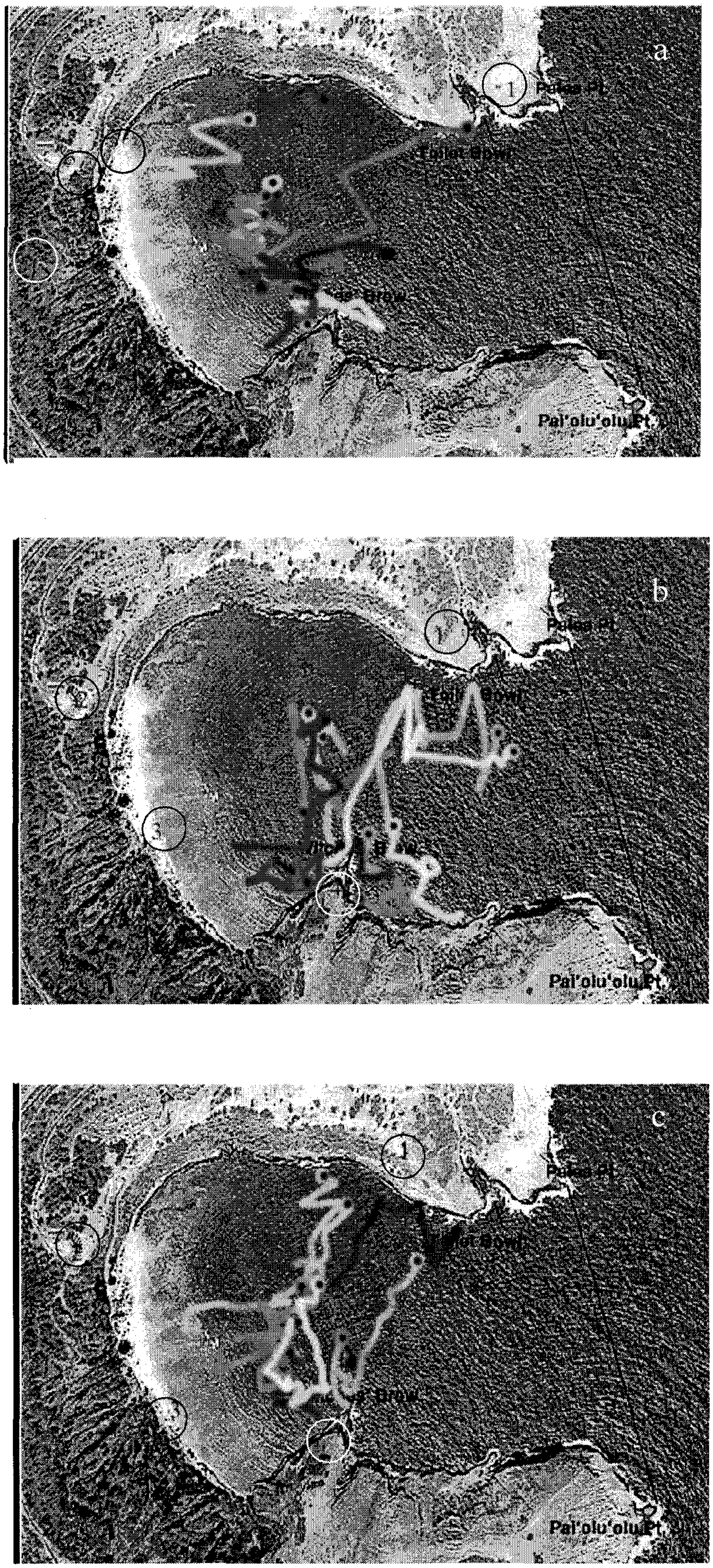


Figure 2.7a-c Drogue analyses of nearshore current pattern in Hanauma Bay for **a)** incoming tide, **b)** outgoing tide, and **c)** mixed tide. Observer positions are circled.

the *Schindleria* or for the larval fishes data. For the log-transformed *Schindleria* data, the R^2(adjusted) was 30% and the peak period (p=0.142) and wave direction (p=0.155) were not highly non-significant (Figure 2.8 a-d). On the other hand, the R^2(adj.) for the larval reef fishes regression was 7.1% with only peak period (p=0.17) being not highly non-significant. For the sea surface temperature and tidal range data, I used the log-transformed catch of all permanent traps (n=59) for both *Schindleria* and larval reef fishes using trap type as a covariate. The *Schindleria* had a negative relationship with sea surface temperature (p=0.075) and a significant positive relationship with tidal range (p=0.017), as the temperature decreased and the tidal range increased, the number of *Schindleria* caught increased (Figure 2.8 e-f). The larval fishes had a positive relationship with both temperature (p=0.115) and tidal range (p=0.102), as the temperature and tidal range increased, the number of larval fishes caught increased.

Surf report: There were twenty-eight data points of log-transformed H1 catches and surf report observations. Only the south shore wave direction was significant (p=0.032) with the *Schindleria* catches; the greater the degree (more southern and western), the higher the catch (Figure 2.9 a-b). The R^2(adj.) for the entire regression was only 22.7%. The H1 catches of larval reef fishes were highly non-normal, so binary regression was used. There were no significant relationships in this analysis, although wind speed did come close (p=0.086); as the wind speed increased, the catch decreased (Figure 2.9 c). I could not use the combined buoy and surf report data in a regression because there were too few degrees of freedom.

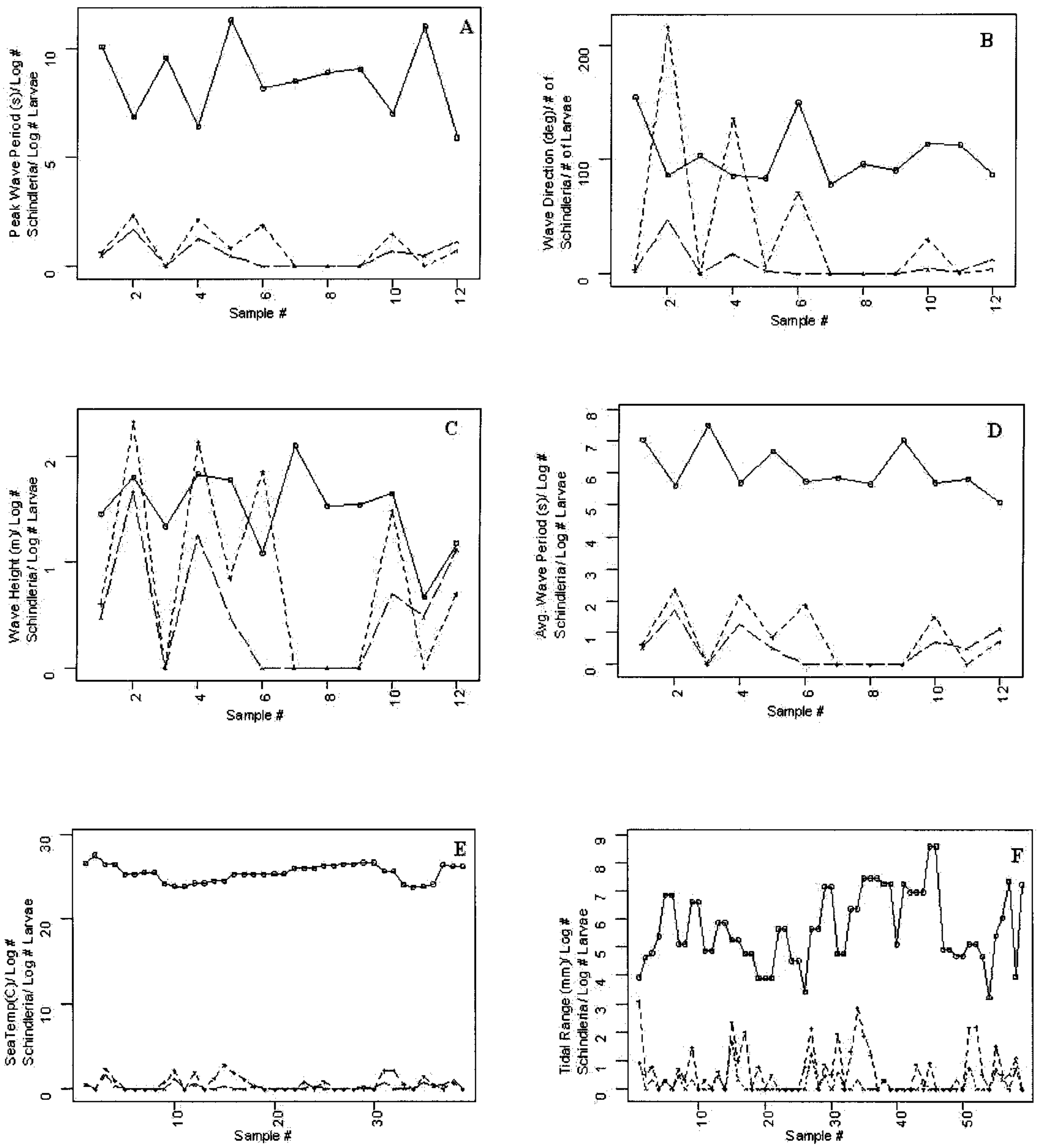


Figure 2.8 Relationship between catch and buoy/tidal data for **a)** peak wave period, **b)** wave direction, **c)** wave height, **d)** average wave period, **e)** sea surface temperature, and **f)** tidal range. For all graphs, the solid line is the buoy measurement, the dashed line is the *Schindleria* catch and the long-dash line is the larval fish catch.

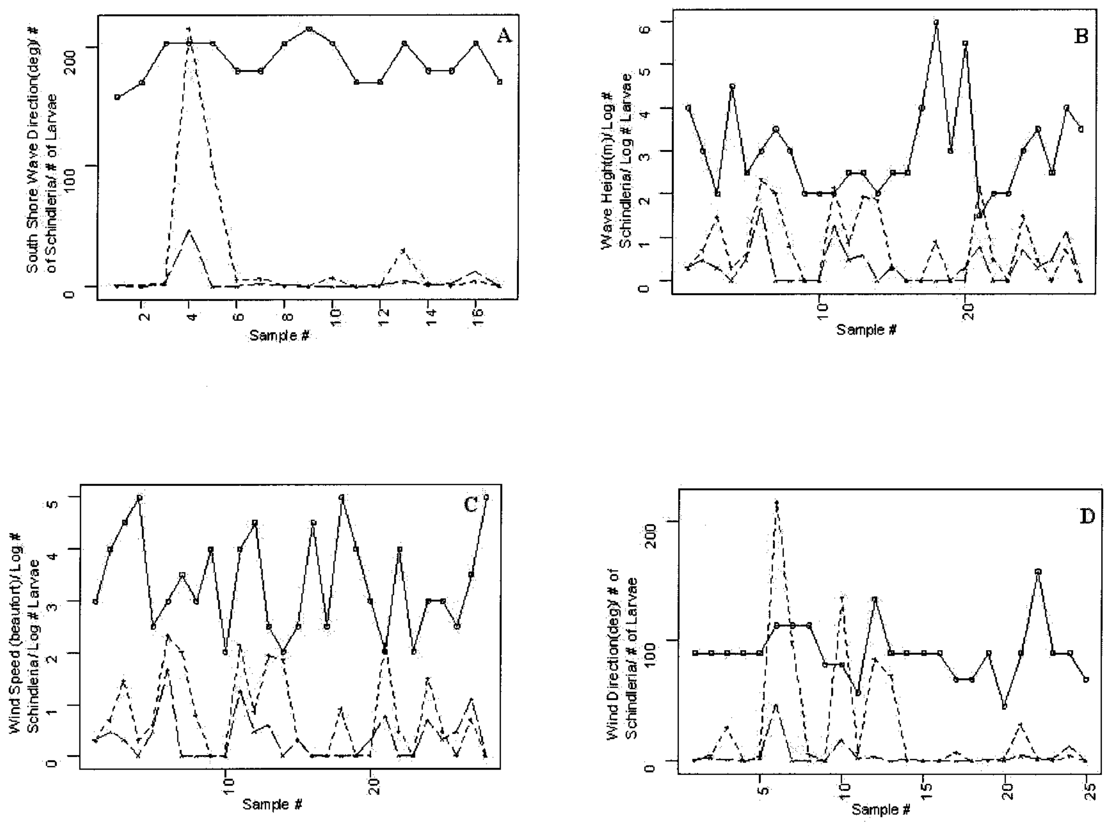


Figure 2.9 Relationship between catch and surf report data for **a)** south shore wave direction, **b)** wave height, **c)** wind speed, and **d)** wind direction. For all graphs, the solid line is the surf report measurement, the dashed line is the *Schindleria* catch and the long-dash line is the larval fish catch.

Adults: Brock and Kam (2000) listed 109 species observed in the Bay. Of these, only species from two genera were caught as larvae in my light traps: *Abudefduf* and *Thalassoma*.

DISCUSSION

These results indicate that, during the study period, the Bay has a severe paucity of late-stage, photopositive fish larvae, approximately 1.5 fish larvae per trap per night. Researchers on the Great Barrier Reef in Australia have found 26.8 fish larvae per trap per night for just one species of *Pomacentrus* (Jones *et al.*, 1999) and 25.7 fish larvae per trap per night for two species *Pomacentrus* and one species of *Dischistodus* (Milicich *et al.,* 1992); Sponaugle and Cowen (1996), working in Barbados, caught 17.5 fish larvae per trap per night of 82 species. Light trap studies have been attempted by several other researchers in Hawai'i: J. Stimson, R. Kinzie, NMFS lab, and were deemed unsuccessful due to the lack of fish catch. Jeff Leis (pers. communication) suggested that the primary factor influencing the low light trap catch numbers in Hawai'i was the absence of species that are caught in large numbers in other places: species of *Pomacentrus*, *Lethrinus*, *Siganus*, *Chrysiptera*, *Neopomacentrus*, *etc*. Light traps are selective sampling devices, but of the three families Choat *et al.* (1993) mentioned that were not caught, at large sizes, by light traps but were caught by other collection methods (purse seines, towed nets), one was Schindleriidae (the others were bothids and carangids). Juvenile attraction devices were also placed in three locations in the Bay and were checked weekly for new recruits; after six months, only three *Dascyllus albisella* settlers were found. So, along with the limited photopositive species in Hawai'i, the low number of larvae in the Bay may be due to its probable high flushing rate (although no measurements have been made), its location directly off the "Moloka'i Express" current, its large number of predators, or, most likely, a combination of these.

The catches over sand habitat were significantly greater than those over the other three habitats. Spatial replication inside the Bay was not possible geologically (except for coral) in the scale examined, and not feasible temporally, logistically, or monetarily in multiple locations. This result is a single datum and must be combined with other similar results (Doherty, pers. communication; Milicich *et al.,* 1992; Sponaugle and Cowen, 1996; Jones *et al.,* 1999) to conclude that larvae may use sand habitat as a waiting room before settling. This conclusion demonstrates that it is important to include varied, especially sand, habitats in MPA design: all life-history stages must be protected, particularly from habitat degradation.

The lack of lunar and seasonal patterns is probably due to the small catch numbers, multiple species included in the analysis, and the highly patchy, large-scale nature of larval distribution. These patterns have been shown to be specific to species and scale (Cowen, 2002). The recorded current pattern in the Bay matched the anecdotal pattern: debris accumulates in Witches' Brew and a lost light trap washed ashore a month later in this western area. The current patterns do not seem to be tidally controlled (the overall pattern of flow was similar during the different tidal phases) and because the drogue studies were done on calm days, the velocity measurements could be the lower boundary—as winds and waves increase, so too would the currents. Although there were the current patterns to provide it, there was no apparent accumulation or retention of larvae in the Bay. The lack of significant differences in the catches between the Witches' Brew and Toilet Bowl sides can probably be explained by the absence of extensive sand or rubble habitat for *Schindleria* and by late-stage larval behavior, specifically strong swimming abilities. Stobutzki and Bellwood (1994) measured the average critical swimming speeds of pre-settlement juveniles of three pomacentrid species to be 38.2 cm/sec and the fastest average current measured inside Hanauma Bay was 3.4 cm/sec; the fishes swam 11 times faster than the measured currents. Larval behavior can probably also explain the lack of significant relationships between catch and the measured small-scale physical factors.

Another surprising result was the high abundance of *Schindleria* adults, especially above sand and rubble habitats. These fishes could be important contributors to the energy budget of a reef because of their abundance and short generation time (37.1 days; Kon and Yoshino, 2002b), which may lead to fast turnover and high productivity. Catches were lower in the summer when temperatures were higher, which might be related to food availability, due to semi-annual tidal peaks and/or increased thermal stratification. However, Watson and Leis (1974) found *Schindleria* to be most abundant in Kane'ohe Bay from late spring to early fall; this opposite finding may be due to the difference in tidal and stratification effects between an open bay (Hanauma) and a lagoonal bay (Kane'ohe). Another paper concluded that their growth rate was also lower during higher temperatures (Whittle *et al.,* in prep.).

The higher catches during southern wave events may be related to geological features of the Bay which block the waves: *Schindleria* may migrate vertically during periods of calm and large tidal ranges [Watson and Leis (1974) had a similar conclusion]. The lack of significant relationships between catch and wind and wave data, along with the 4-5 m depth of my traps suggests that trap functioning was probably not affected during rougher nights. The dip in catches around the full moon also suggests that members of the genus may remain closer to the substrate when predators have a visual advantage. This concurs with Watson and Leis's (1974) lack of *Schindleria* catch during daylight hours; they migrate vertically in lower light conditions.

The concern that MPAs might become sinks for larvae is not justified in this case, at least for some species, because there was not enough late-stage, photopositive larval supply available for predation. The Bay is probably a source for larvae and the large reef fish population (Friedlander *et al.,* 2003; Brock and Kam, 2000) is most likely due to immigration. Therefore, the resident adult fish population is likely producing more successful larvae (possibly for itself and for other areas) than it is eating (simply because there were few larvae to prey upon during the time period of the study), which makes it a source and not a sink for larvae. Larvae were most abundant farthest towards open ocean, so the available larval supply may be influenced by predators farther inside the Bay. The Bay is the largest no-take MPA on O'ahu and if it acts as a source, where are the larvae settling? The issue of connectivity of MPAs (Roberts, 1995) may be important: a network of reserves might help promote successful protection.

In addition, the Bay is likely not recruitment-limited for photopositive species and instead these results suggest that its population of these species is probably structured by post-settlement processes, such as migration, competition, and predation. Adults of photopositive species (Mullidae, Acanthuridae, Synodontidae, Gobiidae, Blenniidae) are present inside the Bay, but were rare or non-existent in light trap catches. The lack of larval supply is probably most influential in the population structure of short-lived species, such as Blennidae and Gobiidae, which would not have resident adults present during bad recruitment years (presumably the study period) if no immigration were occurring. This hypothesis could be tested by mark-recapture studies and observation of juveniles and adults.

CHAPTER 3:

AUDITORY RECRUITMENT CUES

Investigation of sound as a recruitment cue in Schindleriidae (Teleostei: Gobioidei) and larval fishes

Manuscript

by

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ABSTRACT

The lack of knowledge concerning the pelagic stage of larval reef fishes is one of the major hurdles being faced in population studies of reef fishes, design of Marine Protected Areas, fisheries management, and other related fields. Experimental data regarding the cues (chemical, visual, auditory) that larval fishes may use to recruit to an area have only been examined in the last 25 years. Light and light and sound traps were deployed in Kane‘ohe Bay, O‘ahu, Hawai‘i to test the usage, by larval fishes and progenetic *Schindleria*, of sound as a recruitment cue. Nocturnal patch reef sounds were recorded and broadcast using an underwater speaker, an amplifier, a 12V rechargeable battery, and a continuous play tape player (all encased in underwater housing). For both the light and the light and sound traps, a collection bucket was located at the bottom of the trap. Permanent anchor lines were set over sand bottom, at least 40 m from each other, and from the nearest patch reef. Traps (also included were an empty trap and a purely sound trap, both of which caught nothing), using a randomized square design, were deployed, in the Spring/Summer of 2002, 12 times at dusk and retrieved the following morning. A significant difference (p=0.058) was found between the catches of non-larval *Schindleria* in the light and light and sound traps. Surprisingly, the purely light traps caught more fishes. The same trend (p=0.13) was found in the larval shorefishes caught. Reef fishes were extremely rare in all my catches (six total), but the light and sound trap did catch, though not significantly, more larvae than the light trap (p=.104). Analysis of variance (ANOVA) also showed that more *Schindleria* were caught

in the traps closer to the patch reef than those in the far positions (p=0.078). My results indicate that, in Kane'ohe Bay, non-larval *Schindleria* and larval shorefishes may be deterred from recruiting by nocturnal reef sounds, but larval reef fishes may be attracted by sound. In addition, *Schindleria* may reside in larger numbers closer to the patch reef or may need the addition of ambient patch reef sound to locate the light and sound trap.

INTRODUCTION

A currently important topic in larval fish ecology involves the recruitment cues upon which larval supply and recruitment to an area depend. Whereas many researchers conclude that larval recruitment is mainly a function of physical ocean properties (currents, eddies, temperature, tradewinds) (Lobel 1989; Blaxter 1992; Thorrold *et al.*, 1994), others conclude that fine-scale recruitment events may be driven by visual (Kobayashi, 1989; Dufour and Galzin, 1993; Job and Bellwood, 1996), auditory (Stobutzki and Bellwood, 1998; Tolimieri *et al.*, 2000), chemical (Sweatman, 1988), and/or electromagnetic cues. Studies involving visual cues are common, but research on auditory, chemical, and electromagnetic cues are scarce or non-existent.

Sound may be the most important stimulus for long distance recruitment of fishes. It is detectable for 100s to 1000s of meters (more than visual, possibly less than olfactory cues) and it is multidirectional, unlike chemical cues. Reef environments are loud and, in Kane'ohe Bay, snapping shrimp are the major producers of that noise (Au and Banks, 1997). At 1 m from the source, a snap ranges between 183 and 189 dB and 2 to 200 kHz. Fishes with swim bladders (such as those in this study) are sensitive to the pressure changes of sound above 100 Hz and to the particle motion changes of sound below 100 Hz (Myberg and Fuiman, 2002). Detection of acceleration due to particle motion is accomplished in the sac-like organs in the inner ear that contain the otoliths. Different hair cell bundles are scattered throughout the organ and fishes can detect the direction of sound based on which hair cells are most stimulated by their associated otolith (Edds-Walton and Popper, 1995; Lu *et al.*, 1998). In fishes, hair cell numbers increase with development, but it is not known whether larvae are developmentally ready to use sound as a cue. Kenyon (1996) found that young juveniles exhibit poor sound detection and that auditory thresholds decreased rapidly with increasing age (indicating better hearing as the fish age); however, physiological and behavioral studies are not always reconciled. Stobutzki and Bellwood (1998) performed the first published behavioral field study on the use of sound by larval fishes and found that reef fishes were attracted to sound. Tolimieri *et al.* (2000) found that triplefin larvae, but not pilchard larvae, may use sound as a navigational cue. Leis *et al.* (2002) found that the damselfish *Chromis atripectoralis* could distinguish between biological and non-biological sound, but could not locate it.

MATERIALS AND METHODS

<u>*Study site:*</u> The study was conducted on the windward (eastern) side of O‘ahu, Hawai‘i in Kane‘ohe Bay, which is a shallow, multi-use area (Figure 3.1). It consists of fringing reefs, an inner lagoon area, patch reefs, and a barrier reef that is dissected by two

channels, the southern Sampan Channel and the northern Mokolii Channel. The barrier reef extends more than 5 km across the mouth of Kane'ohe Bay. Water enters Kane'ohe Bay over the barrier reef and exits out the channels. Kane'ohe Bay is subjected to small waves, tides, and wind (CRAMP; Smith *et al.,* 1981).

Sound: The shallowness of Kane'ohe Bay, the rapid increase in depth offshore of the Hawaiian Islands, and a previous study (Tolimieri *et al.,* 2000) done in deep, isolated water "using extremely high-level, ambient sounds" (Myberg and Fuiman, 2002) caused this research to focus on a more natural range of projected sound in conjunction with nearby ambient patch reef sound. Nocturnal reef sounds were recorded from a patch reef off the western end of Coconut Island using a hydrophone and a digital audio tape (DAT) recorder. The 30-minute recording was analyzed using Cool Edit (Syntrillium Software, USA) to identify the portion with the greatest frequency range (0-23kHz, Figure 3.2a) and sound pressure range (Figure 3.2 b); a three-minute segment was repeated 20 times and transferred to a cassette tape. The resulting sound was 144 dB at 1 m, approximately 15 dB louder than the ambient sound at the study site.

Trap design and placement: Four different traps were constructed: sound, light, light and sound, and empty. The two traps utilizing light were each fitted with a 6W florescent bulb and a 6V lantern battery in waterproof casing (Figure 3.3). The two traps utilizing sound were each fitted with an Aqua229 underwater speaker (Clark Synthesis Inc., USA,

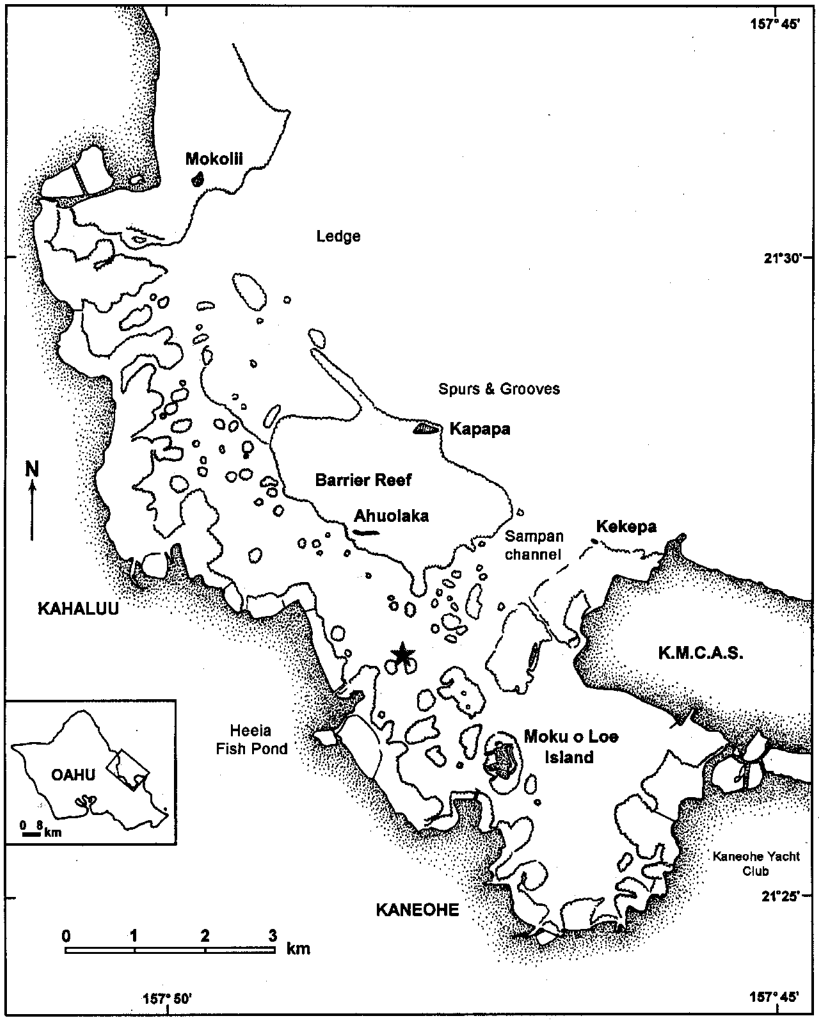

Figure 3.1 Study site: Kane'ohe Bay, O'ahu, Hawai'i. Permanent anchor lines were placed in proximity to an isolated patch reef (marked with star). Map from Greenfield (2003).

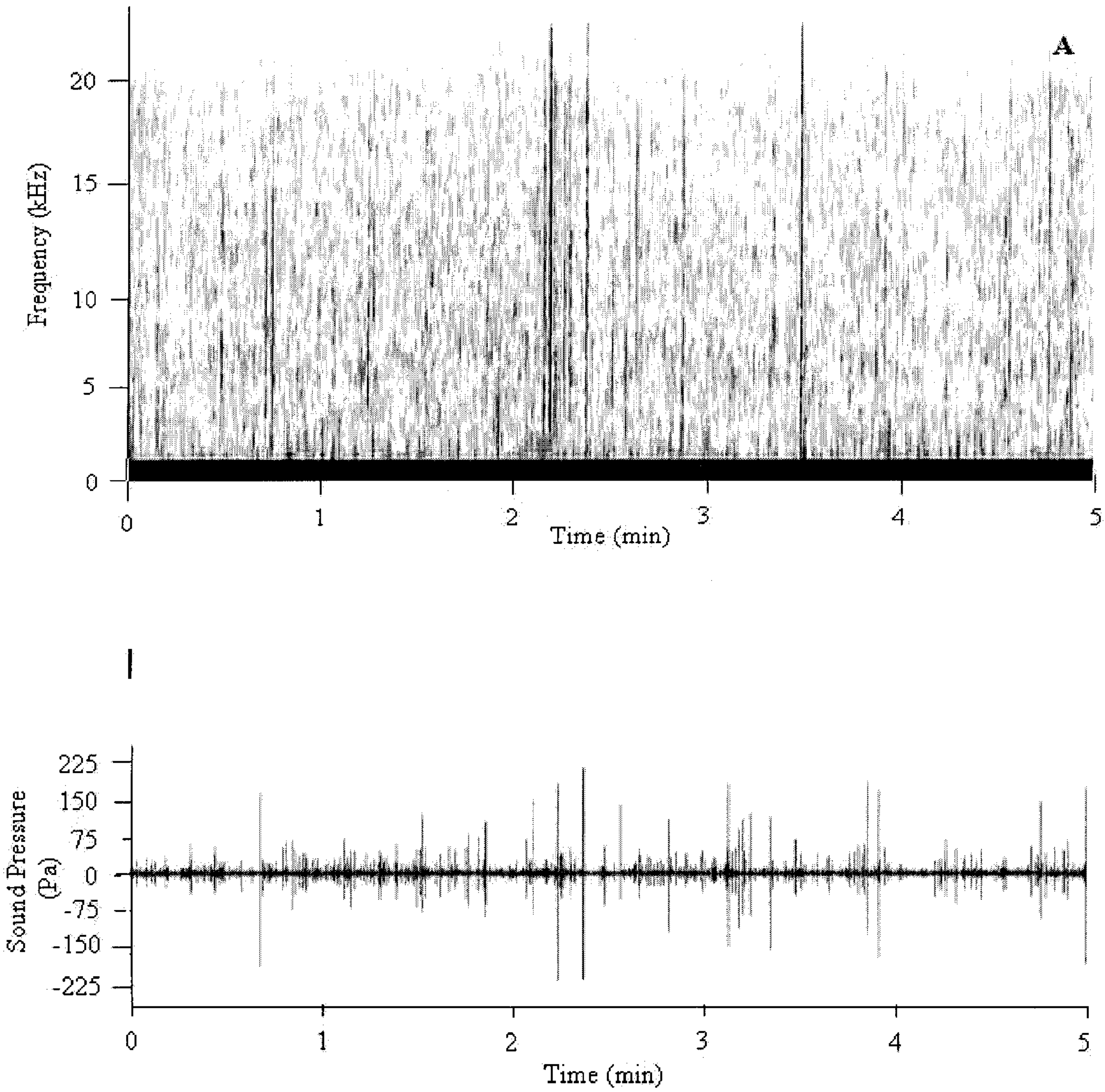

Figure 3.2 Analyses of recorded ambient sound for **a)** frequency range and **b)** sound pressure. The first three minutes were looped.

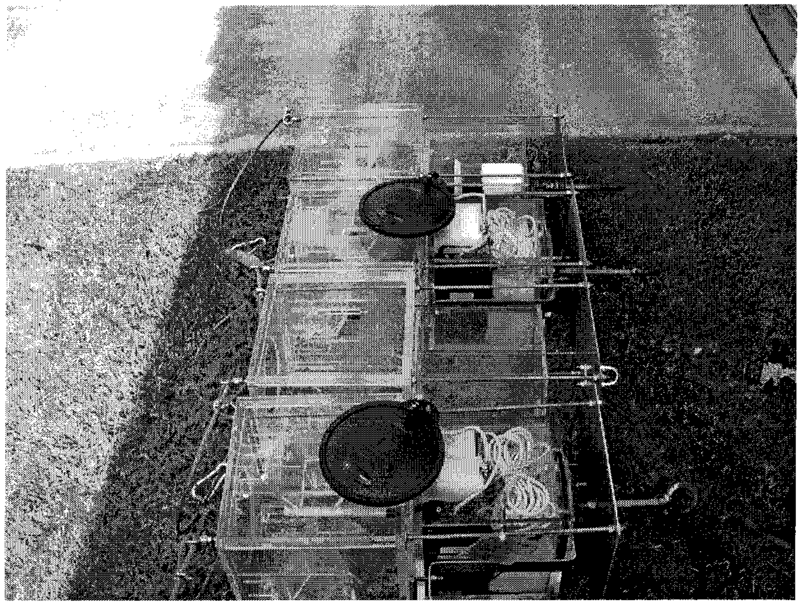

Figure 3.3 Light, sound, empty, and light and sound traps. From top to bottom: the light trap was fitted with 6W florescent bulb and 6V lantern battery in waterproof casing; the sound trap was fitted with an underwater speaker and in underwater housing: an amplifier, a continuous play tape player, and a 12V battery; the empty trap; the light & sound trap was a combination of the light and sound traps. Each trap had a collection bucket, a Plexiglas support structure with entry points for larvae, and stainless steel cable for attachment.

Clark229, 5Hz to 200KHz), and in underwater housing: an amplifier, a continuous play tape player, and a 12V battery (Figure 3.3). In addition, each trap had a collection bucket, a Plexiglas support structure with entry points for larvae, and stainless steel cable for attachment. The traps were attached, at 4m below the surface, using permanent anchor lines in a randomized 40 m X 40 m square design [each trap combination (2^{n+1}), based on proximity to the reef and to each other, was considered to minimize interactions] in the deepest (15m) area of Kane'ohe Bay. Two trap locations were 40m from the nearest patch reef and two trap locations were 80m from the nearest patch reef. All four traps were deployed before dusk and retrieved the next morning. This experiment was repeated 12 times, throughout the lunar cycle, between 30 May and 2 September 2002.

Unfortunately, on the first trap deployment, the light trap was lost (or stolen), so an alternative trap design was used (design by D. Kobayashi, National Marine Fisheries Service Honolulu Laboratory, with my own modifications; based on an earlier design by Floyd *et al.*, 1984) and both versions of the light trap were randomly tested for bias. Over six nights (between 17 September and 9 October), the two traps (the light trap used in the study and the light and sound trap without the sound) were deployed, over a patch reef abutting Coconut Island, Kane'ohe Bay, before dusk and retrieved the next morning.

Species identification: Collected specimens were fixed in 5% formalin, stored in 55% isopropynol, and identified to the lowest possible taxon level (Bruce Mundy, NMFS, unpublished notes; Miller *et al.,* 1979; Okiyama, 1988; Leis and Trnski, 1989; Clarke, 1992; Randall, 1998; Greenfield, 2001).

Physical factors: The Department of Oceanography at the University of Hawai'i at Mānoa deployed a Datawell Waverider buoy (Station ID #98; N 21 ° 24.900 W 157° 40.700) off the Mokapu peninsula that measured Hs (wave height in meters), Tp (peak period in seconds), Dp (mean wave direction in degrees), Ta (average period in seconds), and sea surface temperature in Celsius. The buoy recorded these data every 30 minutes and these measurements were averaged over each night of sampling. Daily tidal range from Kane'ohe Bay (in cm) data was provided by the University of Hawai'i at Mānoa Sea Level Center; because the traps were left out overnight, the ranges of the two calendar dates were averaged.

RESULTS

Species collected: The catches of the 12 nights of sampling amounted to 74 *Encrasicholina purpurea*, 3 *Spratelloides delicatulus*, 5 *Atherinomorus insularum*, 58 *Schindleria pietschmanni, 1 Schindleria praematura,* and 1 *Apogon* sp. in the light trap catches and 46 *Encrasicholina purpurea, 7 Spratelloides delicatulus,* 1 *Atherinomorus insularum,* 17 *Schindleria pietschmanni*, 2 *Apogon* sp., 2 *Asterropteryx semipunctatus*, and 1 unknown reef fish in the sound and light trap (Figure 3.4). The empty trap and the purely sound trap never caught any fishes.

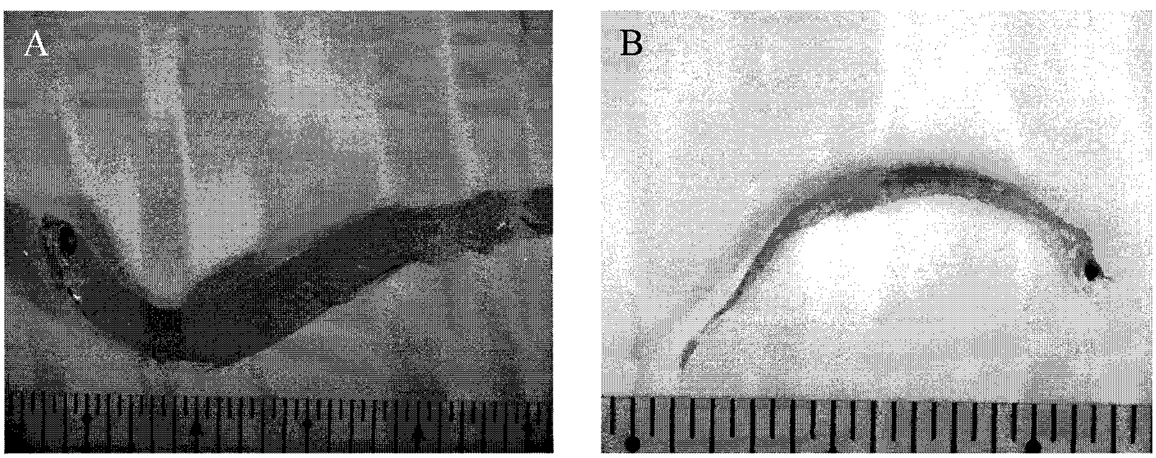

Figure 3.4 Most common fishes caught **a)** *Encrasicholina purpurea* larva **b)** *Schindleria pietschmanni* gravid adult female

Effect of sound: Thirty-seven percent of the light trap catch of *E. purpurea* was caught in one night and 91% of the sound trap catch of *E. purpurea* was caught in a single night (28 August and 2 September respectively; Figure 3.5a). The variable nature of larval shorefish (*E. purpurea*, *S. delicatulus*, *A. insularum*) catches led to non-normal data. A nonparametric test, McNemar's presence/absence Chi-squared test, was used to determine the use of sound by shorefishes. Of the 12 nights, shorefishes were caught in both the light and the light and sound traps three times, no shorefishes were caught in either trap during five samplings, and shorefishes were caught in only the light trap on four occasions. There were no instances were the light and sound trap attracted shorefishes and the light trap did not. The McNemar's presence/absence test ($X^2 = 2.25$, $p=0.13$) did not show significance at the $\Delta=0.05$ level, but this is due to the small sample size (again because of the highly variable catch, specifically the common no-catch nights).

Adult *Schindleria,* a cryptic, progenetic genus, were also caught; only one *Schindleria praematura* was identified from the catches and it was included with the *S. pietschmanni* for analysis. The numbers of these fishes caught were normally distributed throughout the randomized sampling period, so a paired t-test was used (Figure 3.5b). A difference was detected between the catches of the light trap and the light and sound trap with significantly ($p=0.058$) more fishes attracted to the light trap.

Although only six reef fish larvae (*Apogon* sp. and *Asterropteryx semipunctatus)* were caught on three nights during the sampling period, these catches were normally distributed (Figure 3.5c). A paired t-test demonstrated a significant difference ($p=0.104$) at the $\Delta=0.1$ level with these specific reef fish larvae being more attracted to the light and sound trap than to the purely light trap.

As mentioned in the methods, the original light trap was lost or stolen during its first deployment. A different design of light trap was substituted and an experiment was conducted to test trap effect. Five *Apogon* sp. and one *S. pietschmanni* were caught in the soundless light and sound trap, and two *Apogon* sp. and one *S. pietschmanni* were caught in the light trap. The data were normally distributed and the paired t-test showed no significant difference between the trap catches ($p=0.415$).

Physical factors: A multiple regression was used for total catch versus all the physical factors. None of the measurements of physical factors, including wave height, peak wave period, wave direction, average wave period, sea surface temperature, and tidal range, explained any of the variation in my catches of any species.

Distance from reef: Although a randomized design was used so that no bias existed in trap location, an analysis of the catches of the traps in the near versus far positions in relation to the patch reef was conducted. The catches of larval shorefishes and reef fishes showed no significant difference in near/far position catches; however, 58 *Schindleria* were caught in the near position and 18 were caught in the far position (Figure 3.6). The two-way ANOVA using log- transformed data, trap type, and trap position showed more fishes in the near position catches than in the far position catches ($p=0.078$).

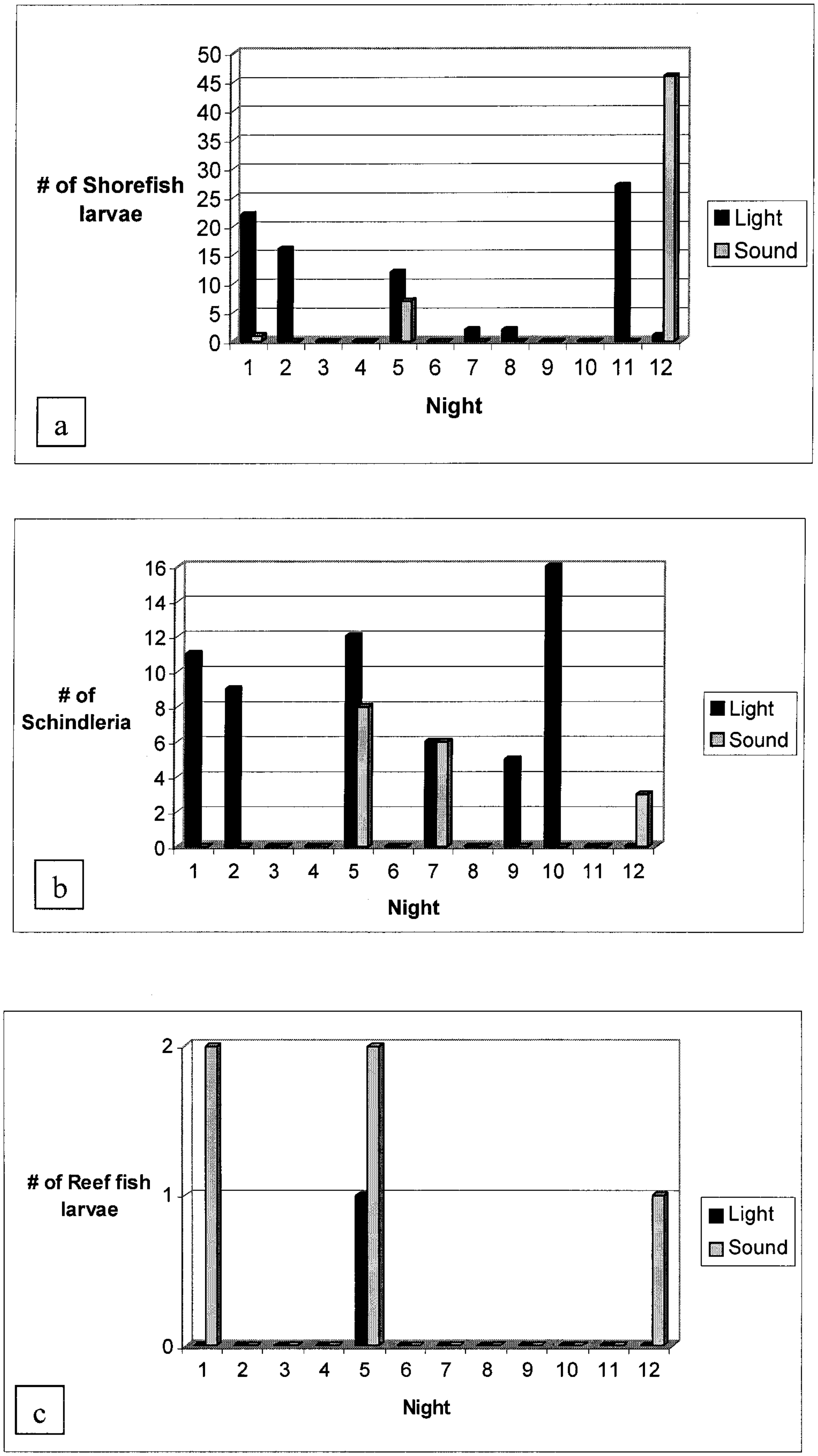

Figure 3.5 Abundance of fishes caught each sampled night for **a)** shorefish larvae **b)** *Schindleria* and **c)** reef fish larvae. Nights are 1-12 and the traps are paired as light and sound (and light).

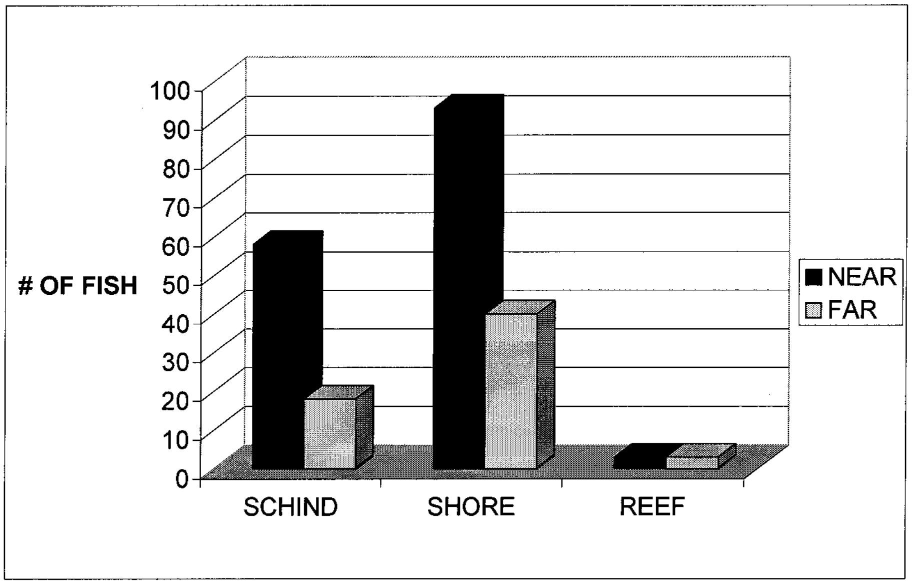

Figure 3.6 Total number of fishes caught in traps closest to the patch reef (40m) vs. farthest from the patch reef (80m) for *Schindleria,* larval shorefishes, and larval reef fishes. The differences in catch were not significant for larval shorefishes (highly non-normal data), and for larval reef fishes, but did show a trend (p=0.078) for *Schindleria.*

DISCUSSION

The foremost conclusion to be drawn from this study is the paucity of late-stage, photopositive fish larvae in Kane'ohe Bay (and Hanauma Bay as found in Whittle, in prep.). Whereas 136 shorefish larvae and six reef fish larvae were caught in 12 nights, Tolimieri *et al.* (2000) caught 15,648 pilchard larvae and 650 triplefin larvae in 14 nights (28 samplings). Kane'ohe Bay has a high retention probability with a flushing rate of eight to 13 days (Smith *et al.,* 1981), but there still were few late-stage larvae caught.

Light trap studies have been attempted, unsuccessfully due to lack of catch, by several other researchers in Hawai'i: J. Stimson, R. Kinzie, NMFS lab. The primary factor influencing the low light trap catch numbers in Hawai'i might be the absence of species that are caught in large numbers in other places: species of *Pomacentrus*, *Lethrinus*, *Siganus*, *Chrysiptera*, *Neopomacentrus*, *etc*. (Leis, pers. comm.)

The hearing ability of *Schindleria* is unknown, as is most of its ecology and physiology, but *Schindleria* were significantly more attracted to traps without sound and shorefish larvae showed the same trend, though it was not significant. These findings indicate that sound is a deterrent for *Schindleria* and shorefishes (when recruiting to an area). The patch reefs of Kane'ohe Bay are noisy and provide habitat for possible predators. The six reef fish larvae that were caught did show a preference for the light and sound traps, which concurs with previous studies (Tolimieri *et al.*, 2000; Leis *et al.*, 2002; Meekan, pers. com.). Sound may be an important cue that larval reef fishes use to recruit to a habitat; however, Leis *et al.* (2003) did find variability in the attractiveness of sound to coral reef fish larvae, even within species, depending on location and time. Also, *Schindleria* adults, when reef-associated, live closer to the patch reefs and therefore are more likely to be in contact with the near position traps. The near trap positions were still 40m away from the closest patch reef, a long distance for a 2cm fish.

This study purposely focused on natural sound levels. A. Myrberg (pers. comm.) hypothesized that sound emitting from a trap would need to be 15dB above ambient noise for fish larvae to detect it, but he also suggested that larvae are probably "stone deaf."

This hypothesis has been contradicted by field studies (Tolimieri *et al.*, 2000; Leis *et al.*, 2002) and this present study demonstrates that sound traps operating at the lower boundary of the loudness spectrum are still effective, as shown by the significant difference in *Schindleria* catch and the trends for larval shore and reef fishes. Leis *et al.* (2003) also found low-level sound (10 dB above ambient at 3m) to be effective. Continued research involving the volume of sound, the type of sound, and the distance of detection should be undertaken.

CHAPTER 4:

ECOLOGY OF SCHINDLERIIDAE

The life history strategy of Schindleriidae (Teleostei: Gobioidei)

Manuscript

by

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ABSTRACT

The cryptic, progenetic genus *Schindleria,* with its two species *S. pietschmanni* and *S. praematura* in Hawaiian waters, has little known about its life history. This research used histology and otolith analyses to ascertain age-growth differences between species and sexes, and the effect of temperature on growth. The otoliths of 148 *S. pietschmanni* and 24 *S. praematura* were analyzed; 74 of the former and 17 of the latter were sexed. In both species, females were significantly ($p=0.007$, $p=0.001$) larger, but they were not significantly older nor did they grow significantly faster within the range examined. For *S. pietschmanni* temperature was negatively related to size ($p=0+$). Size and age were not significantly related, but this was probably due to the limited life history stage examined: all fishes were sexually mature. The most important result of this study was the discovery of the high growth rate for both species: *S. pietschmanni* grew an average of 0.72 mm/day [with a maximum measured total length (TL) of 17.3 mm] and *S. praematura* grew an average of 0.60 mm/day (with a maximum TL of 24 mm).

INTRODUCTION

Gosline and Brock (1960) said of *Schindleria*: "It is almost impossible to see them in the water… they occur in great numbers near the surface around Hawai‘i…indeed, it is not impossible that they are the commonest Hawaiian fishes." Yet little is known about these, possibly, most abundant fishes in Hawai‘i. Cryptic species make up a large portion of the fish diversity, and possibly the energy budget, on reefs (Munday and Jones, 1998; Greenfield, 2003), but they are largely ignored. *Schindleria pietschmanni* is the lightest vertebrate in the world (Bruun, 1940) and, with its congener *Schindleria praematura,* part of its life history is examined in this paper. The genus is progenetic (Kon and Yoshino, 2002a) and is abundant in Hawaiian waters: Watson and Leis (1974) ranked *S. pietschmanni* second in overall abundance with catch being 15.72% of the total in their tows in the Sampan Channel, Kane‘ohe Bay, O‘ahu. S*chindleria praematura* was ranked seventh in overall abundance and was 3.26% of the total in the same location; however, in South Kane‘ohe Bay, *S. pietschmanni* only comprised 0.68% of the total catch and *S. praematura* was only 0.12%.

Schindleria was first identified by Otto Schindler (from Northwest Hawaiian Islands specimens given to him by Victor Pietschmann) in 1932. Schindler identified the fishes as hemiramphids, but, in 1934, Giltay reclassified the fishes as a new family, Schindleriidae. The two species differ in number and position of dorsal and anal fin rays: *S. pietschmanni* (D: 17-18, A: 16-17) has even dorsal- and anal-fin origins, *S. praematura* (D: 18-22, A: 11-14) has a dorsal fin that begins in advance of the anal fin (Jones and Kumaran, 1964). The gut length of *S. pietschmanni* is approximately less than 60% of its total length and is greater than 60% of the total body length in *S. praematura.* Both species have a prominent gas bladder and a unique elongate caudal peduncle (Miller *et al.,* 1979).

Further analysis of this genus has, until recently, focused mainly on its phylogeny (Gosline, 1959; Johnson and Brothers, 1993; Thacker, 1993) which revealed that Schindleriidae lies within the suborder Gobioidei. Thacker (1993) concluded that *S. pietschmanni* was the more derived form because it is smaller and therefore has an "even more extreme paedomorphic condition." Thacker noted that Schindler's species fell into two groups with the females and *S. praematura* being larger (males 11.5-17 mm, females 15-20 mm; males 14-18 mm, females 18-22.5mm); however, no otolith work has been performed to determine age-growth curves for the two species, growth differences between the sexes, and how temperature affects growth rate. Kon and Yoshino (2002b) used otolith analysis to determine age at maturity of one species (see below) of *Schindleria*. They found early maturity at 23-60 days. The authors also hypothesized that, during the colder months of the year, the fish will take longer to reach sexual maturity although no formal analysis was undertaken. Kon (pers. comm.) has identified nine different species of males and four species of females in Okinawa, Japan. This paper focuses on the two previously mentioned described species.

Because of its small size, the reproductive biology of *Schindleria* is known primarily from histological studies or anecdotal evidence. Schindler (1932) first noted the presence of mature oocytes in females of *S. pietschmanni* and the presence of a secretory testicular gland in males. This structure is shared with gobies and would later secure the placement of *Schindleria* within the Gobioidei (Johnson and Brothers, 1993). Thacker (1998) compared the gonad morphology of *S. praematura* to that of 14 other gobioids. Although gross morphology was similar, she found several differences in the gonad microstructure of *S. praematura*, which she attributed to the paedomorphic development of the species, including a reduction of stromal and interstitial tissues within the gonad, absence of visible lamellae within the ovary, and restriction of gonial cells to the anterior gonad in both males and females. The latter is most surprising, as restricted spermatogonial testes were previously known only from atheriniform fishes (Grier, 1981). Thacker also concluded that *Schindleria* are gonochorists (non-sex changers) because females lacked precursor testicular structures found in most sex changing gobies.

The spawning mode for *Schindleria* can only be speculated upon based on the morphology of the gametes. Like other gobioids, *Schindleria* have elliptical oocytes, which bear an enlarged micropyle, or egg cap, at one end. In other gobioids, this egg cap is associated with adhesive threads, which are used to attach the oocyte to the nesting substrate (Thresher, 1984). This morphology may indicate that *Schindleria* are demersal spawners, however, more definitive evidence is necessary. Regardless of spawning mode, it is probable that *S. praematura* are iteroparous (reproduce more than once during their lifetime) because their ovaries typically contain more than one size class of oocytes (Thacker, 1998).

Schindleria are attracted to light, but little else is known about their ecology. Schindleriidae are found in all marine tropical waters except the Atlantic Ocean and the Gulf of Mexico (Thacker, 1993). The family is said to "inhabit coral reefs" (Kon and Yoshino, 2002b) and to be sand-dwellers (Young *et. al.,* 1986). Harris and Cyrus (1996) also pointed out that the breeding period of Schindleriidae is not known, although, in the

Ryukyu Islands, Okinawa, it appears that the generation time averages 37.1 days (Kon and Yoshino, 2002b).

This paper uses histology, otolith analysis, and temperature data to ascertain the possible age/growth differences between sexes and between species of *Schindleria*, and the effect of temperature on growth. Batch fecundity and its correlation with body size, possible location of spawning, a review of gonad morphology, and new morphological characteristics are also discussed.

MATERIALS AND METHODS

Collection: In Hanauma Bay, light traps [design by D. Kobayashi, National Marine Fisheries Service (NMFS) Honolulu Laboratory, with my own modifications; based on the earlier design by Floyd *et al.*, 1984] fitted with a 6W florescent bulb, a 6V lantern battery, and a collection bucket were constructed and anchored using 30 kg weights and stainless steel cable. The samplings occurred at various bottom depths and locations. Using scuba, and carabineers, the light traps were moored within 3 m of the surface. The light traps were deployed 0-4 nights a month, between 14 December 1999 and 31 July 2002, during various phases of the moon. Each morning following deployment, the trapped *Schindleria* were placed in fresh water and frozen.

Fishes collected from Hanauma Bay were used for otolith analyses, but were too degraded for histological work, so three tows were done in the Sampan Channel of

Kane'ohe Bay (N 21 ° 25' W 157° 47') on 27 April 2003, 11 May 2003, and 15 June 2003. Fishes were collected using a 1 m, 505 Πm plankton net towed, 1-3 m deep, behind a 17 ft Boston whaler at 2-3 knots. All tows occurred between 1930 and 2230 hrs and lasted 15 to 20 minutes each. After each tow, the contents of the nets were chilled in cold brine and stored on ice until processing.

Schindleria were identified using a key provided by Bruce Mundy, NMFS Honolulu Laboratory, (modified from Watson *et al.,* 1984; Watson, 1989), and photographed with a digital camera affixed to a dissecting scope. Three body lengths were measured for each specimen. Standard length (SL) was measured as the distance between the tip of the snout and the caudal fin base, total length (TL) was measured as the distance between the snout and the distal tips of the caudal fin rays, and pre-anal length (PAL) was measured as the distance between the snout and anal-fin insertion. Dorsal and anal fin positions were also noted. All measurements were rounded to the nearest 0.5 mm.

Histology: The head of each specimen was removed and frozen for aging and the remaining trunk portion was fixed in buffered formalin (3.7% formaldehyde in seawater). Individuals that contained visible oocytes were classified as females and set aside for batch fecundity measurements (below). All other individuals were decalcified with Cal-Ex (Fisher Scientific), dehydrated in a graded ethanol series, and embedded in glycol methacrylate resin (JB4 Kit, Electron Microscopy Sciences). Cured methacrylate blocks were sectioned at 2-5 um on a microtome fitted with a glass knife. Sections were affixed to glass microscope slides, stained with toluidine blue, and examined for the presence of testes (males) or ovaries (females). Ovaries were classified according to Wallace and Sellman (1981). Testicular tissue was classified according to Nagahama (1983).

Batch fecundity was estimated using the oocyte size-frequency method (Privatera, 2001), assuming the largest mode of oocytes formed the next spawning batch. The relationship between fecundity and SL was evaluated using linear regression analysis.

Otolith work: The sagittae were removed and mounted on glass slides using thermoplastic Crystal Bond (Aremco Products, USA). The increments were counted using transmitted light at 400X on a Zeiss Axioskop compound microscope, a digital camera, and were analyzed using image software (Image 1.47, National Institutes of Health, USA) (Shafer, 2000). Each otolith was independently counted by two persons and the counts were compared. If there was a discrepancy in the counts, the saved images were examined for differences, and a final count was agreed upon.

Buoy: The Department of Oceanography at the University of Hawaiʻi at Mānoa has a data-collecting buoy off the Mokapu peninsula (Station ID #98; N 21 ° 24.900 W 157° 40.700). This buoy recorded sea surface temperature in Celsius degrees every 30 minutes and these measurements were averaged for each day. The age of the fish and date of collection were used to back-calculate the average temperature for the life of each fish.

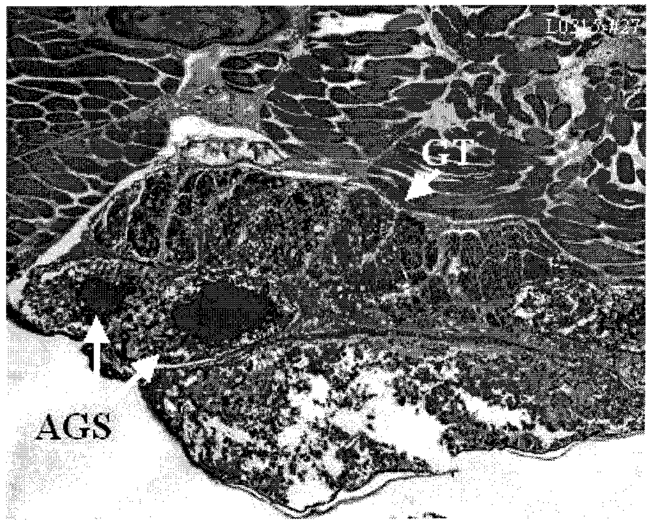
RESULTS

Collections: The light trap collections in Hanauma Bay yielded 3638 Schindleriidae, but only 129 could be used for otolith analysis; the plankton tows in Kane'ohe Bay collected 100 specimens, which were all used for otolith and sexing analysis. The otoliths of 148 *S. pietschmanni* were analyzed; 62 of these were collected using a plankton net and 74 were identified by sex. The otoliths of 24 *S. praematura* were analyzed; 23 of these were collected by plankton net and 17 of these were identified by sex.

Gonad morphology: Thacker provides a thorough review of gonad morphology for both *S. pietschmanni* (1993) and *S. praematura* (1993; 1998). Herein we briefly illustrate gonad morphology of male and female *S. pietschmanni*. Males of both species have testes that are divided into a dorsal geminal portion and a ventral testicular gland (Figure 4.1a). The geminal portion of the testis is lobular, consisting of a series of blind-ended tubes that are subdivided into spermatocysts [spermatocysts are the basic unit of spermatogenesis in vertebrates, consisting of germ cells (spermatogonia, spermatids, or spermatozoa) encapsulated by sertoli cells]. In reproductively active males, spermatocysts showed anterior to posterior trends in development; the most anterior cysts typically contained less-developed germ cells whereas those posteriad contained tailed spermatozoa. In some individuals, spermatocysts were completely absent from the posterior portion of the testis, which instead contained copious amounts of free spermatozoa. The testicular gland did not contain spermatogenic tissue. Instead, it consisted of hollow tubules of secretory epithelium. In many males, the lumen of the testicular gland contained a large mass of darkly stained acellular material (Figure 4.1b).

In females, two populations of oocytes were apparent in ovaries of both *S. pietschmanni* and *S. praematura*. These oocytes differed in size (Figure 4.2a) as well as developmental stage (Figure 4.2b, Figure 4.3), thus both species demonstrate group-synchronous oocyte development, the most common profile for oocyte growth for teleost fishes (Wallace and Sellman, 1981). Only one population of vitellogenic (yolked) oocytes was apparent in either species, indicating that the spawning clutch is recruited directly from previtellogenic stages. Mean batch fecundity was 20.4 in *S. pietschmanni* and 44.3 in *S. praematura* and was not correlated with body length in either species (Table 4.1).

Sex, age, and size: Validation was attempted on the genus, but the fishes did not survive more than a few hours; however, the increment widths were similar to those of other larval fishes. A General Linear Model (GLM) revealed that the size and growth rate of individuals of *S. pietschmanni* differed significantly between plankton net tows and light trap catches with individuals from plankton tows being significantly larger and having a higher growth rate (p=0+, p=0+; Figure 4.4), but the fish were not significantly older (p=0.107). Of the 62 individuals of *S. pietschmanni* collected with a plankton-net, 41 were females, 11 were males, and 10 could not be identified to sex. Males ranged in size from 14-17 mm and females were 14.1-17.3 mm. Females were significantly larger than males (p=0.007), but males and females did not differ significantly in age or growth rate (p=0.872, p=0.342).



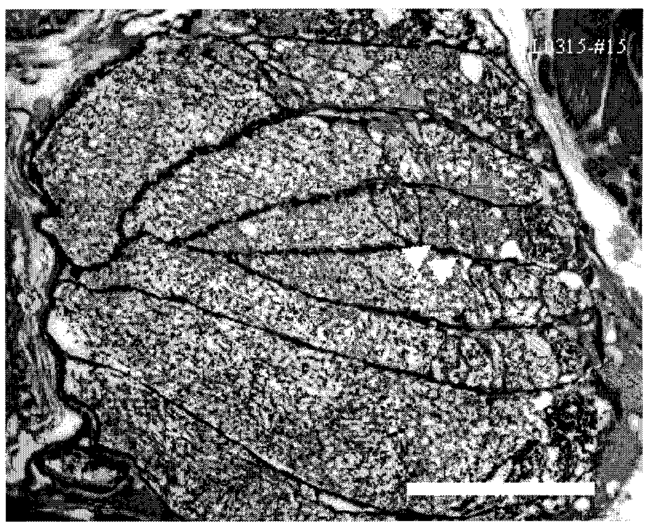


Figure 4.1 a) Transverse section through the gonad of a 13mm male *S. pietschmanni.* Geminal portion of testis (GT) overlies accessory gonadal structure (AGS) which contains dark mass of secreted material. **b)** Sagittal section through geminal portion of testis of a 14mm *S. pietschmanni.* Spermatocysts (arrows) occur in a single row throughout the anterior testis (right side of photo). Posterior testis (left side of photo) contains free spermatozoa. Scale bars are 100 ΓΙm.

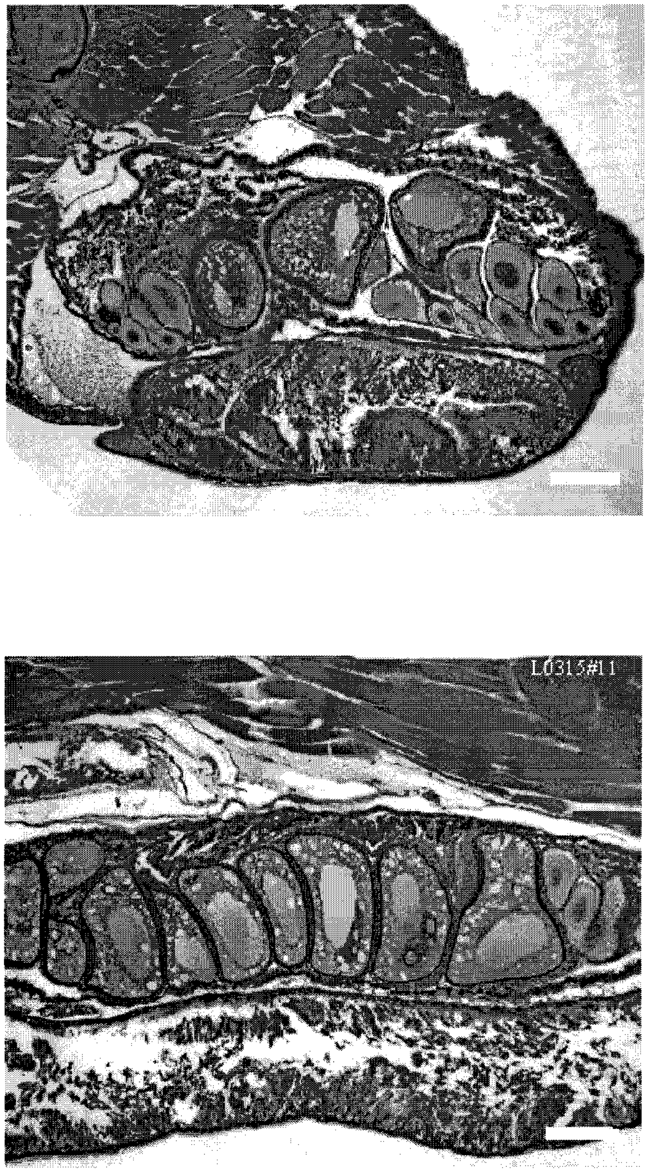


Figure 4.2 a) Transverse section through the ovary of a 14mm *S. pietschmanni* containing both cortical alveolus (CA) and primary growth (PG) stage oocytes. **b)** Sagittal section through the ovary of a 14.5 mm S. pietschmanni. Larger oocytes occur in a single series. Scale bars are 100 Πm.

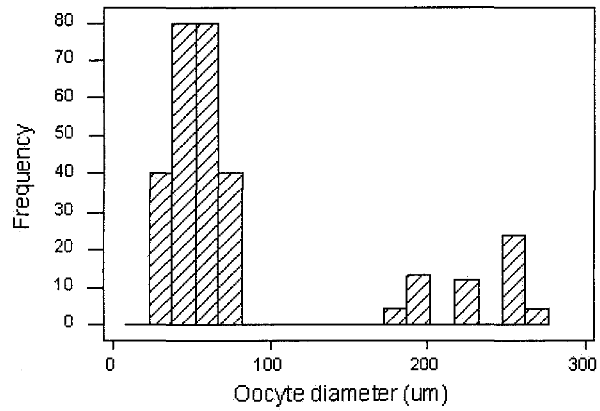


Figure 4.3 Size frequency distribution of oocytes for a 20.8 mm *S. praematura.* Bars to the left indicate primary growth oocytes, whereas those to the right indicate those in cortical alveolus stage. We estimate a batch fecundity of 57 oocytes for this specimen. Scale bar is 100 Πm.

Table 4.1 Batch Fecundity

N	**Mean**	**Min**	**Max**	**SD**	**SL vs. BF**	
23	20.4	14	29	3.9	P = 0.449	*S. pietschmanni*
3	44.3	36	57	11.2	__	*S. praematura*

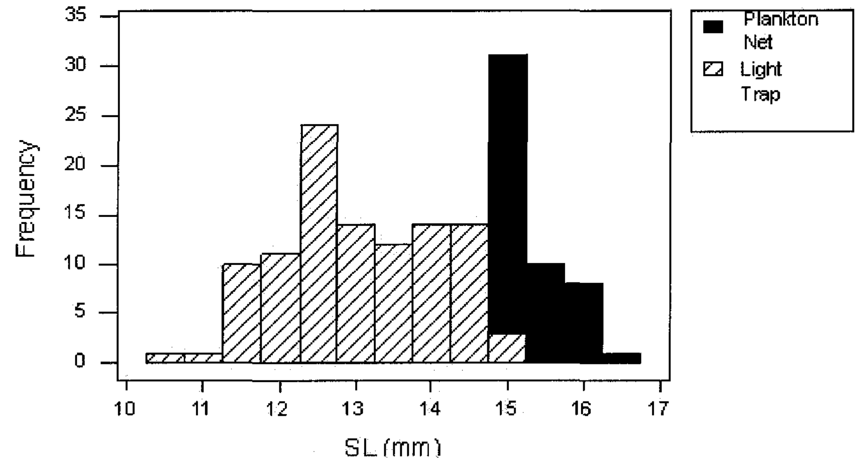


Figure 4.4 Size frequency distribution of SL for individuals of *S. pietschmanni* collected in light traps (hatched bars) and plankton tows (shaded bars). Specimens caught in plankton tows were significantly larger than those from light traps.

Of the 23 individuals of *S. praematura* collected with the plankton net, 9 were males, 8 were females, and 6 could not be identified to sex. Males ranged in size from 18-21 mm and females were 18.5-24 mm. A GLM showed that females were significantly larger (p=0.001), but not older (p=0.066) nor did they have a higher growth rate (p=0.236).

Regression analysis: A regression of size on age and temperature, with an indicator variable for sex, was used for the *S. pietschmanni* caught by plankton tows in Kane'ohe Bay (52 fish). Total length was regressed against sex, age (in days), and average lifetime sea surface temperature (in Celsius degrees). Size of the fish was not related to age (p=0.985) or temperature (p=0.128), but it was significantly related to sex (p=0.001) with females being larger (Figure 4.5). All of the fish were not sexed and a regression on the entire data set (148 fish) revealed that temperature was significantly negatively related to size (p=0+) and age was significantly positively related to size (p=0.02) when sex was not included, but the R^2 (adjusted) for this regression was only 11.3%.

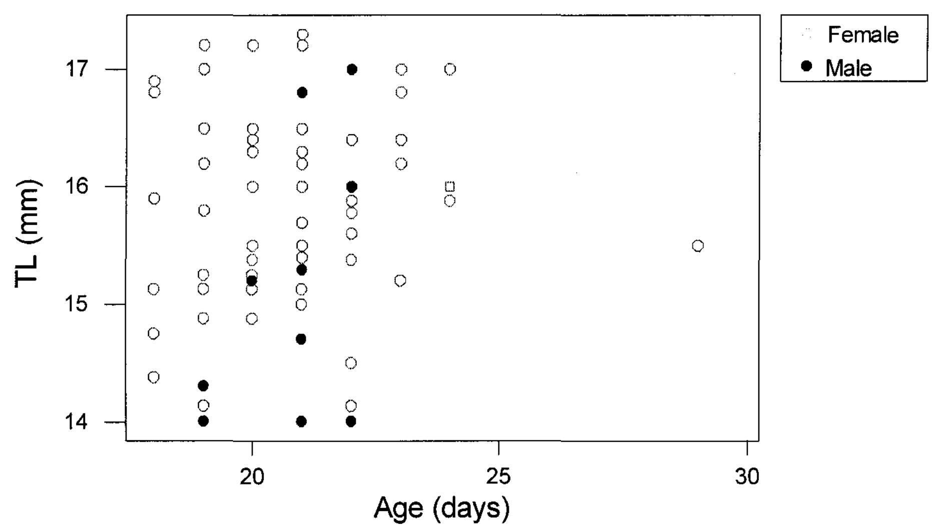


Figure 4.5 Plot of size on age in relation to sex for *S. pietschmanni*. No significant relationship existed between size and age, but females (open circles) were significantly larger than males (closed circles).

The analysis for *S. praematura* did not include the lifetime temperature of the fish because there was very little variation in this measurement. The regression of total length on age and sex revealed that size is significantly related to sex (p=0.039) with females being bigger than males, but that age is not related to size (p=0.514) (Figure 4.6).

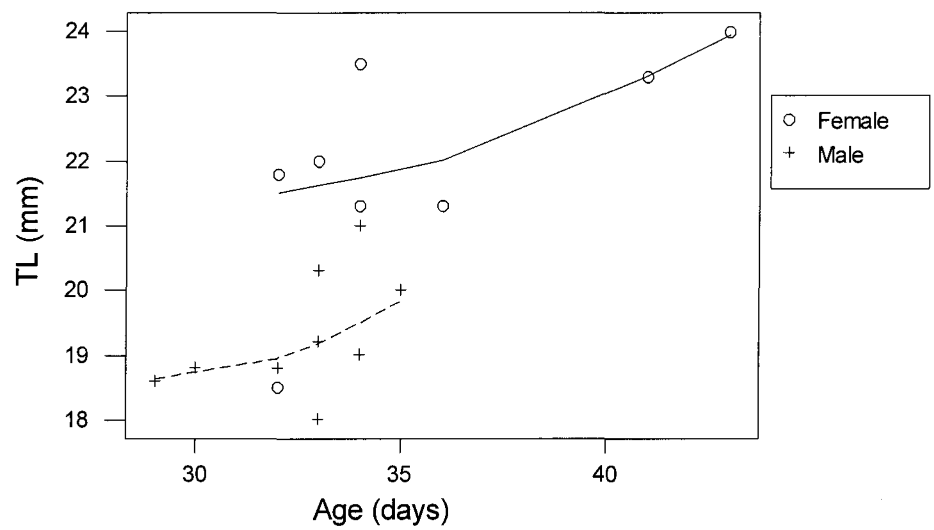


Figure 4.6 Lowess lines for the significant difference between males (crosses) and females (circles) when size was regressed on age and sex in *S. praematura.*

<u>*Growth rate:*</u> The average growth rate for all *S. pietschmanni* was 0.72 mm/day; females grew 0.76 mm/day and males grew 0.72 mm/day (remember, tow specimens were significantly larger). The average growth rate for fish caught in light traps in Hanauma Bay was 0.69 mm/day and for fish caught in plankton tows in Kane'ohe Bay was 0.76 mm/day. The average growth rate for *S. praematura* was 0.60 mm/day; females grew 0.62 mm/day and males grew 0.60 mm/day (remember, tow specimens were significantly larger). A regression of growth rate on temperature for *S. pietschmanni* revealed that fish grew significantly slower at higher temperatures (p=0+) (Figure 4.7).

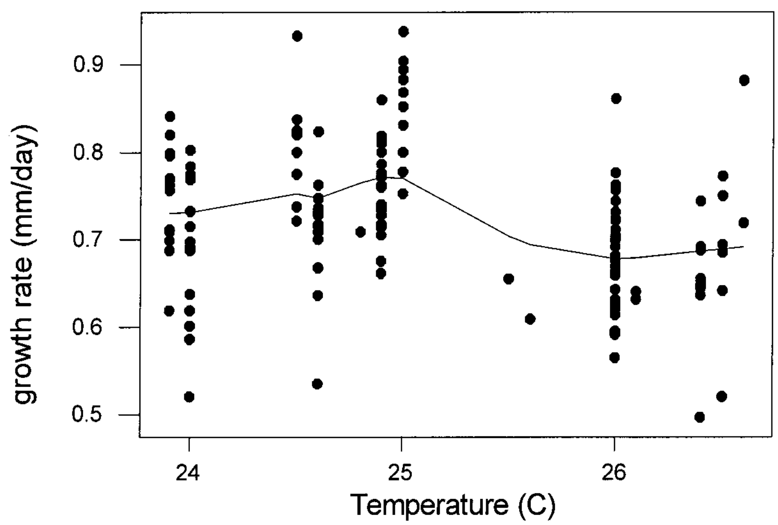


Figure 4.7 Lowess line showing that temperature was significantly negatively related to growth rate for the complete data set of *S. pietschmanni.*

Otolith shape: The sagittae for the two species were notably different in appearance. The otoliths of *S. pietschmanni* were thicker and round in shape (Figure 4.8a). The otoliths of this species did not have an evident elongated primordium, which was one of the characters Johnson and Brothers (1993) used to place Schindleriidae within the suborder Gobioidei. The otoliths for *S. praematura* were thinner and egg- or irregular-shaped (Figure 4.8b).

Figure 4.8a) Distinctively round sagittus of 15.7mm *S. pietschmanni,* aged 21 days. **b)** Egg-shaped sagittus of 18mm *S. praematura,* aged 33 days. Scale bars are 10 Πm.

DISCUSSION

The large size of collected fishes could have been caused by sampling bias, with the smaller individuals extruded through the 0.5 mm mesh and also not attracted to light, or because *Schindleria* may only be reef-associated when they are reaching sexual maturity (the second smallest *S. pietschmanni* was ripe). The age and size of juveniles could not be assessed, so no age-growth curves could be determined. The data had a limited size range, which is evidenced by the lack of significance for both species for the TL/Age regressions (Figure 4.9a-b).

Both species had two populations of eggs present and eggs had a cap indicating demersal spawning. The egg morphology of the eggs found inside a worm tube, and the number of myomeres (muscle segments), the overall body shape (especially the body depth), the PAL, and the straight intestinal primordium of the embryos were all characteristic of *S. pietschmanni* (Bruce Mundy, NMFS; Watson and Leis, 1974; Figure 4.10). Even based on a small sample size for *S. praematura,* batch fecundity was more than twice that for *S. pietschmanni*, but there was absolutely no size overlap between the species with *S. praematura* always being larger.

Earlier work by Thacker (1993) suggested that females were bigger than males, but no aging work was done to determine if females were simply older. In this study, the range of TL for both males and females was almost identical for both species, but the regressions (TL on age and sex) both revealed that females were significantly larger than

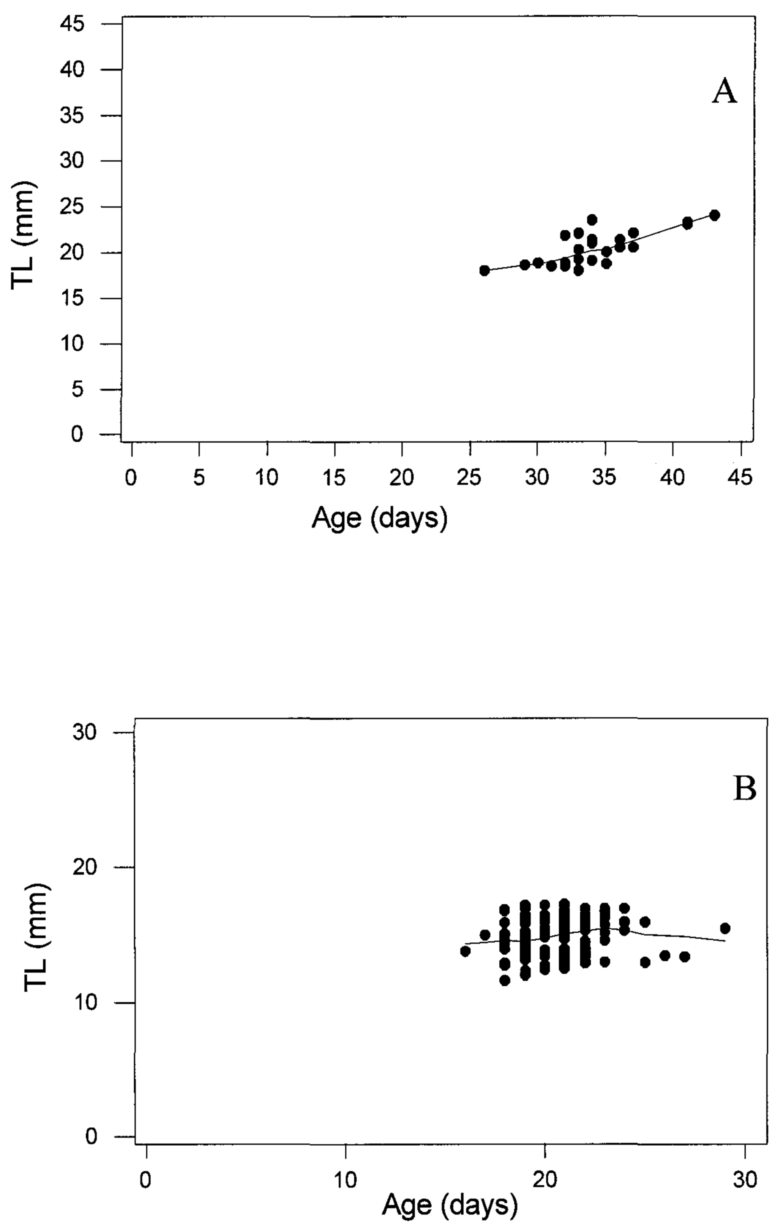


Figure 4.9 The limited age-growth curves for **a)** *S. praematura* and **b)** for *S. pietschmanni* due to collection bias toward larger fishes

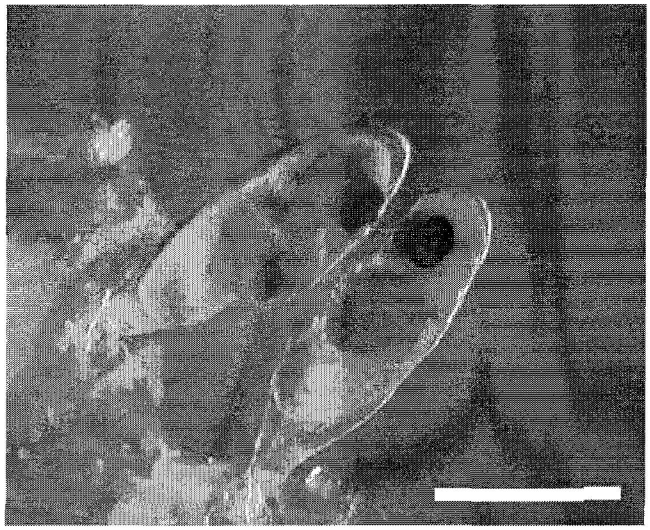


Figure 4.10 Possible *Schindleria* embryos discovered in a polychaete worm tube in Hanauma Bay by Dr. Julie Bailey-Brock. Scale bar is 500 Πm.

males. When the male and female size ranges overlapped, the fishes were of different ages. Our sampling bias prevented us from catching smaller males that were of similar age to the youngest *S. pietschmanni* female and, with exception of one individual, all the youngest *S. praematura* were males; however, the large variation in size at age and our conclusions may change with a less biased sampling protocol (size was significantly related to age in the full *S. pietschmanni* data set, but not in the limited, sexed data set). Only 11 males were used in the *S. pietschmanni* analyses and, in the *S. praematura* analyses, sex was almost significantly positively related to age. The fact that the females were significantly larger, but were not significantly older nor were they growing at a faster rate, does seem contradictory. A combination of age and growth rate, although correlated, may answer the contradiction; analysis on the limited size range may also have created bias. Females may have grown faster than males earlier, during the exponential growth phase, but not during the plateau phase; this hypothesis would allow for the females being larger, but not older and the overall growth rate between the species would have evened out. Temperature was negatively related to growth rate for *S. pietschmanni*. At higher temperatures, the fish grew slower. This is the opposite of what Kon and Yoshino (2002b) found and may be related to food availability, due to spring and fall tidal peaks, in Hawaiian waters.

The most important result of this work is the determination of the growth rates of these species of *Schindleria*. Both species had a high growth rate, with *S. pietschmanni* growing at 0.72 mm/day and *S. praematura* growing at 0.60 mm/day. In a study of the growth rates of demersal reef fishes, Busea (1987) found that small (<51cm) reef fishes grow up to 65% of their maximum length during year one; this translated to 0.18 mm/day for the 13cm fish and to 0.47 mm/day for the 50cm fish. Longenecker and Langston (in press) found that *Enneapterygius atriceps* (maximum size of 30 mm) grew at a rate of 0.34 mm/day. Growth rates of reef fish larvae, which would be approximately the same size as *Schindleria* adults, but in the exponential growth phase, are also comparable: 0.34-0.37 mm/day for *Stegastes partitus* (Sponaugle and Cowen, 1996) and 0.63-0.73 mm/day for *Halichoeres maculipinna* (Sponaugle and Cowen, 1997). The rapid growth of *Schindleria* agrees with the conclusion of hypomorphy by Kon and Yoshino (2002a).

Future research should focus on a obtaining and analyzing a full size range of *Schindleria*; a growth rate estimate from a non-linear model may be even higher.

Thacker (1993) described one “aberrant” adult female *S. praematura* with “red pigment spots along the ventral body surface.” In examining specimens from our plankton tows, we found 26 specimens with this pigment pattern, although the color was orange and not red. The specimens included both species, sexes, and the entire sampled size range. Observation of otolith shape was a reliable character distinguishing the two species; this morphological character could be used for species identification (Figure 4.8a-b).

CHAPTER 5:

SUMMARY AND CONCLUSIONS

Larval fish ecology in Hawai'i is still largely unexplored, but this study has contributed to the understanding of which factors may affect larval supply of photopositive species to an area. There are certainly fewer fish species in the Hawaiian archipelago than in the western Pacific [approximately 680 (420 inshore) species versus 2800; Kay, 1994; Helfman *et al.,* 1997], and never before have similar light trap studies been done in Hawai'i. These results allow for the general comparison of catches in Hanauma and Kane'ohe Bays to those of higher diversity locations throughout the world. The conclusion is clear; there were few late-stage, photopositive larvae at these two sites during the study period. Many photopositive fish families, including Synodontidae, Mullidae, and Acanthuridae (Bruce Mundy, NMFS, unpublished notes), are found in Hanauma Bay (Brock and Kam, 2000; pers. obs.), but were not caught in my light traps. The reasons for the lack of late-stage, photopositive larvae in Hanauma and Kane'ohe Bays are probably complex and include the species present (Leis, pers. comm.), oceanographic patterns (currents, eddies, and/or fronts would be needed to retain larvae around the islands and rapid, long-distance currents would be needed to transport larvae from other locations to Hawai'i), lack of connectivity of Marine Protected Areas (MPAs) (more protected areas would probably produce more larvae by providing adult habitat; Randall, 1996), the patchy nature of recruitment both spatially and temporally (Walsh, 1987), and/or the ineffectiveness of light traps as a collection method in Hawai'i.

From successful research experience in Australia, Doherty (pers. comm.) advised that light traps are most effective in the top 5 m of the water column, over sand habitats, and in the lee of islands. Leis (pers. comm.) added that lagoonal samplings catch more larvae than exposed coastlines. Kane‘ohe Bay is a lagoonal area and Hanauma Bay is an exposed Bay, some traps were placed over sand habitat, and all the traps were within 5 m of the surface. The trap design was based on Floyd *et al.* (1984) and was used successfully (4,980 fishes were caught in light traps versus 994 in push seines and 83 in drift nets) by the authors in a stream. Light traps have been shown to be effective in other locations and my traps did catch fish larvae and were effective for catching *Schindleria,* but these specific traps were never tested elsewhere in the world. Anderson *et al.* (2002) found that light traps were less effective at a high current site (~10.6 cm/s) than at a low current site (~3.3 cm/s). The measured currents in Hanauma Bay were equivalent to those at the low current site. I also found that wind strength, wave height, and wave period were not significantly related to larval or *Schindleria* catch. I would not conclude that the traps were less effective during rougher periods, but this conclusion is relative because sampling was only done on days calm enough to permit shore diving. The lack of larval fish catch makes certain fine-scale distribution conclusions, like differences between species, impossible to ascertain; however, other important conclusions can be drawn from this research.

A high biomass of adults, especially of certain heavily fished species, exists in the Bay (Brock and Kam, 2000; Friedlander *et al.,* 2003) and, although this was not directly tested, these fishes probably produce a large number of larvae (i.e. a source). The paucity of late-stage, photopositive fish larvae caught in my light traps in Hanauma Bay indicates that the MPA is not a sink for these species. So, the source versus sink debate surrounding MPAs has a source example for late-stage photopositive larvae, at least during the time period studied. This study shows that large numbers of these larvae are not entering the Bay and being eaten because the trap over sand had no reef (and, therefore, predator) habitat seaward of it. However, it is possible that the small number of late-stage, photopositive larvae are preyed upon inside the Bay as the outermost traps had higher catches than those farther in, but this result was confounded by habitat type.

This research also touches on, though indirectly, another important question in reef fish ecology, at least for Hanauma Bay. The lack of recruitment of certain species would suggest that the area would be recruitment-limited for these species; however, the high number of adults of photopositive species in Hanauma Bay indicates that this conclusion is probably not true, at least for these species during the three-year study period. This hypothesis is especially relevant for short-lived species, such as Gobiidae and Blenniidae, because older conspecifics would not be able to sustain the population structure during bad recruitment years (presumably the three years of this study) without immigration. Even the species that were caught as larvae were not matched with the adult population; only two genera of larvae caught were observed in the Bay as adults by Brock and Kam (2000). They did not look at nocturnal or cryptic fishes, but they did list 107 other species not found as larvae. The populations are likely controlled by post-settlement factors such as immigration, competition, and predation, but this hypothesis would need to be tested.

In Hanauma Bay, distribution of catches was directly tested in four locations with the major differing factor being substrate type: sand, rubble, and coral, plus a mixed location that included all three of these habitats. Larval reef fishes were caught most often over sand habitat, followed by rubble, mixed, and coral. The sand, rubble, and mixed habitats were in equally deep water, near the mouth of the Bay, so water depth and nearness to open ocean currents were not factors in this comparison; however, fish larvae did have to traverse above extensive coral habitat to reach the coral location. The type of substrate available does not affect the pelagic stage of reef fish until recruitment—larvae must have a chance to settle before being eaten and sand habitat may offer a temporary refuge (Frederick, 1997; Sponaugle and Cowen, 1997). The high catches in the sand location (along with other published, similar conclusions: Milicich *et al.,* 1992; Sponaugle and Cowen, 1996; Jones *et al.,* 1999) highlight the necessity of diverse habitats being included in MPA designation because larvae may be trying to avoid predators by assembling in areas with fewer predators. Protection of these intermediate areas would guard against habitat degradation, such as point-source pollution, anchor damage, and gill netting.

The current mapping of the outer reef of Hanauma Bay was a novel endeavor as, to our knowledge, these are the first direct measurements of currents in this region of the Bay. The results confirmed the hypothesis (due to the accumulation of floating debris) that currents move towards the Witches' Brew (western) area of the Bay during all tidal phases. This current pattern would indicate that more fish larvae should be found in this area due to drift and/or accumulation (there is sand, rubble, and coral habitat present); however, light trap results comparing the catches on the Witches' Brew and Toilet Bowl (eastern) sides of the Bay do not support this hypothesis. The active swimming ability of late-stage larval reef fish can probably overcome the current patterns in the Bay (Stobutzki and Bellwood, 1994). The lack of significance (with the exception of the negative relationship between catch and wind speed) between the other oceanographic factors measured (sea surface temperature, wave height, wave direction, peak wave period, average wave period, wind direction, lunar, seasonal, tidal) and larval fish catch is also attributed to this fact, although the combination of 20 families of fishes in the analyses may also be a confounding factor. This research suggests that habitat type may be more important than small-scale physical oceanographic factors in MPA planning.

The results of the research concerning the use of sound as a recruitment cue were novel or supportive of conclusions by other studies, depending on which species were examined. The novel result, though not significant at the Δ=0.05 level due to the large number of zero catches, was that the shorefishes (*Encrasicholina purpurea*, *Spratelloides delicatulus*, *Atherinomorus insularum)* were deterred from settling by sound. These larval shorefishes can be reef-associated, but do not settle on reefs and, therefore, may avoid reefs because of predators, at this vulnerable stage. Only six larval reef fish were caught in the traps, but a difference (though not at the Δ=0.05 level) was found: more larvae were caught in the light and sound trap than in the purely light trap. This result supports the three other studies done to date on the use of sound by larval reef fishes

(Tolimieri *et al.*, 2000; Leis *et al.,* 2002; Leis *et al.,* 2003; Meekan, pers. com.); larval reef fish may use sound as a recruitment cue to find suitable habitat to settle.

The cryptic, progenetic adult *Schindleria* were abundant in my light trap catches (3600+) and, therefore, may be an important contributor to the energy budget of the study sites, especially for zooplanktivores (certain species of Pomacentridae, Apogonidae, Holocentridae, and *Sepioteuthis lessoniana*, the oval squid) because of the few number of late-stage photopositive fish larvae prey. The short lifespan (37.1 days; Kon and Yoshino, 2002b) and, therefore, high turnover rate and productivity, of *Schindleria* could also contribute to the possible importance of this genus to the energy budget. Because of the greater numbers caught, their distribution was more easily analyzed. Less than 1% of the fish caught were *Schindleria praematura,* 99% were *Schindleria pietschmanni.* In Hanauma Bay, the fish significantly preferred sand and rubble habitats and more were caught around the new moon. Both of these patterns indicate that *Schindleria* may avoid habitats and times of high predation. *Schindleria* abundance was negatively related to temperature; this pattern was confirmed by the low summer catch despite higher effort. This relationship may be related to the semi-annual tidal peaks (Merrifield, pers. comm.), which influence food availability, and current patterns which maximize retention (Watson and Leis, 1974). *Schindleria* were significantly more abundant during times of southern wave direction, which may lead to flat conditions due to the geology of the Bay, high tidal range, and (non-significantly) during lower wave days. They migrated vertically on calm nights.

In Kane'ohe Bay, *Schindleria* were significantly more abundant in the light trap than in the light and sound trap. Reef sound may be used as a deterrent for these adults. From the results of the habitat study in Hanauma Bay, *Schindleria* were more abundant over sand and rubble habitats as compared to coral and mixed habitats. They reside close to reefs, but not on them where predators are more abundant: during my sound experiment more fishes were caught in the traps 40 m from the patch reef than those 80 m from the reef. Although the hearing ability of this genus is unknown, it is possible that they need the added ambient reef noise to reach their hearing threshold (i.e., the sound emitted from the traps was too quiet); however, it is more likely that *Schindleria* adults live closer to the patch reefs and therefore are more likely to be in contact with the near position traps (40 m is still a great distance for a 2 cm fish).

The determination of age-growth curves for the two species of *Schindleria* was impossible due to the collection method used. Only reproductively mature adults were caught. For both species, females were significantly bigger than males. *Schindleria pietschmanni*'s growth was negatively related to temperature, which may coincide with the lower catches during the summer months in Hanauma Bay. This result is an unusual one and conflicts with Kon and Yoshino's (2002b) conclusion for *Schindleria* in Okinawa, but the year-round low productivity of tropical waters and the semi-annual tidal peaks may have a greater influence on food availability than fluctuations in primary productivity alone.

A possible morphological character distinguishing the two species was found: otoliths of *S. pietschmanni* were round in shape, whereas those of *S. praematura* were egg- or irregular-shaped. Finally, the most interesting result of this study was the discovery of the high growth rates of both species: *S. pietschmanni* grew 0.72 mm/day and *S. praematura* grew 0.60 mm/day. These growth rates are more than three times as fast as those of other small reef fish (Buesa, 1987). Schindleriidae have a distinct life history characteristic: they grow rapidly, reach sexual maturity early, and truncate their development.

Future directions: Future research involving late-stage larval fishes in Hawai'i should not use light traps. A different method, such as moored or towed nets, would not allow for as fine-scale assessment, but it would allow for the assessment of species that are not photopositive. Sampling should also be attempted during rougher conditions to allow for a complete picture of distribution. Research involving the larger-scale distribution of fish larvae should use otolith microchemistry, which analyzes where fish have migrated from using trace elements incorporated into the otoliths from surrounding water, and genetic analyses, which assesses relatedness of fish populations using DNA analysis. Unfortunately, the difficulties surrounding the use of light traps make the current design of sound traps ineffective too. The use of sound as a recruitment cue should involve broadcasting sound (natural and/or artificial) around a reef (natural and/or artificial) and assessing the settlement as compared to a control reef. The broadcasting of different sounds (waves, snapping shrimp, non-biological) could determine which particular element of reef noise attracts certain fish. Research in Hanauma Bay should include answers about whether it is a source and which post-settlement processes are structuring the population. Future research on *Schindleria* should include a sampling method that catches the larval and juvenile fishes: plankton towing in open ocean. The age-growth curve could then be completed. And further research on other small fishes should be done to assess how unique *Schindleria* is with its rapid growth rate.

APPENDIX 1

Table A.1 Collection by date and trap location in Hanauma Bay. TB=Toilet Bowl, WB=Witches' Brew, C=Coral, R=Rubble.

DATE	H1	H2	H3	H4	TBC	WBC	TBR	WBR
12/14/99				X				
2/29/00				X				
3/7/00				X				
5/8/00				X				
8/1/00	X	X						
8/3/00	X	X						
8/29/00	X	X						
8/31/00	X	X						
9/26/00	X	X						
9/28/00	X	X						
10/31/00	X		X					
11/2/00	X	X	X					
11/28/00	X		X					
11/30/00	X		X					
1/30/01			X					
2/19/01	X		X					
3/6/01	X		X					
3/26/01	X			X				
4/24/01			X	X				
5/22/01	X		X	X				
5/24/01	X		X					
6/26/01	X			X				
7/3/01	X		X	X				
7/19/01	X			X				
8/22/01	X			X				
9/10/01	X			X				
10/1/01							X	X
10/15/01							X	X
11/19/01	X			X				
11/26/01							X	X
2/4/02	X							
2/11/02							X	X
2/18/02	X							
2/25/02							X	X
3/4/02					X	X		
3/11/02	X							
4/1/02	X				X	X		
4/8/02					X	X		
5/28/02	X							
6/3/02	X							
7/22/02						X		
7/24/02	X							
7/29/02					X	X		
7/31/02					X	X		

Table A.2 Collection by date and trap in Kane'ohe Bay. An "X" indicates that *Schindleria* adults, shorefish larvae, and/or reef fish larvae were caught on that date.

DATE	LIGHT	LIGHT/SOUND	SOUND	EMPTY
5/30/02	X	X		
6/20/02	X			
6/26/02				
7/3/02				
7/9/02	X	X		
7/16/02				
8/8/02	X	X		
8/19/02	X			
8/22/02	X			
8/26/02	X			
8/28/02	X	X		
9/2/02	X	X		

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