1991

Tidepool selection and homing behavior of the bald sculpin, Cinocottus recalvus, on the Central California Coast : with notes on other intertidal fish species

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Order Number 1347159

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TIDEPOOL SELECTION AND HOMING BEHAVIOR OF THE BALD SCULPIN, *CLINOCOTTUS RECALVUS*, ON THE CENTRAL CALIFORNIA COAST, WITH NOTES ON OTHER INTERTIDAL FISH SPECIES

A Thesis
Presented to
The Faculty of the Department of Biology at
Moss Landing Marine Laboratories
and
San Jose State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

By
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December, 1991

APPROVED FOR THE DEPARTMENT OF BIOLOGY

10/25/91

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ABSTRACT

TIDEPOOL SELECTION AND HOMING BEHAVIOR OF THE BALD SCULPIN, *CLINOCOTTUS RECALVUS*, ON THE CENTRAL CALIFORNIA COAST, WITH NOTES ON OTHER INTERTIDAL FISH SPECIES

by Beverly M. Hanna

I used tagging and translocation to study the relationship of specific tidepool characteristics to the distribution, abundance and homing ability of *Clinocottus recalvus* and several other species of intertidal fish in Garrapata State Park, California. A total of 1,000 fishes from 13 species was captured in 16 pools during two distribution surveys. *Clinocottus recalvus* was the most abundant species, represented by 640 individuals. In the homing experiment, 278 fishes from 10 species were tagged and translocated in three pools. Eighty fishes (7 spp.) were recaptured 143 times, 74 of which were in their home pool. Of the 174 *C. recalvus* tagged, 56 were recaptured (32.2% of tagged) and 52 of these had homed (92.9% of recaptured). This is the first evidence for homing in *C. recalvus* , as well as *C. acuticeps*, the northern clingfish, *Gobiesox maeandricus* and two species of stichaeids, *Xiphister atropurpureus* and *X. mucosus*.

ACKNOWLEDGEMENTS

I would like to thank my parents, Phyllis A. and Edward R. Hanna, whose support and encouragement throughout my education are very much appreciated.

I owe many thanks to my committee members, Drs. Gregor M. Cailliet, Michael S. Foster, and Ralph J. Larson for their encouragement, guidance and thoughtful comments in reviewing this thesis. A special thanks to Greg Cailliet for being an inspirational teacher, advisor and good friend.

Many thanks are due to the faculty, students, and staff of Moss Landing Marine Laboratories. Their academic assistance and friendship have made my graduate school experience unforgettable.

This work was funded in part by the Myers Oceanographic and Marine Biology Trust Fund and the David Packard Foundation.

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INTRODUCTION

From the time of the early ichthyologists, rocky intertidal fishes have been studied extensively along the west coast of North America (see Bolin, 1944 for review). This early work consisted primarily of descriptions of new species and their ranges, with little concentration on the behavior or life histories of these cryptic fishes. The shift from purely descriptive intertidal work to experimental science began as fewer and fewer new species were discovered.

In the past 20 years our knowledge of these specially adapted fishes has increased dramatically. However, of the 29 species of Cottidae (9 species of *Clinocottus* and *Oligocottus)*, seven species of Stichaeidae and four species of Gobiesocidae that are residents of the intertidal zone of the North East Pacific (Miller and Lea, 1972), few have been studied in detail (see Gibson, 1982 for review of recent work). Resident intertidal fishes are those that spend their entire lives in a narrow band of coastline between the lowest-low (occasionally in shallow sub-tidal) and the highest-high tides (Gibson, 1969).

Pool characteristics may play an important role in determining fish assemblage structure. Total algal cover and mean pool depth have been shown to affect biomass and species diversity of clinids (Marsh et al., 1978). Recruitment, density, and adult size of *Oligocottus maculosus* are influenced by rock and algal cover, along with the abundance of food and habitats (Pierce and Pierson, 1990). Food resource partitioning may maintain these fish assemblages (Grossman, 1986).

Cottids seem to lack aggression towards each other (Richkus, 1978; Nakamura, 1976a), and actually show a kinesis-type response when placed with another fish (Richkus, 1981). This behavior is perhaps what allows many of these species to co-exist in persistent communities for periods of at least 42 months (> 1 mean generation time for residents) (Grossman, 1986).

Many species of fresh and salt water fishes (salmon, steelhead, *Anguilla* eels, plaice and cod) are capable of returning to a specific area after leaving for long periods of time, or after being displaced experimentally (Harden Jones, 1968). This action is generally called homing and is a complex behavioral mechanism. Territorial reef fishes (Thompson, 1983) and Atlantic herring (Wheeler and Winters, 1984) have also been shown to display homing behavior.

Early tagging experiments indicated that intertidal fishes also had special behavioral adaptations, such as fidelity to a home pool or range and a homing ability. Gersbacher and Denison (1929) discovered that some *Oligocottus maculosus* remained in the same pool at least 10 days after being tagged. Beebe (1934) found that the intertidal goby, *Bathygobius soporator*, would return to its original pool by the next low tide after being displaced to a nearby pool, and Aronson (1951) noted that these gobies seemed to be capable of memorizing the topography of an area, enabling them to return to their home pool.

Homing was defined as "the occurrence of the same fish in the same pool on two consecutive observations of the fish during two different low tides" by Williams (1957), who was the first to seriously test for homing ability in intertidal cottids. He noted that *Clinocottus analis* actively seek out their home pool and remember the route to it, but pointed out that you can not assume it is the pool itself the fish are returning to; it may be a home-site within the pool. He also found that C. *analis* is able to home without light, and stray more often from disturbed pools. He hypothesized that homing may be a survival tactic that allows fish to avoid pools that drain at low tide.

Green (1971a) found that *Oligocottus maculosus* display an innate rhythmic tidal activity that functions as a biological clock, enabling fish to home from unknown pools at high tide. He also suggested that hydrostatic pressure is the most likely cue used by these fish in determining when to leave the pools.

Fish may recognize their home-range by physical or chemical landmarks. Olfaction is the single most important sensory input for homing *Oligocottus maculosus*, although vision also plays an important role (Khoo, 1974). Craik (1981) found that juvenile (20 to 30 mm total length: TL) *O. maculosus* learn the topography of an area and began homing at 30 mm TL, with significantly fewer fish remaining in a transplant area as they increase in age. She hypothesized that memory loss in older fish may cause a decrease in homing ability, although she showed no data to support this.

There are species pairs of cottids from British Columbia to Baja California that replace each other geographically. For example, *Oligocottus maculosus* is the dominant species from Canada south to central Oregon, and *O. snyderi* is the dominant species from approximately central Oregon south to central California (Yoshiyama, et al., 1986). *Clinocottus analis* is dominant in southern California and may be restricted to the north by *C. recalvus* (Williams, 1957). *C. globiceps* lives north of San Francisco and is almost indistinguishable from C. *recalvus,* which lives primarily south of Santa Cruz, CA (Morris, 1951; Yoshiyama et al., 1986).

Clinocottus recalvus is a relatively small (generally < 120 mm TL), intertidal sculpin. Although it is found along much of the N. E. Pacific coast, (from Baja California to Mill Beach, Oregon) (Miller and Lea, 1972), it is numerically dominant only along a limited stretch of the central California coast, from approximately Big Sur to Monterey (Yoshiyama et al., 1986). Eggs are laid on the substrate in March with approximately 900 eggs per cluster, and pelagic larvae settle after 7 weeks at 10.8 mm TL, not fully metamorphosed, but totally demersal. Ten-week old juveniles are 18 to 20 mm TL, 14 week-olds are 24 to 25 mm TL, yellowish-green, much lighter than adults and can be identified with a key (Morris, 1951).

Very little work has been done on the ecology or behavior of *Clinocottus recalvus,* or on the rocky intertidal fish assemblages in which it occurs in central California. Many studies casually mention the less common species and families but rarely examine them experimentally.

This study was designed with two major objectives. The first was to describe and compare the distribution and abundance patterns of young-of-the-year (YOY: < 35 mm TL) and larger size classes of *Clinocottus recalvus,* to that of all other species in the area over time. Pool characteristics such as tidal height, surface area, depth, algal cover and presence or absence of cobbles were measured, along with the species and size composition of fishes in all pools, to evaluate which factors were important to the fish when selecting a pool in which to reside.

The second part of the study used tagging and translocation of fishes over a four month period to test which species and size classes were capable of homing, and to determine if these species display a fidelity or affinity to a home range or home pool. Homing was defined in this study as the return of an individual to its original (first) pool of capture, its "home pool," after being displaced to a new pool. This is compared to Williams' (1957) study where no displacement of fishes was done. Fish that were recaptured in a pool other than their original, or home pool, were called strays.

MATERIALS AND METHODS

Study Site

Field work was conducted at Garrapata State Park, approximately 10 km south of Carmel on an exposed section of the central California coast (Fig. 1). This site was chosen for its relative ease of access and the abundance of pools. The study area (31 x 104 m) was a rocky bench extending south-west from the base of steep granite cliffs and received full wave exposure on nearly three sides. The high surf at this site made sampling impossible during high tide and the winter months. Sixty-six permanent pools with greatly varied sizes (from pot holes to ~15 m^2), and tidal heights ranging from -0.3 to +2.5 m above mean lower low water (MLLW) were counted at the site.

Fish species composition and algal cover were surveyed in 16 of the major pools (Fig. 1). These pools were chosen because they were within the tidal range that could be sampled during most 0.0 m (or lower) tides and were small enough to sample completely in one day, yet large enough to contain a resident population of fishes. They ranged in size from 1.6 x 1.0 x 0.4 m to 12.8 x 12.0 x 0.7 m and were located between -0.2 m and +2.2 m above MLLW. Pool substratum was primarily granite bedrock, with some pools containing cobbles of various sizes, caves, or overhanging ledges. Algal species diversity was high and algal cover varied from near 0% to ~90%. (Appendix 1).

Pool Surveys

Detailed surveys of the 16 sample pools were conducted once in the fall of 1988 (October and November) and again in the early summer of 1989 (June and July) to look for differences that might influence which fish species were present. Pool characteristics such as size, shape, depth (average and maximum), and tidal height (relative to the upper limit of *Laminaria setchelli*, approximately 0.0 m; Ricketts, et al., 1968) were determined. Pools were classified as low (-0.2 to +1.0 m above MLLW), intermediate (+1.1 to +1.3 m), and high (+1.5 to +2.2 m), according to their tidal heights. The percent of algal and invertebrate cover, and the amount of bare and loose rock, were estimated by eye for all pools to find general differences in available habitat between pools (Appendices 2, 3 and 4). No effort was made in this study to determine the amount of sampling error in the percent cover data, so results should be viewed as relative values. Dethier (1984) found visual estimates of algal and sessile organism cover to be quicker and more repeatable than point sampling techniques.

The Percentage Similarity Index for algal cover [$P = \Sigma$ min. (p_{1i}, p_{2i})], where: P = the percentage similarity between samples 1 and 2;

p_{1i} = percent of species i in pool 1;

p_{2i} = percent of species i in pool 2

was calculated for each pool between the two survey periods, and for each pool against all other pools in the same tidal height category for both survey periods (Appendix 5). This index was chosen because it is one of the best quantitative similarity coefficients available, and it takes into account the relative abundances of species, not just presence or absence (Krebs, 1989).

To anesthetize and collect fish, carbon dioxide (CO_2) from a 20 lb. cylinder was slowly bubbled into the pool water through several airstones placed on the bottom. Time required for fish to become anesthetized varied between ~ 5 and 15 minutes depending on the size of the pool. Individuals were captured by skin divers using dipnets, or along the edge of the pool by observers. Each pool was searched until no more fish could be found. After they were identified and measured (mm TL), fish were placed into a bucket of fresh sea water and allowed to recuperate. Pools were re-oxygenated by forcefully pouring in buckets of sea water until the CO_2 was sufficiently diluted. All individuals were then returned to their pool of capture. Species composition, length/frequencies and distribution among pools were determined for all fishes.

Tags

Tags were made of pieces of plastic cut from a 2.5 gallon water jug, shaped into small (~5 mm) ovals, and pierced at one end with a needle. Three-digit numbers were inscribed on each with a diamond-tipped pencil. Ten pound test nylon fishing line was strung through the hole and then affixed to a 10 gauge sewing needle. Tags were kept in numerical order by inserting the needles into a numbered styrofoam board. Individuals of all species, > 40 mm TL (or for stichaeids, > 100 mm TL), were tagged by pulling the needle through the dorsal musculature, then tying first an overhand knot and then a square knot to secure the line. The excess line was cut to approximately 1 cm.

Tagging Experiment

The tagging experiment involved five of the 16 survey pools. Three of the pools (1, 4, 6), chosen for their location and similar tidal heights, were used in the relocation/homing experiment (Fig. 1, Appendix 1). Approximately twice a month between March 31 and August 3, 1989, fishes from each of these three pools were captured and tagged using the methods outlined above. Species, length, tag number, and general condition of each fish and its tag wound (for recaptured fish) were noted. Occasionally a fish was re-tagged if the old tag wound was tearing. Once all three pools had been sampled, all the fishes of one pool were transfered to the next pool and released (i.e., fish captured in pool #1 were transfered to pool #6; fish captured in #6 went to #4; and fish captured in #4 went to #1). This procedure was repeated on each sampling date and the fish were moved from pool to pool in the above order each time, regardless of where they were originally captured.

Two pools (9 and 10), which differed in size, tidal height, algal cover and amount of loose rock, were selected as controls for the effects of tagging (Fig. 1, Appendix 1). Fishes from these pools were anesthetized and tagged, then released back into the same (home) pool. These pools were sampled approximately once a month from April 27 to August 3, 1989.

Pools 1 and 4 were sampled for a different project on two dates (November 10, 1989 and April 26, 1990) after the original study was completed. The size data from these dates for *Clinocottus recalvus* is shown in Fig. 10 for comparison to the other dates. The sampling techniques were the same.

Homing frequency, or "homing success", was defined as the percentage of tagged fish that returned to their original pool of capture (the very first pool in which they were captured) (1, 4, or 6) after being translocated to a new pool. Results were calculated both for the first recapture of individuals and for multiple (repeated) recaptures of the same individuals.

A Kruskal-Wallis test with tied ranks (Zar, 1984) was used to check for differences in the size of new, non-recaptured, *Clinocottus recalvus* entering the tagging pools between sampling dates to find if any months had higher proportions of juvenile recruits.

RESULTS

Pool Characteristics

Low (-0.2 to +1.0 m) tidal height pools (9, 7, 10, 16 and 6) were generally dominated by articulated coralline algae; percent cover of these algae increased 10 to 25% in 1989 over the 1988 values (Appendix 2). Encrusted corallines, *Ulva sp.*, and *Gelidium sp.* also had relatively high cover. The average percent cover of invertebrates was 9% over both periods, while the average amount of bare rock was approximately 25%. Many of these pools contained loose rocks, or had several caves in their walls.

Articulated and encrusting coralline algae were abundant in 1988 with approximately 22% cover each in pools of intermediate (+1.1 to +1.3 m) tidal height (1, 4, 2, 5 and 12) (Appendix 3). By the early summer of 1989 the cover of articulated corallines nearly doubled to 42%. *Codium fragile, Prionitis sp.*, and *Ralfsia sp.* were all present with ≤ 5% cover. The invertebrate cover was greatest (23%) in these intermediate height pools. The amount of bare rock decreased from 11% in 1988 to 6% in 1989.

Coralline algae were dominant in pools at high (+1.5 to +1.7 m) tidal heights (13, 14, 11, 15 and 8), with articulated species averaging 17% cover and encrusted species ranging from 12 to 23% cover (Appendix 4). *Gelidium sp.*, *Rhodoglossum affine,* and *Ralfsia sp.* were also abundant. Red crust algae became the most abundant species in these pools in the spring of 1989, averaging 25% cover. High pools tended to have low invertebrate cover (~ 7.6%) and few loose rocks. The amount of bare rock was greater here (~ 14%) than in the intermediate pools but far less than in most low pools.

Pool 3, located at 2.2 m above MLLW, was dominated by *Prionitis sp.* in both 1988 and 1989. This pool had a high percentage of bare rock (43%, averaged over both surveys) and very low invertebrate cover.

Algal mean percent similarity index values were low and variable (23 to 45%), but indicated that no significant differences occurred among tidal heights or sample dates (Appendix 5). Large confidence intervals signified high spatial and temporal variability of algal cover in all categories.

Fish Survey

One thousand fishes of 13 species were captured in the 16 study pools during the two survey periods (Table 1). *Clinocottus recalvus* was the most numerous species, being represented by 640 individuals, and dominated all but three pools. *Oligocottus rimensis*, represented by 117 individuals, was the second most abundant species overall, but was more than twice as abundant as *C. recalvus* in pool 16. Pool 11, the largest study pool, had the greatest number of fish (392 individuals), and species (11). The two control pools (9 and 10) had eight species each but only 53 and 25 individuals, respectively. The translocation pools (1, 4 and 6) had seven species each, represented by 42, 93 and 34 individuals respectively.

Pools at low tidal heights had between 3 and 6 species and were relatively stable between years, with the same species usually dominating the same pool each season (Fig. 2a). Very few unidentified juvenile cottids were found in any low pool during either season.

Clinocottus recalvus dominated all five pools at the intermediate tidal level in both 1888 and 1989 (Fig. 2b). Pools with loose rock (1 and 12) had more species than pools with solid bottoms (2, 4, and 5) which contained over 80% *C. recalvus*. There were new cottid recruits in four of these five pools in the summer of 1989, but none in the fall of 1988.

Pools at high tidal heights generally had few species (Fig. 2c), except pool 11 (the largest of the 16 pools) that had representatives from seven of the major species. *Clinocottus recalvus* was the dominant species at this level. Only two pools at this height, 13 and 11, had new cottid recruits in 1989. Only one *C. acuticeps* was captured in the fall survey at any tidal level, but this species was quite abundant in the summer sample at all tidal heights.

Small *Clinocottus recalvus* (< 56 mm TL) were more abundant than larger ones during both sampling periods for all pools combined, although all size classes were well represented in 1988 (Fig. 3a). Over 60% of the 338 *C. recalvus* collected during the 1989 survey were new juvenile recruits (< 35 mm TL).

The 62 *Clinocottus acuticeps* captured in 1989 had a normal size distribution, ranging from 35 to 95 mm TL (Fig. 3b). The 56 to 65 mm TL size class had the greatest frequency (22%).

Oligocottus rimensis were generally smaller than the other cottid species found at this site. The majority ranged from 36 to 55 mm TL, although some individuals reaching 75 mm TL were captured during the 1988 survey (Fig. 3c).

There was a shift from large *Oligocottus snyderi* in the fall of 1988 to smaller individuals in the summer of 1989 (Fig. 3d). In 1988 nearly 10% of this species were larger than 85 mm TL. Approximately 8% of the 1989 *O. snyderi* were under 35 mm and none were larger than 85 mm.

Gobiesox maeandricus at this site were generally large individuals, mostly in the 56 to > 95 mm TL range during both surveys (Fig. 3e). However, smaller individuals did occur in both years.

The relationship between tidal height and fish density was variable (Figs. 4, 5). *Clinocottus recalvus* was found at all tidal heights, but had the greatest density between 1.1 and 1.7 m above MLLW, represented by nearly eight fish per m^2 at 1.1 m (Fig. 4). *C. acuticeps* had higher densities (~2/m^2) in pools above 1 m. *Oligocottus rimensis* and *O. snyderi* both had low densities (< 1/m^2). *O. rimensis* was found only in pools below the 1.3 m level and *O. snyderi* was found only below the 0.9 m level.

Gobiesox maeandricus was found in pools up to 1.7 m above MLLW with higher densities in deeper pools containing cobbles (Fig. 5). *Xiphister mucosus* was more widely distributed than *X. atropurpureus*, but neither was found in pools above 1.7 m. Unidentified post larval and juvenile cottids followed a pattern very similar to that of adult *Clinocottus recalvus*, having greater densities in the mid-range pools.

The number of individuals/m^3 for the major cottid species stayed relatively constant in pools up to 2 m^3, then decreased in the larger pools (Fig. 6). *Clinocottus recalvus* was found in densities ranging from 2/m^3 to 75/m^3. One very shallow pool (5) was loaded with juveniles in the early summer and accounted for this one high density value. *Oligocottus rimensis* was found only in pools with volumes of 0.7 m^3 or greater, while *O. snyderi* was found in pools with volumes of 0.4 m^3 and greater.

Gobiesox maeandricus, *Xiphister atropurpureus*, *X. mucosus* and the unidentified cottid juveniles, generally had higher densities in smaller pools with cobbles (up to $8/m^3$), and low densities in the larger pools (Fig. 7). Sampling difficulty due to immovable rocks and CO_2 diffusion in the large pools may partially account for these low densities. These results strongly suggest a surface area and/or volume relationship with fish density.

Tagging Experiment

Pool disturbance appeared to adversely affect the distribution and abundance of fish populations (Fig. 8). While the 11 non-tagging pools had an increase of 20% (from 349 to 420) in the total number of fishes between the Fall 1988 and Summer 1989 surveys, the total number of fishes in the disturbed tagging pools (1, 4, and 6) decreased 59% (from 111 to 46) over the course of the four month tagging experiment. The drop in the number of new fish tagged the first two months corresponded with the increase in number of recaptured fish, which peaked at 32 on May 25, then declined to a low of 11 individuals at the end of the study. The number of small (< 40 mm TL) untagged fishes generally fluctuated between 8 and 19 fishes each sampling day, but reached a peak of 28 fish on July 22.

Tag loss had a small effect on the number of recaptured and homing fishes. Approximately 14 cottids, 1 gobiesocid, and 11 stichaeids were found with missing tags or infected tag wounds. Mortality due to tagging was not observed for any of the 25 cottids, gobiesocids, or stichaeids that were tagged and held in a laboratory for three weeks.

A total of 278 fishes from 10 species was tagged and translocated, while 111 smaller fishes (< 40 mm TL) were not tagged but were still translocated in pools 1, 4 and 6 (Table 2). Eighty individuals, from 7 species, were recaptured

143 times. *Oligocottus rimensis* had the lowest recapture percentage of the major species. The highest number of tags and recaptures, at 135 and 39 respectively (120/37 were *C. recalvus*), occurred in pool 4. Pools 6 and 4 had a similar number of species, but pool 6 had a more even representation of individuals per species.

Ninety fishes (10 species) from pools 9 and 10 were tagged, then replaced back into their home pool (Table 2). The number of species was the same in the two pools (6), but there were large differences in the numbers of individual *Clinocottus acuticeps, Oligocottus rimensis, and Xiphister mucosus*. Of the nine recaptures from five species (10.1% of the tagged fish), only one (a *C. recalvus*) strayed from its home pool. Eight individuals stayed in their home pool (8.9% of the tagged fish and 88.9% of recaptured fish).

Of the 278 tagged fish, 72 individuals (seven species) were recaptured 134 times in their home pool (1, 4, or 6), representing a homing frequency of 25.9% (90.0% of the recaptured fish) for all species (Table 3). Of these 72 individuals, 35 (48.6%) homed only once, and 37 (51.4%) homed more than once. Few fish of any species strayed.

The homing success of *Clinocottus recalvus* was slightly related to the size of the individual (Table 4). One hundred and seventy-four *C. recalvus* were tagged in pools 1, 4 and 6; 56 of these (32.2%) were recaptured. The overall homing success (% of the tagged fish that homed) was 29.3% for all size classes when individuals were counted only the first time they homed. The smallest tagged size class (40 to 49 mm TL) was the least successful, with only 21.6% homing. A large proportion of *C. recalvus* captured during the tagging period was < 40 mm TL and was not tagged (Fig. 9). The number of recaptures increased along with the total number of individuals captured in the 40 to 64 mm size classes, then dropped off sharply through 85 mm. Recaptures reached 100% in some larger size classes, although the total number of individuals was low. Fish that homed 4 - 5 times were from the intermediate size classes, 50 to 70 mm TL.

The mean size (TL) of new, non-recaptured, *Clinocottus recalvus* entering the study area (tagging pools only) differed significantly among sampling dates (Kruskal-Wallis, $H_{(2)(0.001)} = 12.67$; $H = 81.19$, corrected for ties, $P<0.001$) (Fig. 10). It appears that pulses of YOY individuals occurred in early June and again in November 1989. New fish captured during these months had an average total length of 36 mm. There was also a large influx of postlarval (< 20 mm TL) *C. recalvus* in April 1990. New fish captured in the early spring were the largest (57 mm TL average) of all sampling dates.

DISCUSSION

Distribution and Abundance

The quantity and quality of rock and algal cover have been shown to be very important in determining the distribution and abundance patterns of intertidal fishes (Barton, 1982; Green, 1971c; Marliave, 1977; Marsh et al., 1978; Mollick, 1968; Moring, 1981; Nakamura, 1976a; Pierce and Pierson, 1990; Richkus, 1978, 1981; and Wells, 1986). The presence or absence of loose rocks appeared to be an important factor in determining the species composition found in tidal pools in this study. Stichaeids and gobiesocids were rarely found in pools with little or no loose rock, although the pricklebacks were occasionally removed from deep caves and crevices. Undersampling in some pools undoubtedly occurred as it was sometimes impossible to move or remove the larger boulders, and some stichaeids wedged themselves into holes and could not be extracted. In other pools, although a thorough check was done, it is possible that some fishes, particularly the smallest ones, were missed. This was unavoidable with the sampling method used, and it was thought that further searching might cause unrepairable damage to the habitat.

The ability to assess the effects of algal cover on the fish assemblages is confounded by the tidal height and exposure of the pools. Many intertidal fishes, especially the stichaeids, consume specific algae as part of their diet (Barton, 1982; Horn, et al. 1980). Other species, when given a choice, will select a habitat with cover versus one with no cover (Nakamura, 1976a; Richkus, 1981). I had thought that some fishes might select a particular pool in which to reside, based in part on the algal composition and percent cover of that pool. I expected when looking at the algal PSI that individual pools would be more similar to themselves, than to other pools at the same tidal heights each sampling period. However, the seasonal and temporal variation of the algae was very high, and no apparent differences were found between any PSI category (Appendix 5). If fish are using the algae as a basis for home pool selection, it is possible that for some species, simply the presence of algae, rather than the actual composition, is important. More detailed studies are needed in order to determine the actual role algae plays in fish distribution and home pool selection at this site.

Species without the ability to air-breathe may be excluded from pools with high algal cover in the upper intertidal, which are not flushed regularly with fresh sea-water, due to a lack of oxygen (Davenport and Woolmington, 1981). Pools with large quantities of algae should have high O_2 levels during the day, but low pH values at night due to the cessation of photosynthesis and increased CO_2 release from respiration. Cottids in this study were often seen trying to crawl out of the pools after the CO_2 had been added, and up the sides of the bucket when their densities got too high. Wright and Raymond (1978) observed *Clinocottus recalvus* emerging from pools, gulping air into their mouths, then holding it a few minutes before releasing it. This behavior may be responsible for *C. recalvus*'s ability to inhabit the high pools at this site. Davenport and Woolmington (1981) found that this emergence response of British intertidal fishes was not stimulated by CO_2 build-up, inside or outside the fish, but by a lack of O_2 (hypoxia). They observed no effects of salinity, temperature, or changes in pH and CO_2 on the behavior of three species of intertidal fishes.

Distribution patterns are affected by a diverse array of physical and biological factors. Temperature appears to be the most important factor determining the vertical and latitudinal distribution of some species, but is only of secondary importance to others (Barton, 1982; Horn and Riegle, 1981; Nakamura, 1976b). Although not measured, the temperature in the upper pools at this site got quite high during sunny periods, and may have restricted the number of individuals and species in several of the pools (3, 8, 14 and 15) (Fig. 2c).

Green (1971c) found that the primary factor affecting the distribution of *Oligocottus maculosus* on Vancouver Island was exposure to wave action. In exposed areas this species is restricted to the upper intertidal, but it is found at all tidal heights in sheltered areas. The section of Garrapata State Park in this study is exposed to full wave action from three sides. Sampling was restricted to the calmer periods of late spring through fall, but 10 foot seas were still common. Perhaps *Clinocottus recalvus* is especially well suited to this extreme environment, allowing it to dominate this small section of coast, while being out-competed by *O. maculosus* and *O. snyderi* in the north and by *C. analis* to the south. A more extensive study of the central coast would be required to identify the factors involved in these population dynamics. *C. recalvus* and *O. rimensis* are found in high numbers only between approximately Pescadero Pt., CA and Pt. Sur, CA (Yoshiyama et al., 1986). These two species were also commonly found in the canopy of *Macrocystis pyrifera* between Carmel Bay and San Simeon in Miller and Geibel's (1973) study. It is not known how this area's large kelp beds and the dominance of C. *recalvus* and O. *rimensis* are related but there may be a connection.

The size of an individual can be related to its vertical distribution. Most intertidal species segregate by size to some degree, with the young fish more abundant near the upper limit of the species' distribution as shown by the following patterns. Young of the year *Oligocottus maculosus* (< 55 mm) do not occur as low in the intertidal as older fish, and larger fish will only inhabit high pools if they are deep enough (> 10 cm) (Green, 1971c). *Clinocottus analis* gradually moves to lower pools as they get older until eventually many of them move into the subtidal zone (Wells, 1986; Williams, 1957). However, this study found YOY and adult C. *recalvus* primarily in pools of intermediate tidal height (Fig. 2). This may be a species specific or a site specific pattern. Interactive or confounding effects of factors other than tidal height make it difficult to determine which factors limit the vertical distribution of a species.

Fish density is often dependent on tidal height or pool volume. Many species are found almost exclusively in one tidal range, while others appear to be unaffected by this factor (Grossman and DeVlaming, 1984; Moring, 1981; Nakamura, 1976a,b; Pierce and Pierson, 1990; Richkus, 1981; Wells, 1986). *Oligocottus rimensis* and O. *snyderi* in this study were found in significant densities only in pools of low to intermediate tidal heights ($0.3/m^2$, < 1.3 m and $0.3/m^2$, < 0.9 m respectively), while *Clinocottus acuticeps* was captured primarily in pools above 1 m, with densities of $1.0/m^2$ (Fig. 4). C. *recalvus* had an average density of $1.7/m^2$ over the entire tidal height range. These results concur with Green's (1971c) findings on Vancouver Island, British Columbia, and Moring's (1981) study in Trinidad Bay, CA where he found densities of $0.30/m^2$ for *O. snyderi* and $1.36/m^2$ for *O. maculosus.*

Richkus (1978) stated that there was no significant correlation between median pool population and the depth, area, or volume of pools, but he did find high densities of fishes in deep, well-shaded pockets. Wells (1986) found densities of *Clinocottus analis* up to $27/m^2$ (mean $8.5/m^2$) (excluding YOY), but discovered no correlation between tidepool size and population density. He also found that pools with moderate to high algal cover had higher population densities than pools with low cover. I found that pool size appears to influence the number of species present, but only to a small degree. The smallest pool (14) had only 3 species, while pool 11, the largest of the study pools, had 11 species.

However, pool complexity was perhaps more important than size in determining the number of fish species present. Pools with cobbles, holes, and overhanging ledges generally had more species than larger pools with flat bottoms. I also found higher densities of all species examined in pools with small volumes (Figs. 6, 7). Intertidal fishes are generally bottom dwellers, so density and number of species present are primarily dependent on the bottom area of a pool, not the volume. Large, deep pools have a high percent of water volume that is not utilized by these fish. Cover (algae, rocks and caves) was an important factor in microhabitat selection in all pools. Fishes were primarily found bunched together under cover whether the pool had a high or low fish density overall.

Predation pressures by subtidal fishes (Yoshiyama, 1981), birds (Marsh, et al., 1978; Pierce and Pierson, 1990), and small animals (Nakamura, 1976a) as well as by man (Moring, 1979b) can limit the upper or lower distribution of intertidal fishes. While isolated incidences of predation have been recorded, it seems unlikely that predation pressure is enough to significantly alter the population in most areas. The only predation observed in this study was by three shore crabs (*Pachygrapsus crassipes*) that were attempting to carry off small, anesthetized fishes before they could be removed from the pools. This area is also a popular spot for poke-polers and weekend tidepoolers, who may have affected the habitat to a small degree.

Reproduction and Recruitment

Most intertidal sculpins, and many stichaeiods, reproduce in the winter and spring months, and recruitment coincides with the increased productivity of upwelling. Grossman and DeVlaming (1984) found a strong positive correlation between the percent of new *Oligocottus snyderi* recruits appearing in June and July collections at Dillon Beach, California, and upwelling (productivity) and to a lesser degree, photoperiod. In Trinidad Bay, CA, YOY *O. maculosus* appear in April, and dominate the population by September (Moring, 1979a). *O. snyderi* and *Clinocottus recalvus* both showed a similar pattern at Garrapata State Park with a high percentage of YOY in the 1989 summer survey period (Fig. 3 a-e). There was a shift towards smaller *Gobiesox maeandricus* individuals in the spring, but neither *C. acuticeps* nor *O. rimensis* showed increased recruitment during that period, indicating perhaps year around recruitment for these two species.

Larval dispersal and transport, or the lack of it, can greatly influence the population as a whole in a particular area. Marliave (1986) found intertidal larvae of all sizes in schools inshore near the rocks but not along an adjacent beach, suggesting that they resist offshore and possibly longshore dispersal. He concluded that some populations may be relatively isolated genetically. In contrast, Yoshiyama and Sassaman (1987) analyzed geographic patterns of allele frequency for three common species of intertidal cottids and found a uniform pattern indicating free gene flow along the coast. They stated that dispersal of planktonic larvae by coastal currents is apparently sufficient to prevent genetic isolation, although movements of adults might contribute to gene flow among some populations.

In areas of high turbulence, like Garrapata State Park, it seems likely that larvae would have a difficult time returning to shore in large numbers and adult migration could help keep the population re-supplied. My results showed relatively few newly settled larvae, but high numbers of new juvenile and adult fishes in the study area. If adult movement along the coast was occurring, this might account for the large percentage of tagged fish that were never recaptured during the study.

If larvae settled randomly, they would be expected in pools of all tidal heights, but Nakamura (1976b) found that larvae, like the adults, of *Oligocottus snyderi*, are found only in low pools while those of *O. maculosus* are found in high pools. He concluded that larvae invade pools of specific tidal heights and stay there their entire lives. The unidentified post larval and juvenile cottids (< 20 mm TL) in this study (most likely *Clinocottus recalvus* since this was the numerically dominant species) were found, although in fewer numbers, in the same pools, and generally the same proportions, as adult *C. recalvus* (Figs. 4, 5). It is not known if the juveniles remain at the same tidal height their entire lives, as C. *recalvus* were found in pools at all heights in this study, but this seems likely since the densities of juveniles and adults were highest in the same group of pools. These results differ from those of Richkus (1981) and Wells (1986), who found that C. *analis* juveniles were rarely found in the same pools as adults and might act as colonizers of new territory.

Tagging and Recapture

Pool disturbance, by natural or man-made causes, appears to adversely affect the abundance and behavior of some intertidal fish populations (Koop and Gibson, 1991; Matson, et al., 1986; Richkus, 1978; Williams, 1957). In contrast, *Oligocottus maculosus* was not found to be affected by sampling disturbance (Green, 1971b), and Grossman (1986) found that the assemblage structure at Dillon Beach, CA, was unaffected by collecting. The 11 pools in this study used only in the two surveys, showed a slight increase in number of fishes collected over time, while there was an overall decline in the numbers of fishes in the tagging pools during the study (Fig. 8). This decline may be attributed to the continuous disturbance of the prey items and to the rock and algal habitats in these pools. A sharp decline in the total population June 7 may be related to a 3° increase in sea-surface temperatures that week in the area (D. Wilson-Vandenberg, Calif. Fish Game, Pers. Comm.) as the larger fishes may have moved to deeper, cooler water. Only the small, untagged fishes seemed to be uneffected, as their numbers increased slightly. The number of new fishes entering this study area first decreased sharply from 64 on April 27 to 13 on June 7, then rose and stabilized at approximately 30 new fishes for the last three sampling dates. The number of recaptured fishes rose the first month then gradually declined the remainder of the study. This decline in recaptured fishes may be a result of individuals leaving the disturbed area, or of natural mortality as older fishes died at the end of the summer.

Green (1971b) showed that the effects of tagging on individuals was negligible, causing no significant mortality. However, tag loss might be extensive in areas of high turbulence. Green (1973) found tag loss to be a significant factor for *Clinocottus globiceps*. Butterfish, *Pholis gunnellus*, experience a 3.25% tag loss per day in the laboratory, and tag wounds healed in 15-20 days making it gradually more difficult to identify previously tagged fish (Koop and Gibson,1991). Tag loss can be caused by abrasion of water and substrate or tangling in plants (Williams, 1957). Some tag loss may be due to other fish biting the tags and removing them, perhaps mistaking them for prey. Tag loss occurred in this study, as fish with tag wounds were often recaptured. This was especially prevalent in the stichaeids. The low recapture percentage for *Oligocottus rimensis* may be due to the relatively large size of the tags compared to the smallness of this species. The use of smaller, more streamlined tags may prevent some of these problems and increase the recapture and homing percentages of these species in future studies.

Successful homing requires that displaced fish leave the new pool they have been placed in at high tide (Green, 1971a; Richkus, 1981). Rhythmic activity centered at the time of high tide has been shown for several species (Gibson, 1982; Green, 1971b; Ralston and Horn, 1986). Green, (1971a) ruled out temperature, salinity and turbulence as synchronizers for this tidal activity in

Oligocottus maculosus, and concluded that hydrostatic pressure was the most likely variable used by this species in determining when to leave the pools. Gibson (1984) found similar results for *Blennius pholis*, stating they were capable of detecting and responding to slow cyclic pressure changes whose amplitude and duration are similar to those of natural tidal cycles.

Eight species had some degree of recapture success in this study. The recapture rate was greatest for *Clinocottus analis* and *Oligocottus snyderi* at 66.7% and 44.4%, respectively (Table 2). These results were quite high compared to results of previous studies of these two species (Richkus, 1978), and may be due to chance associated with the low numbers of tagged fish in this study.

The recapture rate of *Clinocottus recalvus* in this study is comparable to results of the dominant species in southern California and British Columbia, although the percent of non-recaptured fish was higher: 16.1% of *C. recalvus* were recaptured once, 16.1% recaptured more then once, and 67.8% were not recaptured. Gibson (1967) calculated that 36.2% of *C. analis* were recaptured once, 13.2% were recaptured more than once, and 50.6% were not recaptured. Fewer than 6% of *C. analis* individuals remained in their home pool after 56 days. Richkus (1978) reported corresponding values for *C. analis* of 30% recaptured once, 23% recaptured more then once and 47% not recaptured. After 56 days he found < 10% of the fish remained in their home pool and 20% remained in the area.

The recapture of large proportions of tagged *Clinocottus acuticeps*, *Gobiesox maeandricus*, *Xiphister atropurpureus* and *X. mucosus* was surprising because no other study has suggested that these species might home or maintain home ranges. Barton (1973) find no evidence for homing in his stichaeid study. An ultrasonic telemetry study of the high tide movements of *Cebidichthys violatious* (Ralston and Horn, 1986) suggested that this species might have a home range, but indicated that more data were needed. In my study, although the numbers of the above species tagged and recaptured was low, it seems very unlikely that these homing results were due to random chance, because few individuals strayed. Fish generally either homed or disappeared completely; they were rarely found in any of the other pools.

Surprisingly low numbers of fishes were recaptured in pools 9 and 10 (only 10% of tagged). Since these fishes were tagged but not translocated (same as Williams, 1957 and Richkus, 1978), it was expected that a large proportion of them would remain in these pools over time, assuming they were the home pools of those fishes. The majority of *Oligocottus maculosus* (> 55 mm TL) live permanently in specific pools in exposed to moderately exposed areas, and rarely move more then 10 m from this home pool (Green, 1971b). The relatively long time period between my samplings (~1 month) might partially account for these low numbers of recaptures. Pool 9 was also difficult to sample on days with large swells or low tides higher than -0.3 m. So, it is likely that some fish were missed during the search.

Several studies have suggested that intertidal fishes may have a home range rather than a single home pool (Craik, 1981; Green, 1971b; Ralston and Horn, 1986; Williams, 1957). The results from pools 9 and 10 would seem to substantiate this, except that in only two cases were fishes from these two pools found in any of the other 14 pools in the study area.

The effect of fish size on homing ability is not clear. Green (1971b, 1973) found that age and size had no effect on the homing success of *Oligocottus maculosus* or *Clinocottus globiceps*. However, Craik (1981) found significant differences in homing behavior between three age groups of *O. maculosus*, with age two fish (50 to 70 mm TL) being the most successful. She concluded that one-year-olds were the least successful homers because they move around more, learning and memorizing the area, and that older fish begin to lose the ability to home as their memory fades. My results lend support to Craik's hypothesis that younger fish must first learn the area before becoming successful homers, and they may be the colonizers of new habitats and disturbed areas. Contrary to Craik's findings, I found that larger *C. recalvus* (> 80 mm TL) had higher homing percentages (> 42%) and fewer strays (0) then the younger age classes. So, while there are fewer large fish in the population left to home, it does not appear that they are mentally or physically unable to do so.

Richkus (1978) found a significant correlation between size and number of recaptures, with larger fish being recaptured more frequently. In my study, size did appear to influence the number of times individual *Clinocottus recalvus* were recaptured, but only to a small degree. The larger fish (> 85 mm TL) tended to be recaptured 2-3 times, while those individuals recaptured 4-5 times were of an intermediate size.

Immigrant *Clinocottus analis* are primarily younger fish, and the mean TL of new fish is always less than the mean TL of the population as a whole (Richkus, 1978). The number of new *C. analis* in his study ranged from 48 to 100% of the total population. The new *C. recalvus* immigrating into this study area were also smaller on average than the total C. *recalvus* population in the tagging pools, for any one date. These size differences may be partially due to a lack of adults rather then an increase of YOY, or possibly to random variation. The new fish captured comprised between 54% and 100% (average: 70%) of the total number of individuals. This shows that while some fish do return to their home pool, there is a large adult turnover rate with about 60 to 70% of the C. *recalvus* population in any one area immigrating from elsewhere approximately every two weeks. More extensive study is required to determine from where these fish are immigrating.

Reasons For Fish Homing

Homing appears to be a wide-spread phenomenon in the intertidal zone. Most fish species that have been studied thus far are capable of returning to their original pool of capture, or to a home range, after being displaced to a new area. This type of behavior is similar to territoriality. However, these fishes show no aggressive behavior towards one another as is typical of species with true territories who defend their home range. Homing behavior must be of benefit to the individual or it would not be exhibited by so many species. By returning to the same pool again and again, an individual is assured of being in a place having the necessary conditions for survival at low tide. Possible benefits derived by a fish from a particular pool include adequate food and shelter availability, protection from predators, presence of potential mates and spawning sites, and suitable water temperature, salinity and oxygen concentration.

The long term persistence of these intertidal communities attests to the success of these behavior patterns. In a collection made nearly four years after my original collection at the Garrapata State Park site, the species composition was virtually unchanged, with cottids, gobiesocids and stichaeids the dominant fishes. These results were very similar to the results reported by Yoshiyama et al. (1986) on a Soberanes Point collection made 18 years ago. Similar stable patterns have been observed for intertidal fishes in the Sea of Cortez, by Thomson and Lehner (1976), in South Africa by Beckley (1985), and on the east coast of North America by Collette (1986). Since these intertidal communities have shown the ability to persist for long periods of time, it seems probable that homing behavior, coupled with the individual's physical adaptations of body shape, coloration, and keen senses, etc. may have contributed to this long term success.

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Table 1. Total number of captured fish (all size classes) of each species from both survey periods (September - November 1988; June - July 1989). Does not include fishes that were captured and tagged during the homing experiment in pools 1, 4, 6, 9 and 10. Abbreviations for the major species are shown. S = the number of species captured in each pool, N = the number of individuals of each species captured in each pool.

	POOL #																
Spp.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	TOTAL
C. recalvus (C. r.)	20	26	5	83	76	11	10	8	22	8	283	39	10	12	1	26	640
C. acuticeps (C. ac.)	4	7	6	1	2	2	3	9	1	4	17	2	2	1	0	1	62
C. analis (C. an.)	2	2	0	1	1	0	4	0	0	1	10	0	0	0	0	0	21
O. rimensis (O. r.)	4	0	0	5	4	1	0	2	10	1	25	7	3	0	0	55	117
O. snyderi (O. s.)	0	0	0	1	0	4	3	0	6	0	21	1	1	0	0	15	52
O. maculosus (O. m)	0	0	0	1	1	0	0	0	8	0	9	0	0	0	0	0	19
G. maeandricus (G. m.)	6	0	0	0	0	7	0	2	1	1	4	4	2	2	0	2	31
X. atropurpureus(X. a.)	1	0	0	0	0	6	0	0	4	7	0	0	0	0	0	0	18
X. mucosus (X. m.)	5	0	0	1	0	3	0	0	0	2	9	1	0	0	0	0	21
S. marmoratus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	2
A. purpurescens	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2
X. fucorum	0	0	1	0	0	0	0	0	0	0	12	0	0	0	0	1	14
G. montereyensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
S	7	3	3	7	5	7	4	4	8	8	11	6	5	3	1	7	13
N	42	35	12	93	84	34	20	21	53	25	392	54	18	15	1	101	1000

Table 2. Number of tagged and recaptured fish by species in pools 1, 4, 6, 9 and 10 for entire tagging period (no tagging was done on Aug. 3). All tagged fish (> 40 mm TL) were counted. Numbers are given as: total # caught / number of recaptured fish, for each species. S = number of species captured and tagged in each pool. Only the first recapture was counted for each individual.

POOL NUMBER

SPECIES	1	4	6	9	10	#TAGGED	#RECAPS	% RECAP
Clinocottus recalvus	28/10	120/37	26/9	21/2	6/2	201	60	29.9
C. acuticeps	4/2	2/1	7/2	0	14/2	27	7	25.9
C. analis	0	0	3/2	0	0	3	2	66.7
Oligocottus rimensis	5	5	4	20/1	0	34	1	2.9
O. snyderi	0	1/1	4/3	4	0	9	4	44.4
O. maculosus	0	1	0	0	0	1	0	-
O. rubello	0	0	0	1	0	1	0	-
Gobiesox maeandricus	5/1	1	19/5	5	5/1	35	7	20.0
Xiphister atropurpureus	7/2	3	16/3	0	4	30	5	16.7
X. mucosus	8/1	2	6/1	0	8/1	24	3	12.5
Anoplarcus purpurescens	0	0	1	0	1	2	0	-
Scorp. marmoratus	0	0	0	1	0	1	0	-
N (tot.#tagged/#recap)	57/16	135/39	86/25	52/3	38/6	368	89	
S	6	8	9	6	6	12	8	

Table 3. Homing success of the major fish species in pools 1, 4, and 6. Counts of Homing are the number of times that all individuals of a species were recaptured in their home pool. The 11 in parentheses denotes one *Clinocottus acuticeps* individual that was recaptured two additional times after the regular study was over. Number Strayed is the number of individuals of a species that were recaptured in a pool other than their home pool.

SPECIES	NO. INDIV. THAT HOMED	COUNTS OF HOMING	NO. STRAYED
Clinocottus recalvus	52	102	4
C. acuticeps	4	9 (11)	1
C. analis	2	2	0
Oligocottus snyderi	3	6	0
Gobiesox maeandricus	5	8	0
Xiphister atropurpureus	4	4	2
X. mucosus	2	3	1

Table 4. Homing success of different size classes of *Clinocottus recalvus* in pools 1, 4, and 6 over the four month tagging period. Individuals were counted only the first time they were recaptured.

SIZE CLASS (mm TL)	NO. TAGGED	NO. RECAPTURED	NO. RECAPT. IN HOME POOL	% OF TAGGED THAT HOMED
40 - 49	37	9	8 (88.9 %)	21.6
50 - 59	60	19	17 (89.5 %)	28.3
60 - 69	45	16	15 (93.8 %)	33.3
70 - 79	17	5	4 (80.0 %)	23.5
80 - 89	7	3	3 (100 %)	42.9
90 - 99	4	2	2 (100 %)	50.0
100 - 109	3	1	1 (100 %)	33.3
110 - 119	1	1	1 (100 %)	100.0
TOTALS	**174**	**56**	**51**	**OVERALL: 29.3%**

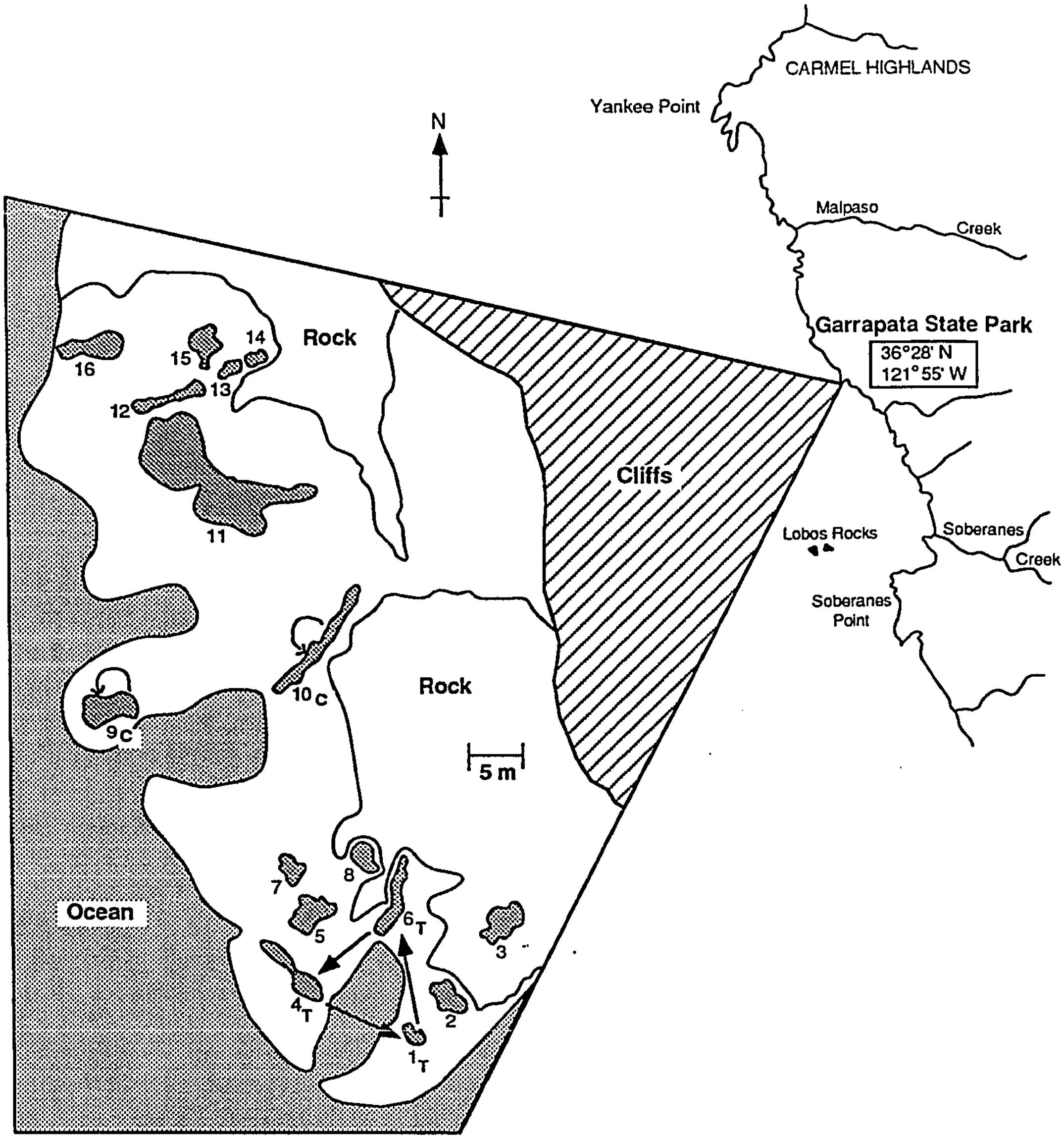
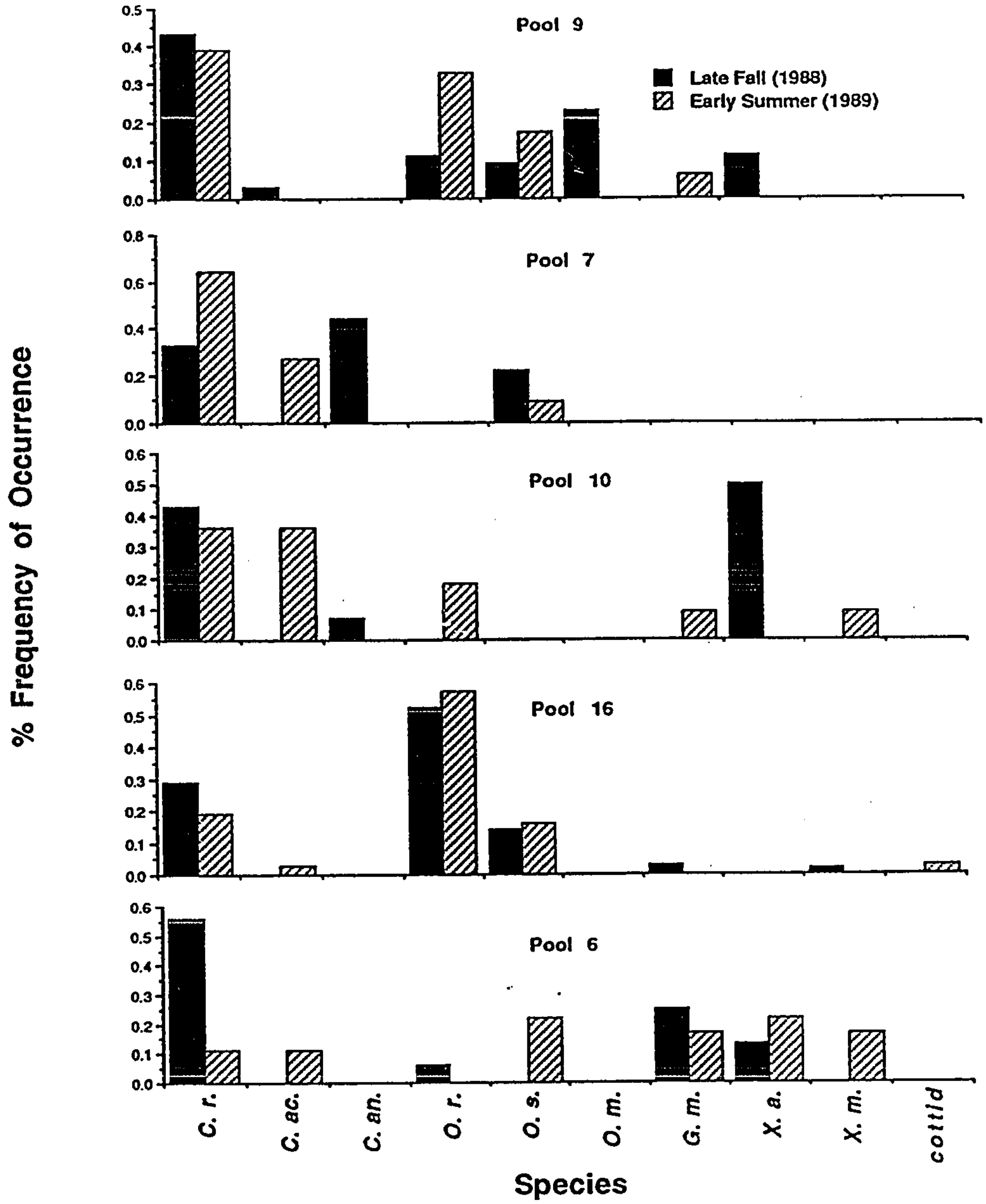
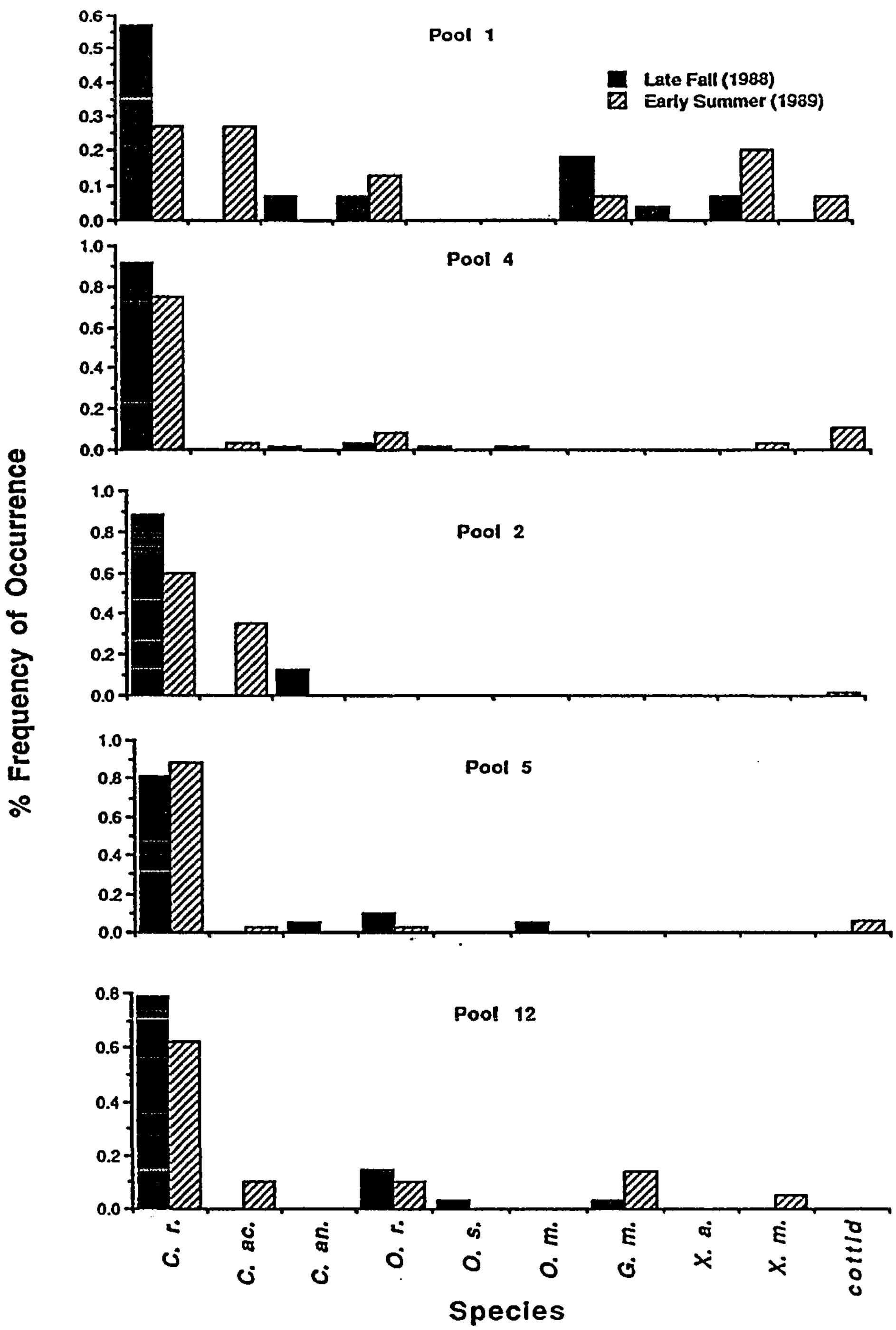


Fig. 1. Location of study area in Garrapata State Park, California, with enlargment of the 16 study pools (shaded areas). The pools used in the tagging experiment (1, 4, 6) are denoted with a "T" and the direction of displacement is shown with the arrows. The control pools (9, 10) are denoted with a "C". All fishes were replaced back into the latter.

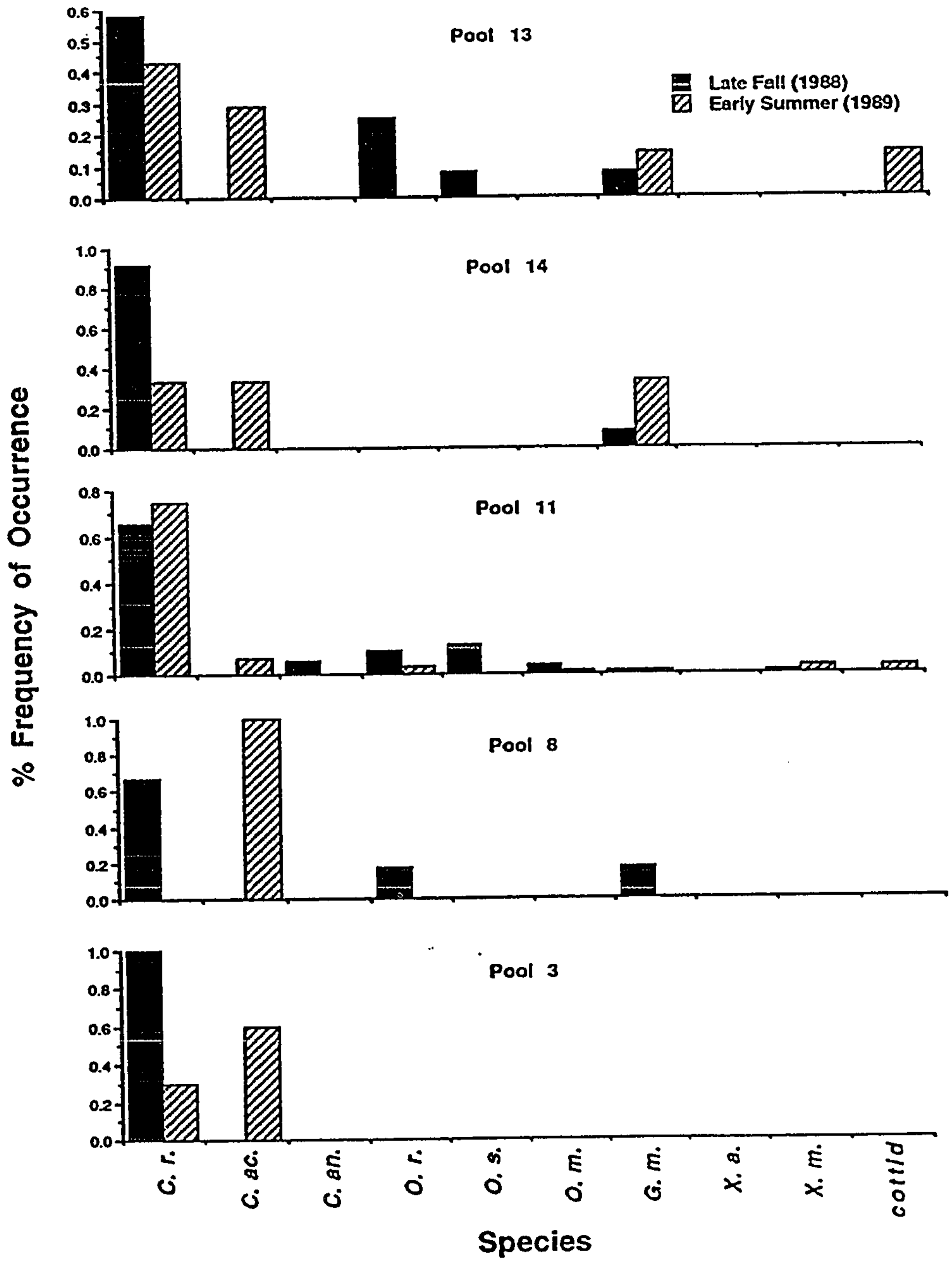
Fig. 2. Percent frequency of occurrence of the "major" (more than five individuals) fish species during the two survey periods, fall 1988 and summer 1989. Pools were divided into three tidal levels: (a) Low (-0.2 to +1.0 m above MLLW); (b) Intermediate (+1.1 to +1.3 m); and (c) High (+1.5 to +2.2 m). The next three pages are arranged with lower pools at the top and higher pools at the bottom. See Table 1 for species names. Unidentified cottid juveniles (~ < 20 mm TL) are shown as "cottid". Note the y-axes are different.



a). Low tidal heights: -0.2 to +1.0 m above MLLW.

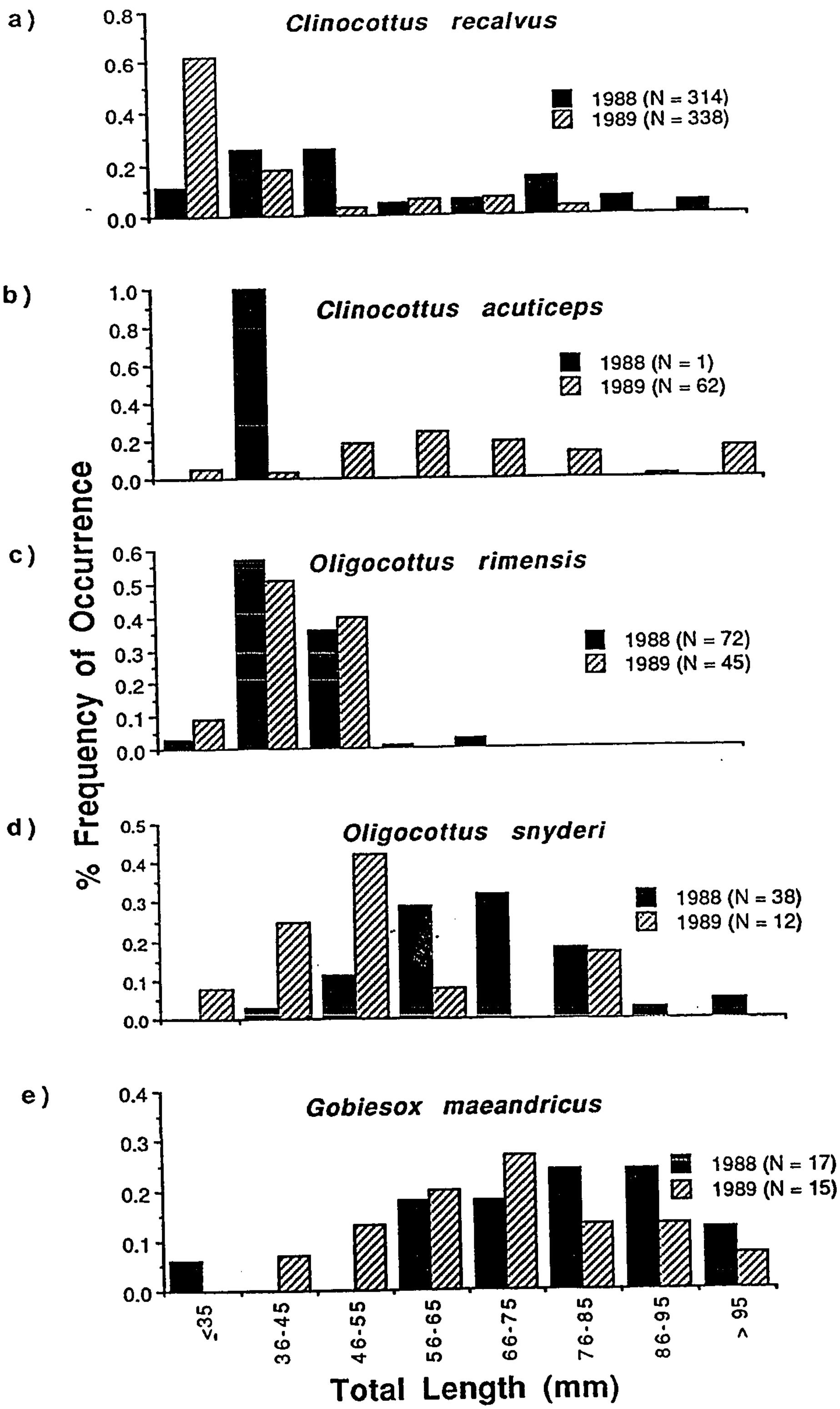


b). Intermediate tidal heights: +1.1 to +1.3 m above MLLW.



c). High tidal heights: +1.5 to +2.2 m above MLLW.

Fig. 3 (a - e). Size frequency distributions for the five most abundant species; data from all pools combined. 1988 and 1989 are shown, with the number of individuals for each period indicated. Note the y-axes are different.


a)
Clinocottus recalvus
1988 (N = 314)
1989 (N = 338)
0.8
0.6
0.4
0.2
0.0
b)
Clinocottus acuticeps
1988 (N = 1)
1989 (N = 62)
1.0
0.8
0.6
0.4
0.2
0.0
c)
Oligocottus rimensis
1988 (N = 72)
1989 (N = 45)
0.6
0.5
0.4
0.3
0.2
0.1
0.0
d)
Oligocottus snyderi
1988 (N = 38)
1989 (N = 12)
0.5
0.4
0.3
0.2
0.1
0.0
e)
Gobiesox maeandricus
1988 (N = 17)
1989 (N = 15)
0.4
0.3
0.2
0.1
0.0
% Frequency of Occurrence
≤35
36-45
46-55
56-65
66-75
76-85
86-95
> 95
Total Length (mm)

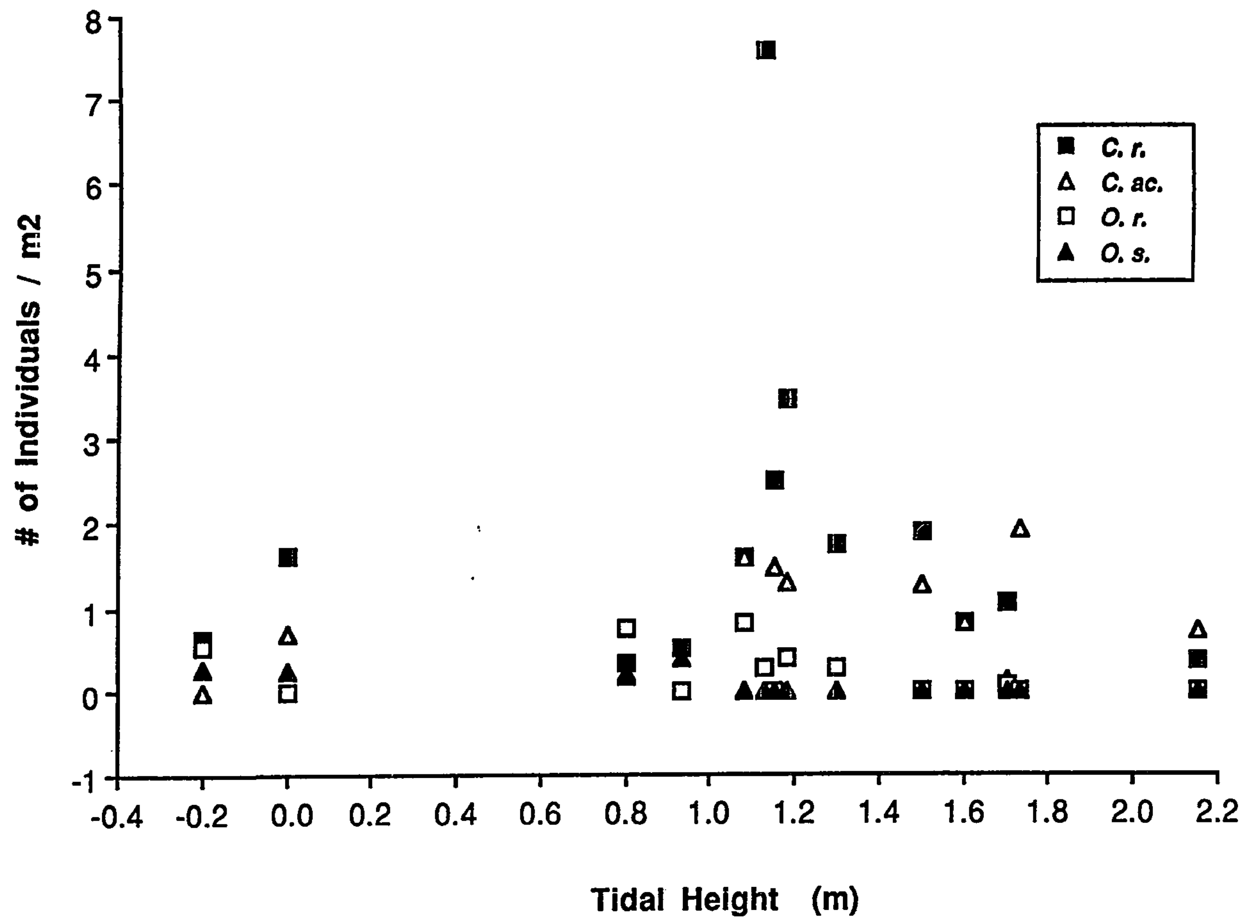


Fig. 4. Relationship of density estimates and pool tidal heights of the four dominant cottid species.

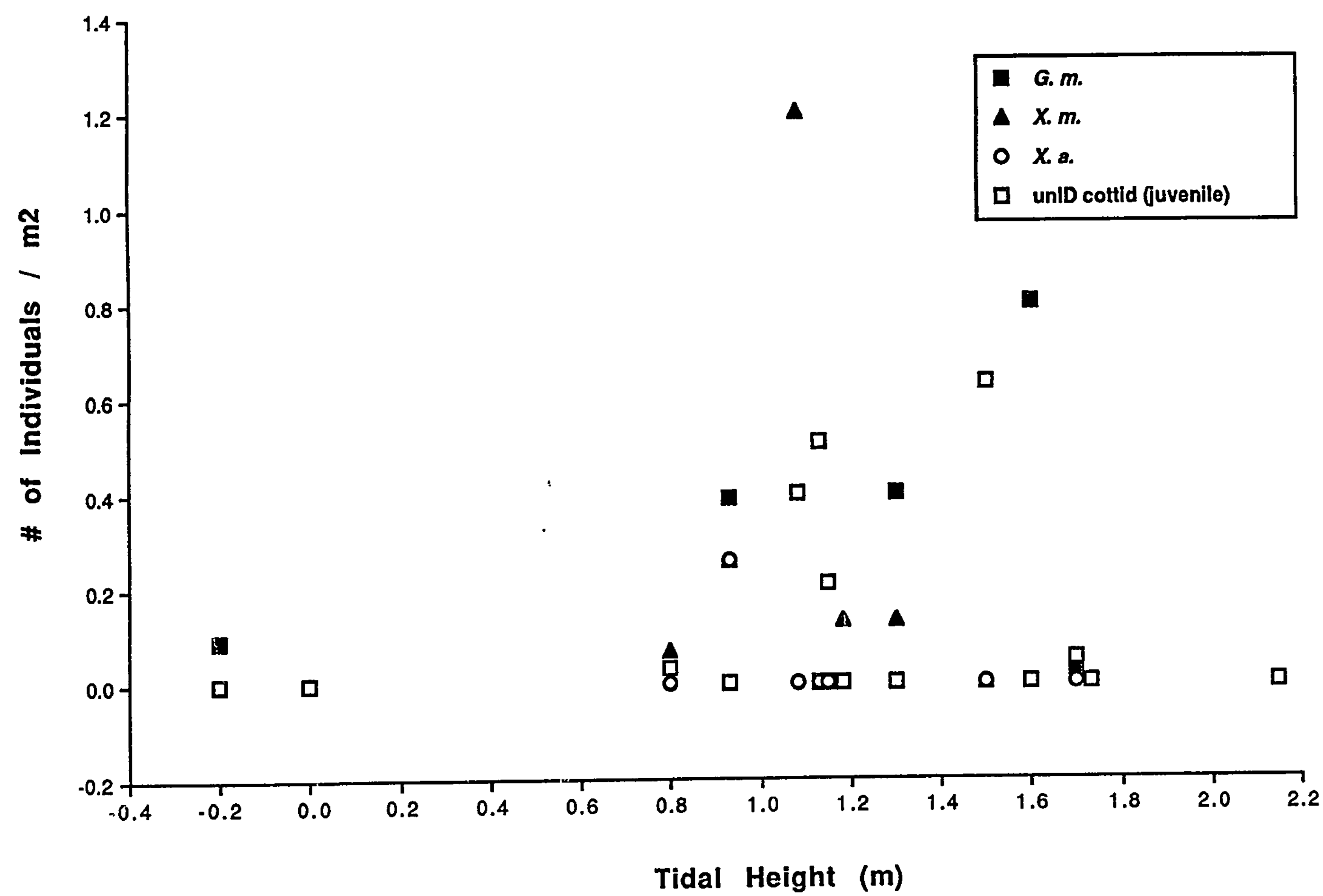


Fig. 5. Relationship of density estimates and pool tidal heights of gobiesocid, stichaeid, and juvenile cottid fishes.

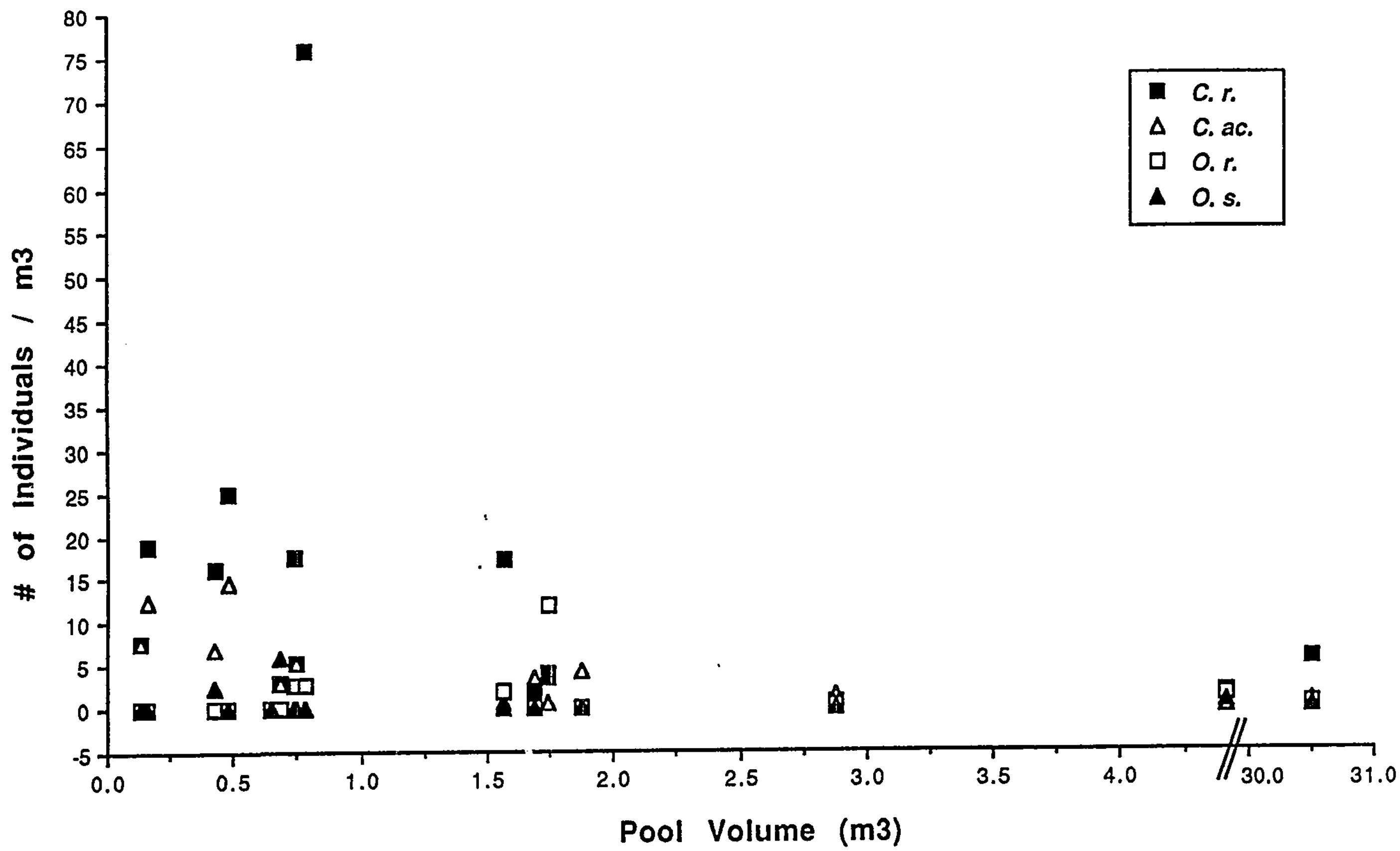


Fig. 6. Relationship of density estimates and pool volumes of the four dominant cottid species.
Note the break in the X-axis.

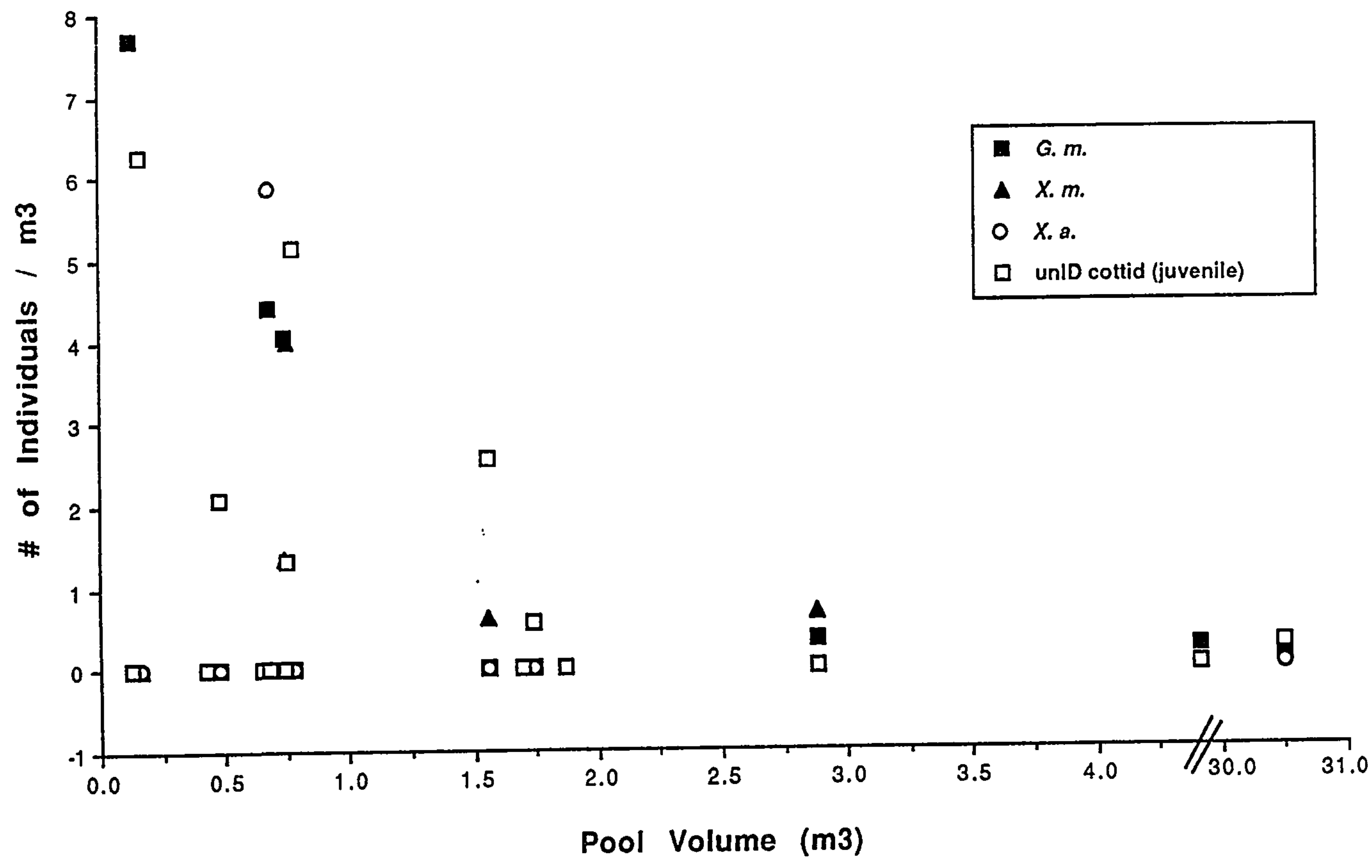


Fig. 7. Relationship of density estimates and pool volumes of gobiesocid, stichaeid, and juvenile cottid fishes. Note the break in the X-axis.

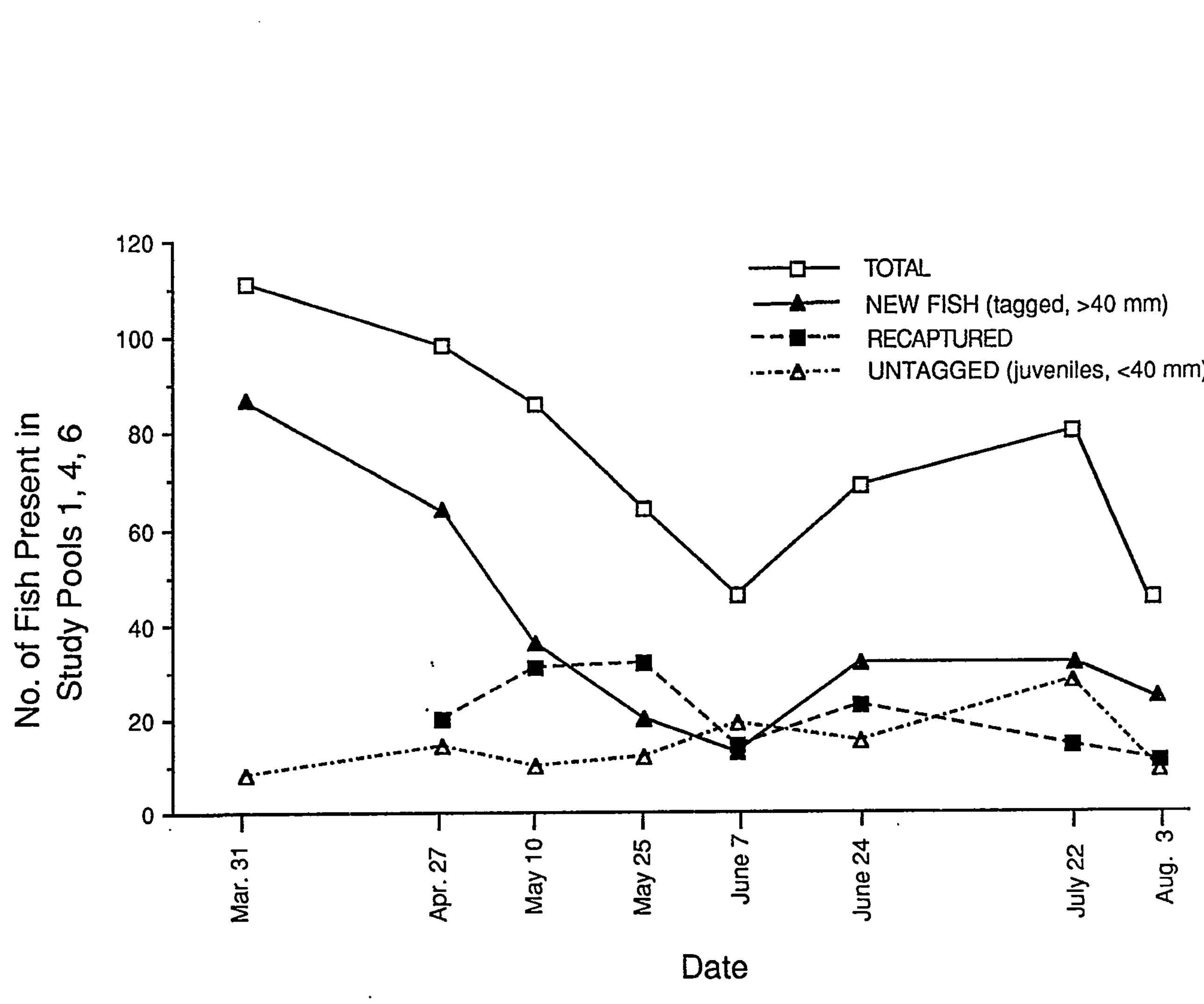


Fig. 8. Number of fish of all species captured in study pools 1, 4, and 6 over the course of the tagging experiment (1989). Total number of fishes, number of newly tagged fishes (> 40 mm TL), number of recaptured fishes, and number of untagged fishes (< 40 mm TL) are shown for each date. No new fish were tagged August 3.

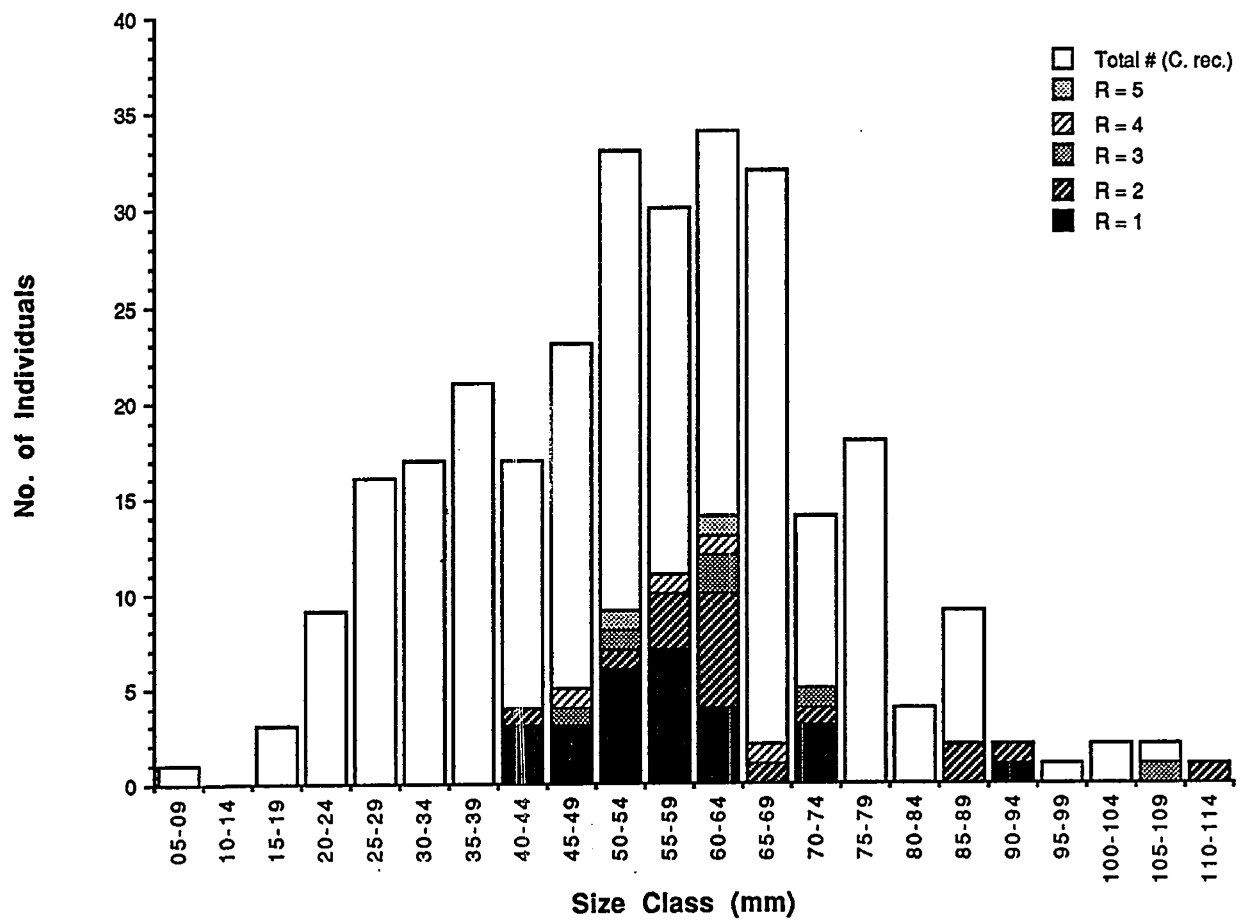
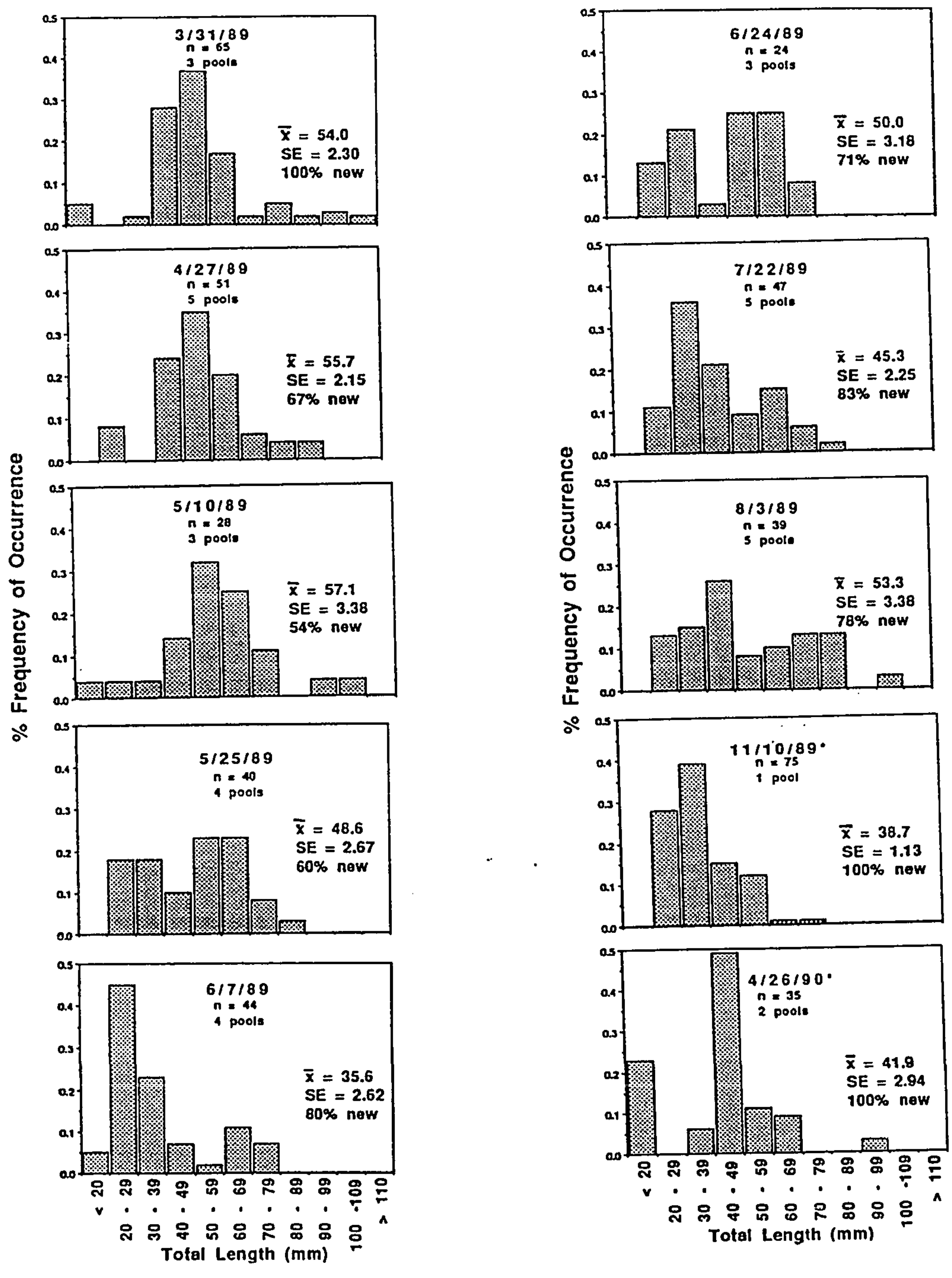


Fig. 9. Number of times individual *Clinocottus recalvus* of different size classes were recaptured (R) in pools 1, 4 and 6 compared to the total number of *C. recalvus* captured during the tagging study in these three pools. No tagging was done on fish < 40 mm TL.

Fig. 10. Size frequencies of new (untagged) *Clinocottus recalvus* captured in pools 1, 4, 6, 9, and 10 during the tagging experiment. Number of fish captured and the number of pools sampled are shown for each date, along with the average size ($\bar{x}$) of the new individuals and one standard error (SE). The difference in mean TL was significant to 0.001 between sampling dates using Kruskal-Wallis (∂ = 0.05). The percent of new, immigrating *C. recalvus* is shown for each date. Dates with (*) were not part of the regular study (see text).



% Frequency of Occurrence
3/31/89
n = 65
3 pools
x̄ = 54.0
SE = 2.30
100% new
4/27/89
n = 51
5 pools
x̄ = 55.7
SE = 2.15
67% new
5/10/89
n = 28
3 pools
x̄ = 57.1
SE = 3.38
54% new
5/25/89
n = 40
4 pools
x̄ = 48.6
SE = 2.67
60% new
6/7/89
n = 44
4 pools
x̄ = 35.6
SE = 2.62
80% new
6/24/89
n = 24
3 pools
x̄ = 50.0
SE = 3.18
71% new
7/22/89
n = 47
5 pools
x̄ = 45.3
SE = 2.25
83% new
8/3/89
n = 39
5 pools
x̄ = 53.3
SE = 3.38
78% new
11/10/89*
n = 75
1 pool
x̄ = 38.7
SE = 1.13
100% new
4/26/90*
n = 35
2 pools
x̄ = 41.9
SE = 2.94
100% new
0.0
0.1
0.2
0.3
0.4
0.5
< 20
20 - 29
30 - 39
40 - 49
50 - 59
60 - 69
70 - 79
80 - 89
90 - 99
100 -109
> 110
Total Length (mm)

Appendix 1. Descriptions of study pools.

POOL #	APPROXIMATE DIMENSIONS (m) (L x W x D) (Max. depth)	RANK BY VOLUME	HEIGHT ABOVE MLLW (m)	DESCRIPTION
1	2.5 x 1.0 x 0.3 (0.7) V= 0.75 m^3	9	1.1	The most S.W. pool. Pile of large rocks in deepest section - fish most likely under sampled.
2	3.0 x 1.6 x 0.1 (0.4) V = 0.48 m^3	13	1.2	Directly inland from #1. Has one medium sized cave, no loose rocks.
3	4.7 x 1.8 x 0.2 (0.5) V = 1.69 m^3	6	2.2	Directly up cliff from #2. Water temperature gets quite high on sunny days.
4	6.5 x 1.2 x 0.2 (0.7) V = 1.56 m^3	7	1.2	Has deep cave at north end and large overhang in center. Narrow and shallow in middle - almost two separate pools.
5	4.1 x 1.9 x 0.1 (0.3) V = 0.78 m^3	8	1.1	Pool has several islands and two small caves. It is directly inshore from #4.
6	3.8 X 0.9 X 0.2 (0.4) V = 0.68 m^3	11	0.9	Large and small rocks line most of bottom. Water from large pool flows directly into this one as the tide rises making sampling difficult.
7	3.3 x 1.3 x 0.1 (0.3) V = 0.43 m^3	14	0.0	Large rock island and two large caves on east side.
8	3.6 x 1.3 x 0.4 (0.8) V = 1.87 m^3	4	1.7	Resembles oval bathtub. Quite barren, no caves.
9	4.4 x 2.5 x 0.4 (1.0) V = 4.40 m^3	2	- 0.2	West end is quite deep with many small holes along walls. East end is shallow with little relief. Floods quickly from large pool as tide rises. This pool is out on the end of a peninsula surrounded by a large pool and a channel.
10	12.2 x 1.2 x 0.2 (0.5) V = 2.88 m^3	3	0.8	Several large rocks in pockets and many smaller rocks along bottom. Many holes and crevices. Pool is inland compared to others in the study.
11	12.8 x 12.0 x 0.2 (0.7) V = 30.72 m^3	1	1.7	Several deep pockets and shallow fingers. Pool is almost cut in half by a rock bridge. The northern end is shallower and the flora is quite different.
12	6.2 x 1.2 x 0.1 (0.4) V = 0.74 m^3	10	1.3	East end has a ~ 0.3 m deep cave and a deep pocket with loose rocks. Rest of the pool is shallow. Pool 11 drains into this one.
13	1.6 x 1.0 x 0.1 (0.4) V = 0.16 m^3	15	1.5	Has several medium sized loose rocks and an underwater bridge that nearly cuts off north arm. South end very shallow.
14	2.5 x 0.5 x 0.1 (0.4) V = 0.13 m^3	16	1.6	Drains into pool 13. Small loose rocks in center. Fairly far inland.
15	3.4 x 1.9 x 0.1 (0.2) V = 0.65 m^3	12	1.7	Several rock islands, very barren, warm water.
16	5.8 x 1.5 x 0.2 (0.5) V = 1.74 m^3	5	0.8	Most northern pool, adjacent to large channel. Pools 11, 12, 13, 14 and 15 all drain into it.

Appendix 2. Percent cover of all algal species, sessile invertebrates, bare and loose rock in pools at low tidal heights (-0.2 to +1.0 m above MLLW) for both survey periods (1988, 1989).

POOL NUMBER

SPECIES	1988 9	1989 9	1988 7	1989 7	1988 10	1989 10	1988 16	1989 16	1988 6	1989 6
Articulated corallines	30%	50	20	30	15	2	35	60	5	15
Encrusted corallines	10	10	5	5	20	2	15	20	15	10
Codium fragile	5	1	1	1			1			
Prionitis sp.	5		5	5	5	1	3	1		5
Pelvetiopsis limitata		2	1			1				1
Ulva sp.	5	3	35	40						2
Colpomenia peregrina			1	1						
Gelidium sp.			5		10	5	15	10		2
Rhodoglossum affine		2			10	5				5
Green scum algae						1				1
Egregia menziesii	5	5					5			
Microcladia borealis										1
Ralfsia		2				3	2		10	10
Iridaea sp.		2		1						10
Gigartina corymbifera										2
Plocamium violacum	2		1							
Phyllospadix sp.			10							
Laminaria sp.							2			1
Desmarestia sp.										
Lessoniopsis littoralis		1								
Ceramiun sp.				5				1		
Cladophora sp.										
Mastocarpus papillatus										
Encrusting red										
Invertebrates	30	15	5		5	5	10	5	5	10
Bare Rock	3	7	10	10	35	75	17		65	25
Loose Rock	5	2	2	5	50	10	2	5	40	30

Appendix 3. Percent cover of all algal species, sessile invertebrates, bare and loose rock in pools at intermediate tidal heights (+1.1 to +1.3 m above MLLW) for both survey periods (1988, 1989).

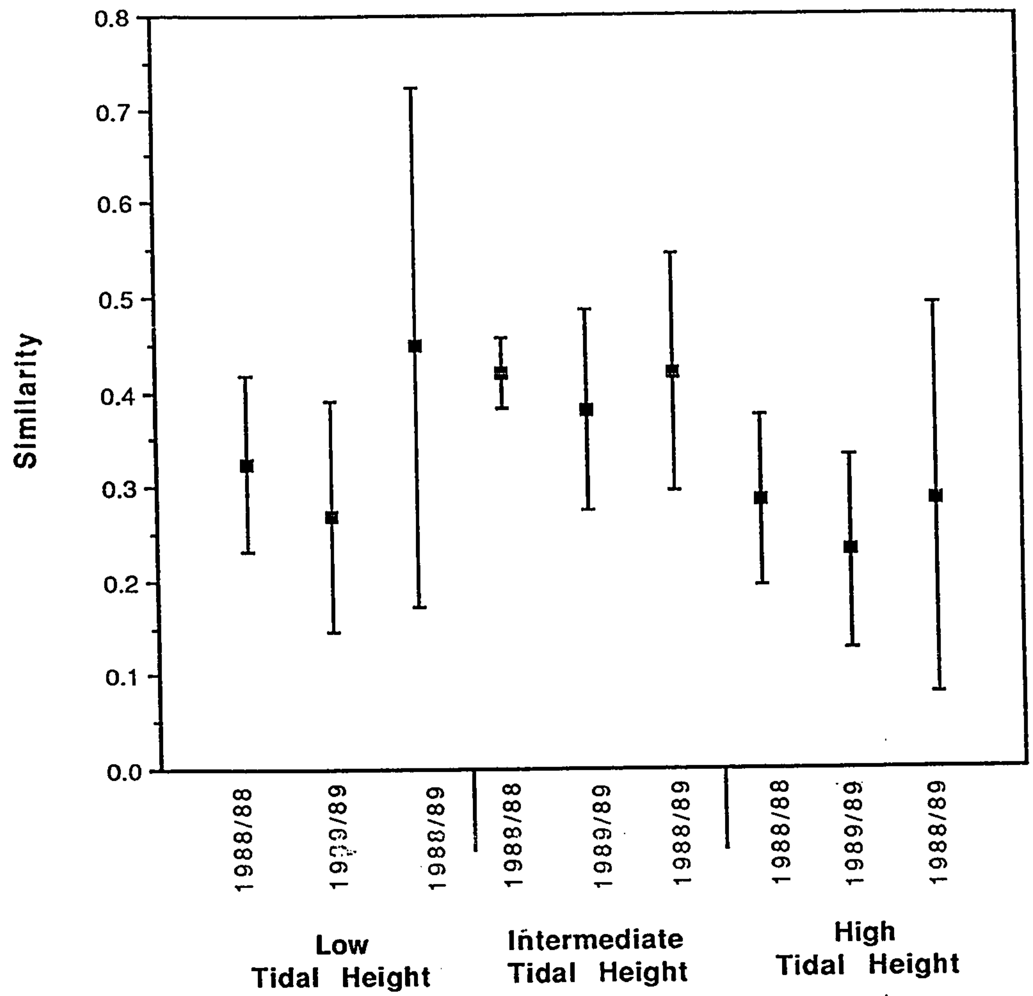
POOL NUMBER

	1988	1989	1988	1989	1988	1989	1988	1989	1988	1989
SPECIES	1	1	4	4	2	2	5	5	12	12
Articulated corallines	20%	20	35	50	19	20	20	50	25	70
Encrusted corallines	25	25	20	5	30	25	10	5	20	
Codium fragile		3	10	5	5	5	10	2	3	
Prionitis sp.	2	3	5	2			5	1	2	
Pelvetiopsis limitata		3				1	2	1		
Ulva sp.							10	5		
Colpomenia peregrina			1		1					
Gelidium sp.							5	5	5	
Rhodoglossum affine							5	2		
Green scum algae	5									
Egregia menziesii			2	1						
Microcladia borealis			1	2		1		2		
Ralfsia		10		3		5	2	1	10	
Iridaea sp.							3	1		
Gigartina corymbifera										
Plocamium violacum			1							
Phyllospadix sp.									2	
Laminaria sp.		1		1						
Desmarestia sp.				1						
Lessoniopsis littoralis										
Ceramiun sp.										
Cladophora sp.									3	1
Mastocarpus papillatus										
Encrusting red										15
Invertebrates	20	25	25	25	35	35	22	30	10	5
Bare Rock	23	10		5	10	8	3	5	20	
Loose Rock	5	25		1		5	3	5	15	10

Appendix 4. Percent cover of all algal species, invertebrates, bare and loose rock in pools at high tidal heights (+1.5 to +2.2 m above MLLW) for both survey periods (1988, 1989).

POOL NUMBER

	1988	1989	1988	1989	1988	1989	1988	1989	1988	1989	1988	1989
SPECIES	13	13	14	14	11	11	15	15	8	8	3	3
Articulated corallines	25%	40	5	30	10	15	30		10	5	1	
Encrusted corallines	10		15	5	10	10	5	60	20	40	1	5
Codium fragile												
Prionitis sp.		10		10	15	10			5	5	30	45
Pelvetiopsis limitata											10	
Ulva sp.					5				5			
Colpomenia peregrina												
Gelidium sp.	10		5		5	10			5			
Rhodoglossum affine	15	5	20		20	15	10		3		5	
Green scum algae									3			
Egregia menziesii									5			
Microcladia borealis									2			
Ralfsia	15		20		4		20		5	25		5
Iridaea sp.									15			
Gigartina corymbifera									2			
Plocamium violacum												
Phyllospadix sp.												
Laminaria sp.												
Desmarestia sp.												
Lessoniopsis littoralis												
Ceramiun sp.												
Cladophora sp.					10	15						
Mastocarpus papillatus					1							
Encrusting red		40		50		5		20				
Invertebrates	5	5	10	1	10		25	10	5	5	1	5
Bare Rock	20	5	25	5	10	10	10	10	15	30	50	35
Loose Rock	10	5	10	5	5	3			5	2	2	5



Appendix 5. Mean percent similarity indices (with 95% confidence intervals) of algae among Low, Intermediate and High tidal height pools.