Larvae of Nearshore Fishes in Oceanic Waters near Oahu, Hawaii

Thomas A. Clarke
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ABSTRACT

Larvae of over 50 families of nearshore fishes were taken in oceanic waters about 13 km offshore of the leeward (southwest) coast of Oahu, Hawaii during 1977-78. The five most frequently taken families (Labridae, Parapercidae, Serranidae, Gobiidae, and Carangidae) made up over 50% of the total nearshore larvae. Most other families were taken very infrequently. Comparison of catch data from three types of nets indicated that 1.25-m diameter bongo nets often sampled larvae as well or better than a 3-m Isaacs-Kidd trawl and that smaller, 70-cm diameter bongo nets were often as effective as the larger nets for certain abundant taxa. Only a few taxa showed evidence of seasonal patterns in abundance. Irregular temporal variability in abundance of some taxa may have been related to occasional recent influxes of surface water from closer to shore. Most larvae taken were late preflexion stage or older. Densities of even the most abundant taxa were rarely greater than 0.001 m$^{-3}$. The nearshore fish larvae were not dominated by taxa with large larvae or with larvae possessing apparent specializations to pelagic existence. Most taxa taken were pelagic spawners as adults, but larvae of demersal spawners were roughly as well represented as demersal spawners are among the nearshore fish fauna. Previous studies of waters closer to shore probably sampled insufficient volumes for any but a few exceptionally abundant taxa. Sampling with volumes filtered of the order of $10^4$ to $10^5$ m$^3$ will be necessary to determine if the dominant taxa taken by the present study are ever more abundant closer to shore.

Introduction

Most species of nearshore marine fishes have pelagic eggs or larvae which are subject to dispersal away from adult habitat. Consequently, recruitment to adult populations is controlled not only by survival during the pelagic stages but also by the probability of return of premetamorphoric larvae to inshore areas suitable for settlement. The role of egg and larval dispersal in the population dynamics of tropical inshore fishes has recently received much attention (McFarland and Ogden 1985). Losses due to dispersal away from suitable habitats may be more important in limiting recruitment of nearshore fish populations of steep sloped oceanic islands than populations along more extensive and broader continental coastlines (Walsh 1987). For the most part, aspects or consequences of dispersal have been inferred from shore-based studies of spawning and recruitment (Victor 1984), adult life-history characteristics (Barlow 1981), or ages of settlement estimated from otolith increments (Brothers and Thresher 1985). There is little direct knowledge of the distribution, density, and size composition of larvae of inshore fishes.

Most available data on fish larvae near oceanic islands are from relatively close to shore. Leis (1982) found that larvae within a few km of shore in Hawaii were dominated by a few species, most of which were demersal spawners. Larvae of most common inshore fish families with pelagic eggs were rare or absent. Larvae of several inshore families have been reported from oceanic waters well removed from adult habitats (Richards 1984), and some inshore taxa have larvae with apparent adaptations to pelagic existence (Leis and Rennis 1983). Based on abundance of certain groups of larvae relative to total larvae in a series of samples from Hawaii, Leis and Miller (1976) concluded that larvae of inshore families which spawn demersal eggs were more abundant close to shore and that larvae of families which spawn pelagic eggs were more abundant offshore. They did not, however, provide or compare actual densities of different types of larvae from different locations. In fact, there are few quantitative data...
available on densities of larvae of inshore fishes in oceanic waters.

This paper reports on the larvae of inshore fishes taken in oceanic waters near the Hawaiian Islands. The larvae were taken during a 16-month long program that repeatedly sampled the upper layers with three different types of nets. Although the program was originally designed for investigation of vertically migrating oceanic fishes and the collections were dominated by oceanic taxa, larvae of inshore taxa were also regularly taken. The data on the latter provide the opportunity for more quantitative consideration of composition, abundance, and seasonality than was previously available for offshore waters and also permit more definitive comparison with data from areas closer to shore.

**Methods**

All samples were taken along a track roughly parallel to and ca. 13 km off the leeward coast of the island of Oahu, Hawaii (between 21°18′N, 158°15′W and 21°30′N, 158°23′W). Water depth along the transect was 2000 m or greater, and the macrozooplankton and micronekton in the area were dominated by oceanic species (Clarke 1980). Samples were taken on short cruises between August 1977 and October 1978. Most cruises were within 1–2 days of new moon of each lunar month during the period. Because of scheduling difficulties, there was no cruise in January 1978; the cruise for November 1977 was 4–5 days after full moon; and the cruise for February 1978 was at full moon. Thus 15 of the 16 lunar months covered were sampled, and 13 at or close to new moon. The cruises are subsequently referred to by year and month, e.g., 78-03 for March 1978. (New moon occurred twice in October 1978. For convenience, the cruise during the second new moon was designated 78-11 in spite of the fact that the cruise was taken sequentially along the southern end of the transect. The exceptions to the standard sampling were: only three IK tows on 77-09 and 77-12, no BB tows on 77-12, and only two or three SB tows on the first five cruises (77-8 through 77-12). Additionally, two IK samples were taken during each of two other cruises in the same area at full moon in both March and April, 1978. A total 62 IK samples, 28 pairs of BB samples, and 50 pairs of SB samples were examined.

All nets were equipped with flowmeters and time-depth recorders. For the few cases where one or the other device malfunctioned, the missing value of either flow or maximum depth was estimated from plots of flow vs. maximum depth of the satisfactory tows. Volumes sampled were determined from flowmeter data and mouth area. Because the sampling program was originally designed for vertically migrating mesopelagic fishes, the maximum depths were purposefully much greater than needed for sampling of inshore fish larvae. Current studies with opening-closing nets (Boehlert and Mundy, NMFS, Honolulu Laboratory) as well as preliminary analyses of nearshore fish larvae from many horizontal IK tows taken in the study area from 1969 to 1974 indicate that few, if any, occur deeper than ca. 100 m. Consequently, the total volume sampled by each tow was multiplied by the ratio of 100/maximum depth to provide the volume sampled in the upper 100 m only, a more appropriate value for this study.

The means (and ranges) of volumes sampled in the upper 100 m per tow by each type of net were IK—31,919 m³ (23,400 - 56,250 m³); BB (both nets)—6582 m³ (3450 - 15,200 m³); SB (both nets)—781 m³ (326 - 1604 m³). For each type of gear, the variability in volume filtered per tow was almost exclusively due to variability in flow/time (as opposed to deviations from the wire out schedules or total duration of tow) and was apparently caused by unexplained variation in the ship’s speed. The effect was compounded because maximum tow depth was inversely correlated with flow/time. Consequently, both the volume/tow and the ratio of 100/maximum depth were higher for faster tows.

There were also great differences in the relative volumes filtered per cruise by each type of gear. For individual cruises, the IK tows filtered 6.5–20.4 times the volume filtered by the BB tows and 23.5–83.9 times that filtered by the SB tows. Overall the IK tows filtered 10.53 times the volume filtered by the BB tows and 46.88 times that by the SB tows. The volume filtered by the BB tows was 3.3–12.3 times the SB volume for individual cruises and 4.45 times the SB volume overall. For the 13 cruises where at least three SB tows were taken, the range of BB:SB...
volumes filtered was 3.5–6.8. (The above comparisons involving the BB exclude 77–12 when no BB tows were taken.)

Samples were preserved and held in 4% formaldehyde-seawater solution. The IK samples were sorted under 3× magnification. Subsequent rechecking of selected samples under a dissecting microscope at 10× indicated that negligible numbers of fish larvae over 5–6 mm long and 5–10% of the smaller larvae were missed by the routine procedure. The BB and SB samples were sorted under a dissecting microscope at 10×. Rechecking indicated that practically no fish larvae were missed by routine sorting. Standard lengths or, for preflexion larvae, notochord lengths were measured to the nearest 0.5 mm. For both types of bongo samples, the catches and volume sampled from both nets combined were used for analyses and presentation. The SB samples with 0.183-mm nets obviously retained smaller larvae than those with 0.333-mm nets, but since such small larvae attributable to nearshore families were so infrequent in the samples, the data from both types of SB samples were pooled for analyses.

Fish larvae from inshore taxa were separated from those of oceanic groups. The latter, mostly myctophids and stomioids, usually constituted over 90% of the total larvae. Two major groups which are solely or partly inshore, the Pleuronectiformes and Anguilliformes, were not further identified and are not considered in this paper. Almost all late preflexion and postflexion larvae were readily identifiable to either nearshore or oceanic taxa, and the former were usually identifiable to family. Among the very small (<2–3 mm) early preflexion larvae there were a substantial number that I did not definitely class as either oceanic or nearshore. Based on my observations of larger, identifiable oceanic larvae during the sorting and identification process, the great majority of these “unknown” preflexion larvae were probably of oceanic perciform or perciform-like taxa, such as melanoids, *Huwella* spp. and similar epigonids, stomioids, or perhaps even some myctophiforms, whose very early larval stages have not been described. These unknown preflexion larvae were smaller and less-developed than the smallest identifiable specimens of most nearshore taxa, and there were no apparent “connecting links” between them and larger nearshore larvae in the material. (Fairly continuous series of sizes and developmental stages were present for the few nearshore taxa whose size range included very small larvae.)

Identification of nearshore larvae below family was variably possible. Many families taken almost certainly included more than one form of larvae, but numbers were too low to assemble definitive series for reliable discrimination. In other cases, distinct forms were evident and often attributable to genera or species known from Hawaii based upon meristics, previously published descriptions, or developmental series that were assembled from available material. In many families, where the meristics of different genera or species overlap, tentative or “most likely” identifications of different forms were based upon frequency distribution of counts. Frequently, forms could not be discriminated from each other at the smallest sizes. For most larvae identified to genus it was usually not certain that either one or more than one species were included; consequently, I have omitted the conventional “sp.” or “spp.” after generic names.

Most nearshore taxa were taken very infrequently, and even for the abundant taxa, data from all cruises were pooled for density estimates and between gear comparisons. Even then, total catches of the SB and often the BB were ≤5 for many taxa and considered inadequate for further analyses. Catches of a few very abundant taxa were high enough for meaningful comparison of densities and size composition between cruises with high catches and the remainder of the data. Otherwise, numbers were too low and variability too high for meaningful within or between cruise comparisons. Size compositions were compared using the Kolmogorov-Smirnov test; differences were considered significant if the resultant probability was ≤0.05. Interpretation of differences in density estimates was very conservative. Differences of less than ± 50% were considered likely to be due to chance and small numbers, and the data were carefully examined to assure that apparent differences were not due to one or two extremely high catches.

## Results

A total of 5192 larvae were definitely and 74 tentatively identified to one of 53 families of nearshore fishes. Some families could be further broken down into size groups, lower taxa, or recognizable different forms, with the end result of 122 different categories of nearshore larvae (Table 1). Additionally there were two unidentified forms of larvae, each represented by seven individuals, which were probably nearshore forms but whose meristics were unattributable to any known Hawaiian families. (One of the unidentified forms resembled uranoscopelids most closely and the other, apogonids.) Only 26 postflexion specimens, some damaged, were neither clearly of oceanic families nor definitely attributable to any nearshore family, but there were 550 “unidentified preflexion” larvae.

The nearshore larvae were dominated by a few forms (Table 2). The 20 most abundant families made up over 90% of the total. The Labridae alone accounted for almost 25% of the total, and the five most abundant families accounted for over half. Among lower taxa, *Parapercis*, *Labrid*, *S*, and *Luzonichthys earlei* made up almost 25% of the total larvae, and the top twenty forms made up over 50%. For the great majority of larval forms listed in Table 1, the numbers of specimens collected were so few that further comment beyond the record of their numbers and size...
Table 1

Numbers and size ranges of nearshore fish larvae collected from oceanic waters near Oahu, Hawaii during 1977-78. For each taxon, the number and size range of positively identified specimens are followed by the number and size range of specimens that could only be tentatively identified (“No.?”).

<table>
<thead>
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<th>Taxon</th>
<th>Size</th>
<th>No.</th>
<th>Size</th>
<th>No.?</th>
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<td>Size (mm)</td>
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<td>(8-8.5)</td>
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<td>Trachinocephalus myops</td>
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<td>(4.5-40)</td>
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<td>(11)</td>
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Table 1 (continued)

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<td>90 (7-25)</td>
<td></td>
<td>Diodontidae</td>
<td>21 (2.5-20)</td>
<td>1 (3)</td>
</tr>
<tr>
<td><em>Goby B</em></td>
<td>55 (5.5-12)</td>
<td>1 (4.5)</td>
<td>Ostraciidae</td>
<td>4 (2-21.5)</td>
<td>2 (2)</td>
</tr>
<tr>
<td><em>Goby D-3</em></td>
<td>37 (5.5-10.5)</td>
<td>4 (8.5-10)</td>
<td>Unident. A</td>
<td>6 (11-18)</td>
<td>1 (4)</td>
</tr>
<tr>
<td><em>Goby D-5</em></td>
<td>42 (4.5-11.5)</td>
<td>3 (8-10.5)</td>
<td>Unident. B</td>
<td>7 (5-21)</td>
<td></td>
</tr>
<tr>
<td><em>Goby R</em></td>
<td>13 (7-10.5)</td>
<td>2 (3.5)</td>
<td>Unident., postflexion</td>
<td>26 (3-15)</td>
<td></td>
</tr>
<tr>
<td><em>Goby C</em></td>
<td>3 (7-8.5)</td>
<td></td>
<td>Unident., preflexion</td>
<td>550 (1-7)</td>
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Table 2

<table>
<thead>
<tr>
<th>Families</th>
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<tr>
<td>Rank</td>
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<td>1. Labridae</td>
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<td>2. Parapercidae</td>
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</tr>
<tr>
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</tr>
<tr>
<td>4. Gobiidae</td>
<td>334</td>
</tr>
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<td>5. Carangidae</td>
<td>332</td>
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<tr>
<td>6. Acanthuridae</td>
<td>251</td>
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<td>7. Mullidae</td>
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<tr>
<td>8. Synodontidae</td>
<td>203</td>
</tr>
<tr>
<td>9. Scorpaenidae</td>
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</tr>
<tr>
<td>10. Pomacanthidae</td>
<td>157</td>
</tr>
<tr>
<td>11. Callionymidae</td>
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<tr>
<td>12. Microdesmidae</td>
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<tr>
<td>13. <em>Symphurus</em></td>
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<td>14. Eleotridae</td>
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<td>15. Apogonidae</td>
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<td>16. Scaridae</td>
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<td>17. Pomacentridae</td>
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</tr>
<tr>
<td>18. Blennidae</td>
<td>74</td>
</tr>
<tr>
<td>19. Lutjanidae</td>
<td>73</td>
</tr>
<tr>
<td>20. Schindleriidae</td>
<td>52</td>
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</table>
Estimated densities of frequently collected taxa of nearshore fish larvae in the upper 100 m of oceanic waters near Oahu, Hawaii, 1977-78. Densities were calculated from catches of three different nets: a 3-m Isaacs-Kidd mid-water trawl (IK), 1.25-m diameter bongo nets (BB), and 70-cm diameter bongo nets (SB). Values are not given for cases where the total catch was < 5 individuals. Densities based on all sizes or cruises are indicated by "all." Otherwise, inequalities under "Size" indicate inclusion of only large or small sizes of certain taxa, and cruise numbers (see text) under "Cruise" indicate separate consideration or exclusion ("X") of data from certain cruises with exceptionally high catches (see text).

### Table 3

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Size (mm)</th>
<th>Density (No./1000 m³)</th>
<th>Cruise</th>
<th>Density (No./1000 m³)</th>
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<tr>
<td></td>
<td></td>
<td>IK</td>
<td>BB</td>
<td>SB</td>
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<td>Synodus</td>
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<td>0.456</td>
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<td></td>
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<td>0.500</td>
<td>0.604</td>
</tr>
<tr>
<td></td>
<td>&lt;22</td>
<td>0.019</td>
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<td>Apogoninae</td>
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<tr>
<td>Carangidae</td>
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<td>0.097</td>
<td>0.359</td>
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<td>Labrid</td>
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<td>1.408</td>
<td>1.300</td>
<td>17.478</td>
</tr>
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<td>0.100</td>
<td>0.250</td>
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<tr>
<td>Labrid</td>
<td>&gt;10</td>
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<td>0.433</td>
<td>0.276</td>
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<td>0.006</td>
<td>0.027</td>
<td>0.048</td>
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<td>0.894</td>
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<tr>
<td>Serranid A</td>
<td>all</td>
<td>0.007</td>
<td>0.103</td>
<td>0.121</td>
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<tr>
<td>Symphysanodon</td>
<td>all</td>
<td>0.058</td>
<td>0.016</td>
<td>0.217</td>
</tr>
<tr>
<td>Serranid A</td>
<td>&gt;20</td>
<td>0.040</td>
<td>0.098</td>
<td>0.97</td>
</tr>
<tr>
<td>Serranid A</td>
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<td>0.028</td>
<td>0.266</td>
<td>0.773</td>
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<tr>
<td>T. myops</td>
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<td>0.362</td>
<td>0.698</td>
<td>0.942</td>
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<tr>
<td>Serranid A</td>
<td>78-03</td>
<td>0.009</td>
<td>0.163</td>
<td>0.121</td>
</tr>
<tr>
<td>Serranid A</td>
<td>78-07</td>
<td>0.073</td>
<td>3.103</td>
<td>0.121</td>
</tr>
</tbody>
</table>

Ranges is not merited. Results for the more frequently taken taxa are presented in the following individual accounts.

**Synodontidae**

The great majority of synodontids were Synodus (Table 1). These were taken on all but one cruise, but densities were markedly higher than average on 77-11 (Table 3) when over a fourth of the specimens were taken. There was, however, no significant difference in size composition between the 77-11 specimens and those from the remainder of the cruises. The overall median length was 17 mm and 75% of the specimens were between 10 and 26 mm. Although the IK caught all but one of the 14 specimens over 27 mm, there was no significant difference in size composition between IK and BB catches (Fig. 1). The estimated density from the BB data was considerably higher than that from the IK. Larvae from the SB catch were significantly smaller in size than those from the BB catch (Fig. 1), and the largest in the SB catch (21 mm) was only 4 mm longer than the median size for the BB catch. For larvae < 22 mm, the estimated density from the SB catch was almost twice the BB estimate.

**Trachinocephalus myops** was taken between August and March. Only one specimen was taken by the SB. The IK captured 9/11 of specimens over 22 mm, while the BB captured the same fraction of those 22 mm or less. The remaining synodontids taken were either definitely or probably small Saurida.

**Ophidiidae**

Neither of the two types of ophidiid larvae were taken frequently (Table 1). For both, sizes between small larvae and nearly transformed individuals were absent. Fourteen of the Brotula multiharbata were 3-13 mm long, while the
remaining four were 26-60 mm. Five specimens of ophidiid X were 6.5-15 mm and the other nine were 27-40 mm. Ophidiid X may prove to be either a pelagic or deep benthic rather than a nearshore species.

Holocentridae

Holocentrine larvac were taken only in July, August, and September. Seven specimens (tentatively identified) were small (1.5-2.5 mm), early preflexion larvae taken on 77-08. Ten of the 17 myripristine larvae were taken in October, but the remainder were scattered throughout the other cruises.

Zeniontidae

Zenion was taken on two-thirds of the cruises; captures were scattered throughout the year. Almost half the specimens taken (13) were >13 mm long and taken by the IK. Two large specimens (30 and 38 mm) were females carrying vitellogenic oocytes. Thus it is not certain that Zenion should be considered a nearshore species.

Scorpaenidae

Scorpaenids <5.5 mm long could not be reliably identified beyond family, but, like the larger larvae, most were probably Scorpaeninae (Table 1). Among the larger scorpaenines, Scorpaenodes spp., which were distinguishable by the parietal spines and dorsal spine counts, were taken on most cruises, but not in large numbers. The remaining scorpaenines all had the same fin ray counts (D = XII, 9; A = III, 5; PI = 16, or rarely 17, 18) and could belong to any of the genera known from Hawaii except Scorpaenodes. There were obviously a great many forms among these specimens, but only two could be reliably distinguished on the basis of body pigment. All but one specimen of scorpaenid E were taken between November and March, and all but one of scorpaenid F in February or March.

A distinct form attributed to Dendrochirus barberi on the basis of fin ray counts was taken in a few samples. The remaining scorpaenids were Setarchinae. Four of these (4.5-9 mm) were Setarches sp. The others were either definitely or tentatively Ectreposebastes. (Some individuals less than 5.5 mm could not be definitely identified.) Ectreposebastes imus is a deep-water species which migrates well off the bottom at night (Struhsaker 1973); adults have occasionally been taken in IK tows at depths between ca. 500 and 1000 m in the same study area.

Apo gonidae

Other than a few specimens of Pseudamiops taken between July and November, the apogonids collected (Table 1) were all apogonines that were not identifiable to species. At least four different forms were taken, but the distinguishing features, principally body shape and pigment on the fin rays, appeared to become less useful with increasing size. Consequently, many larger specimens and those with damaged fin rays could not be assigned to one of the forms. Apogonine A, an elongate form, was represented by about 40 specimens 4-22 mm long. Twenty of these were taken in 77-08, but the rest were scattered throughout the year. A stubbier form (possibly Apogon erythrinus) was represented by at least 10 individuals 3.5-10 mm long; these captures were scattered throughout the year. Two other forms, intermediate in body shape and similar to each other, were represented by six or fewer individuals. The size ranges of apogonines captured were about the same for both BB and IK, but the BB density estimate was much higher than the IK's (Table 3). Those captured by the SB were mostly 4-5 mm individuals.

Carangidae

All but one of the carangid larvae were taken from July through November. The great majority were taken on 78-10, and estimated densities for that cruise were much higher than for the other cruises (Table 3). About 80% of the carangids were small (2-6 mm). Based upon pigmentation, body shape, and head spination, all but five of these were almost certainly either Decapturus, four species of which occur in Hawaii, or Selar crumenophthalmus. Both genera are coastal pelagic and, particularly for Decapturus, spawning could occur well away from shore. Among the
larger larvae, both genera were identified based on fin ray counts (Table 1). Pigmentation differences indicated that at least two forms of Decapterus were present. Scymenteroides lyan was taken in a few samples, and several larvae of Seriola were taken in a single sample from 78-10. The more strictly demersal types of carangids were represented by only two and possibly three small Caranx larvae.

**Chaetodontidae**

Except for a single larva of Forcipiger, all chaetodontid larvae were apparently Chaetodon. Dorsal and anal counts from 31 large, undamaged individuals were XII–XIII, 21–24 and III, 17–20, respectively. Most were XIII, 21–23 and III, 18–19. While species or even species groups could not be discriminated by counts, clearly several of the Hawaiian species of Chaetodon with higher counts were not represented in the samples. Chaetodon larvae were taken on all but four of the cruises, but 16 were taken on 78-03 and 78-04. Seven of the total of eight with twelve dorsal spines were taken on 78-02 or 78-03. Most Chaetodon were taken by IK; the BB, however, caught four of the five specimens <6 mm long. The remaining specimens were almost completely separated into two size groups: 11 (6–12 mm) and 19 (19–31 mm). Seven of the smaller group were the specimens with twelve dorsal spines taken in February or March.

**Lutjanidae**

Lutjanid larvae were taken almost exclusively in the late summer and fall. Over two-thirds of the Lutjanus larvae were small (3–5.5 mm) individuals taken in 77-08 when density estimated from the BB was over 1/10³ m³ (Table 3). One small individual was taken in June and two in July. The larger ones were taken from August through October of both years. All Aprion virescens were taken in August, and Pripptomoides larvae were taken from July through October.

**Mullidae**

Over half (130) of the mullid larvae were small (<5 mm) individuals taken by BB or SB tows. These were most abundant in 77-08 (Table 3) when 139 of the mullids were taken; 69 and 35 were taken in single SB and BB tows, respectively. The 78-10 and 78-11 cruises caught 18 and 33 mullids, respectively. The remainder, including all sizes, were scattered throughout the rest of the cruises. Presumably owing to extrusion through the IK and BB meshes, the SB density estimates were much higher than for the larger nets. Even if only the mullids >9 mm were considered, the SB density estimates were by far the highest and the IK’s the lowest (Table 3).
June larvae from all three types of gear were dominated the study area, particularly six large individuals taken in Serranid A' was very similar to Serranid A and was represented in the samples by only three small and questionably identified specimens. On the basis of other material from Serranid A larvae were relatively large (10-18 mm). The most frequently taken serranid was the anthine, Luzonichthys ear/ei. (Larvae of this species, identified as “probably Anthias sp.” are illustrated by Leis and Rennis 1983, fig. 17.) It was taken on every cruise, but 50% of the total catch was of relatively small individuals taken in June. The June larvae from all three types of gear were dominated by 7-11 mm individuals, which made up 64% of the catch (Fig. 3). Larvae of this size were a minor fraction of catches from the rest of the year; 77% of those from other cruises were metamorphic or apparently metamorphosed individuals >20 mm long. As might be expected, the small Luzonichthys ear/ei were more effectively sampled by the SB and BB (Table 3). Even for large larvae and juveniles from all cruises, the BB and SB estimates were similar and considerably higher than that from the IK data. The maximum size captured by the SB was only 2 mm smaller than the largest IK specimen.

Serranidae

The most frequently taken serranid was the anthine, Luzonichthys ear/ei. (Larvae of this species, identified as “probably Anthias sp.” are illustrated by Leis and Rennis 1983, fig. 17.) It was taken on every cruise, but 50% of the total catch was of relatively small individuals taken in June. The June larvae from all three types of gear were dominated by 7-11 mm individuals, which made up 64% of the catch (Fig. 3). Larvae of this size were a minor fraction of catches from the rest of the year; 77% of those from other cruises were metamorphic or apparently metamorphosed individuals >20 mm long. As might be expected, the small Luzonichthys ear/ei were more effectively sampled by the SB and BB (Table 3). Even for large larvae and juveniles from all cruises, the BB and SB estimates were similar and considerably higher than that from the IK data. The maximum size captured by the SB was only 2 mm smaller than the largest IK specimen.

Four forms of serranid larvae were probably Anthias. Serranid A was taken only from December through March; 65 of the 70 specimens were from 78-03. All but four Serranid A larvae were relatively large (10-18 mm). Serranid A' was very similar to Serranid A and was represented in the samples by only three small and questionably identified specimens. On the basis of other material from the study area, particularly six large individuals taken in May 1974, it appears distinct from Serranid A. All known captures of this form were from May through August. Both these forms have nine anal rays. On the basis of dorsal ray counts, Serranid A is probably Anthias ventralis and Serranid A' is probably A. fucinus. Serranid B and Serranid C both have seven anal rays, and were very distinct from each other. Serranid B was taken at almost all times of the year, while Serranid C was taken only from February through July. Based on fin ray counts, the former is probably A. bicolor, and the latter, A. thompsoni.

The only other serranid form taken more than a few times, Serranid D, was taken throughout most of the year. This form, whose fin ray counts were most similar to those of Odontanthias fuscipinnis, apparently metamorphosed at a smaller size than the above serranids; the largest specimens already appeared metamorphic and several had scales. At least five other types of serranid larvae were taken. Except for one damaged specimen whose counts were those of Liopropoma, all others were anthines, but had counts not directly attributable to any known Hawaiian species. There were also several types among the small, pre-flexion serranid larvae taken. Many showed some resemblance to Serranids B, C, or D, but direct “links” between small specimens and the series of larger individuals were not available. Surprisingly, almost none of the small, preflexion serranid larvae appeared likely to be Luzonichthys ear/ei, the most frequently taken serranid larvae.

Pseudogrammidae

All but one pseudogrammidae larvae had fin counts of Pseudogramma polyacantha. Most (80%) of the specimens were taken in either 78-02 or 78-03, but the others were scattered throughout the year. A single larva with counts of either Aporops or Suttonia was taken in 78-08.

Symphysanodon

Almost 70% of the Symphysanodon larvae were taken in 78-03; 1-8 individuals were taken on 10 other cruises scattered throughout the year. The size composition of the March catch differed significantly from that of the remaining catches. The former was dominated by 11-16 mm larvae, while the latter were mostly <8 mm (Fig. 4). The BB data provided higher estimates of density than did the IK (Table 3). The SB was apparently effective at catching only the small larvae, and caught none at all on the peak 78-03 cruise. Three much larger Symphysanodon (50-56 mm) were taken in the study area by a 5-m IK trawl sample in May 1974. Gill raker counts on these indicated they were S. maunaloae.

Sphyraenidae

Sphyraena larvae were taken on only seven cruises and mostly in the fall (33% in 77-08 and 42% in 78-10). Most
were taken by the BB, but the size composition from all three types of gear was similar.

**Labridae**

At least 13 different forms of labrids were represented, many of them by substantial numbers (Table 1). The most abundant labrid (and second most abundant taxon collected) was Labrid S, probably Cheilinus (cf. Leis and Rennis 1983, fig. 49B). It was taken on all cruises. There was no indication of a seasonal trend in abundance or size composition. The highest density observed, based on BB data from 78-07, was only about twice the mean (Table 3) and not markedly higher than that for several other cruises. Most were taken by IK or BB. Despite the larger volumes sampled by the IK, the BB caught more individuals than the IK and provided higher estimates of density than either the IK or SB (Table 3). Size compositions from the IK and BB were similar; the peak numbers were at 6–6.5 mm with few <5 mm and none >8 mm. The SB caught few >4.5 mm.

Two other forms of the tribe Cheilinini were also taken frequently. Labrid B (probably Cirrilitus jordani) was taken on all but three cruises, but 71% were taken in either 78-07 or August (both years). Similarly to Labrid S, the largest specimens were only 8 mm long. Labrid N (Pseudochelinus sp.) was taken on all but two cruises. Except for a high catch on 78-03, most were taken on late summer and fall cruises. Labrid N apparently reaches considerably larger sizes in the plankton than either of the two other Cheilinini taken. The BB provided higher density estimates than the IK for Labrids B and N; the SB estimate for the latter was similar to that of the BB (Table 3).

The most frequently taken labrid of the tribe Julidini was Labrid 3 (probably Pseudojuloides cerasinus, cf. Miller et al. 1979, as “Labrid L-3”). Labrid 3 was taken on all but 4 cruises, but density was markedly higher than average on 78-03 (Table 3). Size composition overall was bimodal with about 30% of the larvae in the 4–6 mm range and over 50% >11 mm (Fig. 5). The SB provided the highest density estimate for the small larvae. The BB provided a higher estimate than the IK for larvae >11 mm, but there was a significant difference between the two nets in size composition of the catch. The IK catch was dominated by larger larvae than that of the BB (Fig. 5).

Labrid T (either Thalassoma or Gomphodus, cf. “Thalassoma” of Leis 1983) was taken on all cruises, but 75% of the specimens were taken from 77-10 to 78-03. Size composition of larvae from this period was similar to that of the remaining larvae. Most Labrid T larvae and almost all >6 mm were taken by IK or BB. There was no difference between the size compositions of IK and BB catches, but the latter provided a much higher density estimate (Table 3).

Two forms of the tribe Novaculini were taken regularly. Labrid G (Gymnolutes lecule) was taken on almost all cruises, but 75% of the catches were from February through May. The BB and SB provided much higher density estimates than the IK (Table 3). The size compositions of Labrid G from all three nets were similar; catches were dominated by large, >11 mm, larvae. Labrid X (Xyrichthus) was very similar in form to Labrid G, and could not be unequivocally discriminated from it until the dorsal fin elements were complete (or undamaged). This accounted for the large number of questionably identified specimens in Table 1. Even including the questionable specimens, Labrid X was absent from samples from April through July, and all but 'our specimens were taken either from October through November (both years) or from February through March.

Four forms of labrid larvae had the same fin counts (D/A:IX, 12/III, 12) as several genera of the Julidini and of Novaculichthys. Labrid O (cf. Leis and Rennis 1983, fig. 49D) was taken in most months, but over half the total specimens were from 78-02 and 78-03. Labrid E, a very elongate form, was absent from most of the late summer and fall cruises and was most frequently taken in 78-03. (Even in the largest specimens of Labrid E, it was difficult to discriminate the last dorsal spines from the first dorsal rays, and the dorsal fin counts could conceivably be XI, 10.) The minimum size captured for both these species was fairly large compared to the other labrid types. Two other less frequently taken forms with the same counts were Labrid T’, which was very similar to Labrid T and was probably one of the Julidini, and Labrid D, a deep-bodied form. Other, infrequently taken forms were Labrid S, which resembled Labrid S but had counts of either
Labrid or Suezichthys, and a single specimen with counts of Polylepion russelli.

Scaridae

The most frequently taken scarid larvae were scarines with relatively round eyes (Table 1). Scarine A had melanophores on the dorsal edge of the caudal peduncle; Scarine B lacked this pigment. The size ranges of the two forms overlapped but specimens of Scarine A tended to be smaller. Thus the scarine larvae could represent only one form which loses the dorsal pigment at variable size. Both scarine forms were taken throughout the year, with the highest catch (12) in 78-03. The scarid larvae with distinctively narrow eyes, presumably Calotomus, were mostly larger than the largest scarine larvae, but were less abundant. They were taken on all but 5 cruises; almost half the total were, however, taken in 78-02 or 78-03.

Pomacentridae

Most of the pomacentrid larvae taken (Table 1) were small (3-6 mm) with fin elements insufficiently developed for further identification; several were only tentatively identifiable as pomacentrids. Almost all of these small larvae were taken on one of three cruises: 77-08, 78-03, or 78-11. Larger individuals were identifiable to genus. Chromis A, which was taken only in 78-02 and 78-03, had counts of either C. struhsakeri or C. verater. Chromis B, which was taken in 78-02, 78-03, and 78-06, had counts within or close to the ranges of either C. agilis or C. hanui; some could conceivably have been C. leucurus. Chromis C were probably either C. acares or C. vanderbilti. A few specimens each of the other known Hawaiian pomacentrid genera were taken (Table 1).

Acanthuridae

Larvae of Naso were taken on almost all cruises but were more abundant during June-November. Eighteen very small (1-2 mm), tentatively identified specimens that had not yet developed the "acronurus" body form were taken in 78-10 and 78-11. The three largest individuals (one at 37 mm and two at 34 mm) were exceptional catches; the next largest were 24 mm. Only 5% of the larvae were >20 mm long and only about 25% were over 10 mm. The SB did not catch any Naso over 6 mm long. The size compositions of the BB and IK catches were significantly different and indicated that the IK was more effective for the large Naso larvae (Fig. 6). For larvae >6 mm, however, the density estimate from the BB was slightly higher than that from the IK (Table 3). Both dorsal and anal fin ray counts of 64 individuals ranged from 27-30, and did not exclude any known Hawaiian species. Most counts, however, were 27-29/27-29 indicating that these larvae were most likely N. unicornis.

Small (<6 mm) acanthurid larvae which could not be identified to genus were taken in low numbers throughout most of the year. Except for a few Zebrasoma flavescens, the larger individuals had either eight or nine dorsal spines. The former were considered Ctenochaetus and the latter, Acanthurus in spite of known, but infrequent, overlap in
Parapercidae

Parapercis larvae were the most numerous type taken in the samples. All large individuals with completely formed dorsal and anal fins were *Parapercis schauinslandi*, and there were no indications of more than one form among the smaller larvae. *Parapercis* were taken throughout the year. Catches varied greatly between cruises but without any apparent seasonal pattern. Highest catches were in 77-0S (91 individuals), 77-11 (200), and 78-03 (57). The high catches in 77-0S and 78-03 were largely due to single BB samples, but all three types of gear and most individual tows captured higher than average numbers in 77-11. Size composition of both IK and BB catches from 77-11 differed significantly from catches by these nets on the remaining cruises. The larvae from 77-11 were dominated by smaller individuals than those from the rest of the cruises (Fig. 7).

For data from all cruises, the SB catches of *Parapercis* differed significantly in size composition from those of the IK and BB; larvae >4 mm were relatively poorly represented in the SB data (Fig. 7). The size compositions of the BB and IK catches were more similar, but still differed significantly. Larvae 6–8 mm tended to be relatively better represented in the BB data (Fig. 7). The same trend was present, but not significant, in the 77-11 data alone. For the pooled data, the BB density estimate was slightly higher than that of the SB and much higher than that of the IK (Table 3). For 77-11, the SB estimate was by far the highest, but was based on only two tows one of which collected 15 *Parapercis* larvae—almost a third of the total SB specimens from all cruises.

Blenniidae

Most blenny larvae were salariines (Table 1). These were taken on nine cruises scattered throughout the year, but over two-thirds of the total were from either 77-08, 78-03, or 78-11. All but three specimens were either under 8 mm or over 15 mm long. The BB caught slightly more of the smaller group and only slightly fewer of the larger than did the IK. The SB specimens were mostly small, but the largest, 27 mm, was almost as large as the largest IK specimen. Most of the large specimens were taken in 78-03 and most of the small ones in 77-08 and 78-11. Fin ray counts, where possible, indicated that most were probably...
Girrpectes; only two of the 20 counted could possibly have been Exallias brevis. Some of the small specimens, without complete dorsal and anal fins, were possibly Istiblennius spp. Other types of blenny larvae were very infrequent. In addition to three large Plagiotremus sp., only one small unidentified blenniid and nine omobranchs were taken. Eight of the latter were from 77-68.

Schindleriidae

Schindleria praematura was taken on all but four cruises, but over half (25) were from 77-08. S. pietschmanni was taken much less frequently (Table 1); six of the seven were taken on 77-08. Within a few km of shore, S. pietschmanni appears to be the dominant species, and both species are much more abundant and routinely taken (Leis 1982).

Eleotridae

Larvae of Eleotris sandvicensis, a catadromous species which spawns in brackish water, were taken on all but two cruises, but appeared to be most abundant in late summer-fall. Over half were taken on either 77-08, 77-09, or 77-11. The size range taken was very narrow; 80% were 3-6.5 mm long, and over half were 6-6.5 mm. IK and BB catches were similar to each other in size composition and dominated by slightly larger larvae than in the SB catches. The SB and BB density estimates were similar to each other and far above that from the IK (Table 3).

Gobiidae

Gobiids were one of the most frequently taken families. The majority belonged to one of four relatively elongate forms. Goby A, which is probably a species of Oxyurichthys, was the commonest (Table 1). It was taken throughout the year and on all but five cruises, but catches were concentrated in 78-02 (30 individuals), 78-03 (22), and 77-11 (20). Over 70% of the total were >15 mm long. Goby B (probably O. lonchotus) also occurred throughout the year, but half were taken on either 78-03 or 77-11. Nearly 75% of the larvae were >9 mm long. Goby D-3 and Goby D-5 were very similar forms, but with different fin ray counts; the counts of each are, however, shared by several species of Hawaiian gobies. Both forms occurred throughout the year and on most cruises, but almost 30% of Goby D-3 were taken on 77-11. Size composition and maximum size caught by the IK and BB were similar for each of the above four forms, but BB density estimates were considerably higher (Table 3). For the three forms taken sufficiently often by the SB, the density estimates were similar to those from the BB.

Five less frequently taken types of goby larvae could be identified based on either unique fin counts or previous descriptions. Four of these—Eviota epiphanes, Bathygobius, Asteropteryx semipunctatus, and Psilogobius mainlandi—are known to occur at much higher densities in waters closer to shore (Watson and Leis 1974; Leis 1982; Miller et al. 1979). Most of the Eviota and Bathygobius and all Asteropteryx were taken in 77-08. Larvae of none of the above four species nor of Kellogia oligolepis appear to reach sizes comparable to the four elongate forms.

Goby R, which was taken on only five cruises, was more robust than any of the other goby larvae and also had a longer more pointed snout. The latter suggested Fusigobius, but Goby R’s dorsal and anal ray counts were too low. Among the larvae under unidentified Gobiidae (Table 1), there were at least four more distinctive, but unidentifiable forms, none of which were represented by more than three individuals. Other unidentified gobies either did not exactly fit any of the forms mentioned above or were too damaged or too small for identification.

Microdesmidae

Ptereleotris heteroptera was taken only during August-March with highest catches during the fall months. Almost 20% of the total came from two IK samples with high catches of small individuals. Over 60% of the specimens were <12 mm long. For both the entire size range and large (>11 mm) larvae alone, the SB density estimates were higher than those of the BB and both much higher than that of the IK (Table 3). Gunnellichthys curiosus was taken throughout the year and on all but four cruises. Over half the larvae were longer than 20 mm with only two <10 mm. The SB caught only three Gunnellichthys; the largest was only 15.5 mm. The BB, however, caught almost as many larvae as the IK and provided a higher density estimate even for the larger larvae (Table 3).

Callionymidae

Callionymid larvae were taken on all but one cruise. Abundance varied greatly between cruises, but there was no obvious seasonal pattern. There were at least six and possibly more different forms among the callionymid larvae. None of the specimens, however, appeared to be Calliurichthys decoratus, whose larvae are common in shallow inshore areas (Miller et al. 1979). Accurate counts of dorsal and anal fin rays were possible only for the largest individuals, and only one individual, an 8.5-mm Eleutherochir pogonathus could be identified beyond family on the basis of counts. In most other specimens with the fins apparently developed, the dorsal/anal ray counts were 8-7/7-9. The commonest form, Callionymid A was distinguished by a rounder head profile than the others and very light or no pigmentation until about 5 mm. The other forms were distinguished solely upon pigment pattern, but intergrades or questionable individuals were frequent enough that the data were not tabulated separately. As might be expected
for such small larvae, the IK was the least effective and the SB the most effective sampling gear (Table 3).

Discussion

Gear Comparisons

For most taxa or size classes of larvae considered in Table 3, the density estimates from the IK were markedly lower than those from the BB, and the latter estimates were often lower than those from the SB. In many cases between gear differences in density estimates were accompanied by differences in size composition of the catch. Such gear specific differences were not unexpected given that the three types of gear differed in mouth size, towing speed, and mesh size, each of which would affect bias due to avoidance or mesh escapement or both. Bias due to avoidance would be expected to be less for the larger and faster of any two nets, but bias due to escapement through the meshes would be greater because of the larger meshes and perhaps, as suggested by Munk (1988), greater towing speed. The degree of each type of bias would vary with size of the larvae, but in opposite directions, and both types of bias could be operating over part or even all size ranges considered.

Based on analyses of the much more abundant myctophid larvae from the same samples, Clarke (1983) indicated that larvae less than 6–8 mm long and fish less than 25–35 mm long were seriously undersampled by the BB and IK, respectively, because of mesh escapement, but that it was unclear that mesh escapement was serious at larger sizes because avoidance of the SB and BB, respectively, may have contributed to the apparent superior performance of the larger nets for larvae or fish larger than the above size ranges.

The same difficulties in interpreting the data on nearshore larvae are exaggerated because of lower densities relative to volumes filtered—especially by the SB. Nevertheless, most of the between gear differences in estimated density and size composition appear related to differences in error due to mesh escapement. This is most nearly certain in taxa such as carangids, mullids, and callionymids, where the great majority of larvae were small (≤6 mm) and the SB estimates were by far the highest and the IK estimates by far the lowest (Table 3). Such sizes would be least likely to avoid the SB, and losses through the meshes of the BB and especially the IK were almost certainly substantial. Error due to escapement through the meshes of the larger net was also indicated in most cases where there were significant between gear differences in size composition of the catch. In all cases except the IK-BB comparison for Parapercis, the catch from the smaller net was dominated by smaller fish. The differences in density estimates and size composition could have resulted from escapement of the small, more abundant larvae through the coarser meshes of the larger net. The differences in size composition could, however, have resulted in part because of avoidance of the smaller net by large larvae. In some IK-BB comparisons (e.g., Centropyge and Labrid 3) and many BB-SB comparisons (e.g., Symphysodon and even small forms such as Labrid S and Eleotris sandvicensis) the smaller net appeared ineffective at sampling large larvae.

If such bias due to avoidance were operating at the large end of the size range, it effectively canceled some of the losses due to mesh escapement for the large nets and means that densities of small larvae were even more seriously underestimated than the comparisons of total densities would indicate.

Several lines of evidence indicate that even the large larvae of many taxa were underestimated by the IK because of mesh escapement. For several taxa there were no differences in size composition between IK and BB catches, and for Parapercis, the BB catch was dominated by slightly larger fish than that from the larger IK. In these cases and also most comparisons of density estimates of large larvae only, the BB estimate was still higher than that of the IK. The IK estimate was higher than the BB estimate only for large Centropyge and similar to the BB estimate only for large Nasso. Except for such deep-bodied larval types, it appears that there were substantial losses of all sizes of larvae through the meshes of the IK. Error due to mesh escapement would normally be expected to decrease with increasing size and result in differences in size compositions between the BB and IK, but results of Munk (1988) indicate that the higher speed of the IK may have resulted in a disproportionate increase in loss of larger larvae of certain taxa. Munk’s results indicated that higher speed increased loss of large herring larvae but did not change loss rates for the small larvae.

The apparent superior performance of the IK for catching large Centropyge indicates that these robust, well-developed larvae and juveniles were avoiding the BB and certainly the SB. On the other hand, avoidance of the BB was apparently not a serious problem for the taxa whose density was better estimated by the BB for even large sizes. As mentioned above there were several taxa for which the SB appeared ineffective at capturing larger individuals, but for others, such as Luzonisichthys earlei, the SB caught individuals nearly as large as the largest in the IK catches. The SB provided the same density estimate for large L. earlei as the BB. Given that the SB and, for many taxa, the BB tows sampled insufficient volumes to expect many or any captures of large, relatively rare individuals, it is possible that avoidance of the smaller nets was not a serious problem for many of the taxa collected.

The above considerations of mesh escapement and avoidance are admittedly speculative and imprecise because there were no between gear tests of any single variable such as net size without confounding differences in other variables, and the diversity of apparent effects of mesh escapement and avoidance is not unexpected given the diversity in shape, maximum size, and probable swimming and
sensory abilities of the many different taxa considered. The results overall indicate, however, that, except for its ability to sample larger volumes per unit time, the IK used here was the least effective sampler for most taxa because of losses due to mesh escapement. Where densities were high relative to volumes sampled, the SB and BB appeared to be the most effective nets for small and large larvae, respectively. Future studies of such larvae should employ mid-water trawls with finer mesh than normally used, or perhaps consider scaling up a bongo-type net to a size that can sample adequate volumes in a reasonable amount of time. The several indications that avoidance of the bridgeless bongo nets was not a serious problem indicate that a larger version of the BB used here might be more effective overall than a fine-meshed midwater trawl.

Temporal Variation

For many of the abundant taxa, a large fraction of the total catch was from one or two cruises, e.g., Synodus and Parapercis on 77-11, and Luzonichthys earlei on 78-06. On 77-08 and 78-03, high catches of several taxa coincided. The 77-08 cruise collected peak numbers of Apogonine A, Lutjanus, and mullids, as well as unusually high (but not maximal) catches of carangids, Sphyraena, pomacentrids, Parapercis, and salariines. The 78-03 cruise (and to some extent 78-02) was marked by high catches of scorpionids, Centropyge, serranid A, Pseudogramma, Symphysanodon, several labrids, scarids, pomacentrids, Acanthurus, Ctenochaetus, and Goby A. In all the above cases, the catches were higher than normal for at least three of the four IK samples and often for the majority of samples of both types of bongos. (The smaller nets appeared to be ineffective at sampling certain large forms, e.g., Centropyge and serranid A, and thus collected few or none even during peak months.) The high monthly totals consequently did not appear due to chance encounters with one or two small scale patches of high density.

Although these occasional, and often coincident, high catches could conceivably have resulted from peaks in output of eggs and larvae from the benthic populations, many were more likely the result of recent and more rapid than usual movement of water into the study area from inshore. The evidence for this is strongest for 77-08. First, the high catches were not repeated in 78-08 or any adjacent months of either year. Secondly, the high catches of several taxa, particularly Lutjanus and mullids, were due primarily to very small, presumably recently hatched larvae. Finally, several taxa (Crytallodontes cookei, omobranchines, Schindleria spp., Eviota, Bathygobius, and Asteropterix) taken exclusively or nearly so on the same cruise are known to occur routinely within a few km of shore (Leis 1982; Clarke, unpubl. data). All of these indicate that water from close to shore had been transported to the study area very recently before that particular cruise. Unfortunately, insufficient physical data were collected on any of the cruises to directly test this hypothesis.

The high catch of small Luzonichthys earlei in 78-06 was also unlikely due to a seasonal peak in reproduction since large L. earlei were taken in roughly comparable numbers throughout the year. Similarly, there were no hints of seasonality in the data for Parapercis or Symphysanodon that would correlate with the very high catches of these in 77-11; in particular, the high catches were not repeated in 78-11. Recent movement of water from areas of high density seems the most likely explanation for these peaks, but it is difficult to explain why such water carried only one or a few species. Perhaps these were seasons when only a few species are abundant in nearshore waters. Alternatively, larval distributions around the islands may be narrowly zoned and recently transported water may have come from a zone where larvae of only one or a few taxa were present at high densities.

Data from 78-03 differed in several respects from that of other cruises which caught high numbers of larvae, and their interpretation is constrained because of inadequate flowmeter data for all gears were considerably higher than unexplained reasons, the towing speeds estimated from average for these two cruises. (The mean speeds for 78-02 and 78-03 were taken regularly throughout the other cruises. None are known to be more abundant close to shore, but it is conceivable that the high catches resulted from recent movement of water into the study area from somewhere (perhaps further offshore) where these taxa routinely occur at high densities.

Another possible explanation for the peak catches in 78-02 and 78-03 is that these cruises sampled available larvae much better because of higher towing speeds. For unexplained reasons, the towing speeds estimated from flowmeter data for all gears were considerably higher than average for these two cruises. (The mean speeds for 78-02 and 78-03 were about 12%, 25%, and 45%, respectively, higher than the overall means.) This had the obvious effect of increasing volumes sampled per tow, but these differences were far from sufficient to explain the high catches. It is, however, possible that the higher speeds crossed a major "threshold" for avoidance of all types of gear by the larger sizes of larvae and that densities of larvae were actually similar to other cruises, but catches were higher because of reduced error due to avoidance for all three types of gear.
If occasional high catches of some taxa are ascribed to
circulation events, seasonal trends in occurrence or abun-
dance were evident for only a few of the frequently col-
lected taxa. Centrolophus S3, serranid A, and Ctenochaetus
appeared restricted to the winter and early spring months. 
Lutjanus and indeed all lutjanids were restricted to late sum-
mer and fall; this pattern has been noted by Leis (1986)
based on catches from a number of different years. Trachi-
ocephalus myops and Pieroeditis heteroptera were taken only
during August through March. Naso and several types of 
labrid larvae were taken over all or most of the year, but
abundances were high only over shorter periods. Some of
the less frequently taken taxa, such as holocentrids, also
appeared to be present or more frequent during certain
seasons.

Both the general lack of seasonality in abundance and
most instances of apparent seasonality fail to support
Lobel’s (1978) hypothesis that spawning seasons of inshore
fishes are timed to coincide with the period (December–
June) when ocean current patterns might favor retention
of larvae near the islands. The apparent seasonal peaks in
abundance of some labrid larvae agree with seasonal pat-
terns of recruitment of several Hawaiian labrids reported
by Walsh (1987), but otherwise the observed patterns of
larval abundance (or lack thereof) correlate poorly with
Walsh’s evidence for a summer peak in recruitment of
many reef fishes.

Size Composition

The very early stages of inshore fish larvae are apparently
only rarely transported as far offshore as the study area.
For the great majority of taxa, the smallest larvae taken
were at either late prefexion or early postflexion stages.
Except for the coastal pelagic carangids, multiple captures
of early prefexion stages occurred in only a few cases: 
holocentrids and mullids in 77-08 and Naso in 78-10. Ad-
mittedly, it is possible that there were more, but unrecog-
nized early prefexion larvae of nearshore families present
in the samples, but for reasons given in the methods sec-
tion it is unlikely that the number of misidentifications
were sufficient to substantially alter the above statements.

The largest specimens of the more abundant taxa were
probably close to the maximum size for the pelagic stages.
For the majority of abundant taxa it appeared that all sizes
between late pre-/early post-flexion and the maximum size
were either about equally represented or at least reasonably
likely to occur in offshore waters. Eight types of larvae,
however, were represented primarily by relatively large and
presumably near-settlement size larvae. These were Centro-
lophus, Luonichthys earlei (except in 78-06), serranid A, labrids
O and E, Calotomus, goby A, and Gunnellichthys. In these
taxa, and perhaps for some of the less frequently taken taxa,
even the early to middle postflexion stages appear to be
rarely advected very far offshore.

Four abundant taxa (Chaetodon, Symphysanodon, Labrid
3, and salarinids) were exceptional in that the size com-
position of larvae appeared bimodal. A few of the rarer
taxa (ophidiids, Polymixia, dactylopterids, and tetradont-
tiforms) also appeared to be represented mostly by either
very small or very large individuals. Bimodal size-fre-
cquency distributions could result from periodicity in spawn-
ing. Alternatively, the peak of small individuals could
simply represent the most abundant age group while the
peak at larger sizes could represent an accumulation of
older individuals with a wide range of ages, but small dif-
fences in size. Victor (1986a) has shown that labrid lar-
vae can delay metamorphosis and continue to grow for long
periods after the probable minimal size and age for settle-
ment has been reached but that growth is greatly slowed
after the latter point.

Densities

The average densities of even the most abundant taxa were
very low (Table 3). Only Parapercis and Labrid S regularly
occurred at levels of 10^3 m^-3. Carangids, mullids, and
Luonichthys earlei occurred at similar or higher densities only
on single cruises. For the many taxa that were taken less
frequently than those in Table 3, the average densities
would be on the order of 0.0001-0.01/10^3 m^-3. Because it
is likely that most taxa do not occur throughout the entire
0-100 m stratum, densities within the actual depth range
would be higher. Even if larvae occurred only within a
10 m deep stratum and densities thus were 10 times higher
within that stratum, filtering a volume of a few hundred
m3, typical of most plankton tows, would be woefully in-
adequate. Even a volume of the order of 10^3 m^3 would
be insufficient for all but a few taxa at a few times. As is
illustrated by the results from the SB tows in this study,
such volumes filtered simply would not be expected to catch
most taxa.

Lobel and Robinson (1988) reported densities of 0.3–
6.8/10^3 m^-3 for inshore fish larvae at five stations in and
near an eddy off the island of Hawaii. These values are
much higher than most averages reported here and were
exceeded for only a few species on a few cruises. Lobel and
Robinson’s results must, however, be interpreted with cau-
tion because they are based on few samples. A single sur-
face and a single near-surface tow, each of which apparently
sampled about 1–2 x 10^3 m^3, were taken at each station.
Consequently, the density for any taxon collected could
not be less than ca. 0.3/10^3 m^-3. The 44 different density
estimates in their table VI are based on only 130 specimens;
23 estimates, apparently on single captures per station.
With the exception of carangids, only two nearshore taxa
were taken in substantial numbers—both at the same sta-
tion. More data are necessary to determine if the reported
densities of these two taxa are routinely encountered, if they
are only associated with eddies or similar recent transport
from inshore, or if the present study may have ineffectively sampled near-surface depths (see below).

Sale (1970) reported on larval acanthurids taken by a large pelagic trawl at two locations close to the area sampled by the present study. Using estimated towing speed and mouth opening of this trawl (Higgins 1970), Sale's catch data indicate that densities of acanthurid larvae were only 0.001-0.002/10³ m⁻³, about 100 x lower than those estimated from this study (Table 3). Part of the difference is due to capture of smaller and more abundant larvae by the nets used here, but even considering only the same size range as reported by Sale, the estimates from the present study are still very much higher. Apparently all sizes of acanthurids were seriously underestimated owing to escapement through the coarse (19-mm stretch) meshes of the wings of the large pelagic trawl.

Faunal Composition

The larvae collected represent most of families of Hawaiian inshore fishes, and the most abundant taxa were all from families that are abundant in the nearshore habitats. Nevertheless, several taxa that appear to be very abundant as adults in nearshore habitats were poorly represented or absent in the offshore samples. Some common taxa from shallow water areas which were absent or poorly represented were holocentrids, *Kuhlia*, *Kyphosus*, demersal carangids, and pomacentrids other than *Chromis*. Similar, abundant taxa from slightly deeper but still nearshore areas (Struhsaker 1973) were *Glossanodon*, *Aulopus*, *Chlorophthalmus*, *Polymixia*, and *Synagrops*. The meristics of larval *Acanthurus* and *Chetodon* indicate that some species, such as *A. triostegis* and *C. miliaris* which are very abundant inshore, were either probably absent or at best poorly represented among the larvae collected. Although adult abundance inshore is obviously not the sole determinant of larval abundance offshore, it is difficult to postulate why the above taxa were so poorly represented. There is no indication that they differ strongly in fecundity, reproductive output, spawning mode, or larval development period from related taxa that were taken frequently. Their absence or rarity in the present samples may indicate that, even within genera, larval behavior differs enough to affect degree of dispersal to offshore waters.

It is also possible that some taxa of inshore fish larvae were absent or underrepresented in the present samples because they occur in the upper few m of the water column and were poorly sampled owing to the ship's presence directly ahead of the nets. With the exception of the carangids, the most important taxa from the present study are either absent or relatively poorly represented in Lobel and Robinson's (1988) data from near surface tows in oceanic waters off the island of Hawaii. At one of their stations, larvae of holocentrids and the pomacentrid *Abudefduf abdominalis* occurred at very high densities. Neither of these were taken very frequently during the present study and may, like some of the other poorly represented taxa, prove to be more abundant very close to the surface.

The inshore fish larvae from the study area were not dominated by taxa with relatively large larvae. Although larvae of several abundant families reach rather large size (15 mm or more) before metamorphosis, families with small size at metamorphosis (parapercids, eleotrids, callionymids) were, if anything, more abundant. Within the most abundant family, the labrids, there is a great range of maximum sizes of larval types (Leis and Rennis 1983). Several forms of labrids taken in this study reach almost 20 mm as larvae, but the most abundant labrid, *Labrid S*, and *Labrid B*, the sixth most abundant, apparently metamorphose at less than 10 mm.

Although relevant data on larval stage durations are few, they indicate that at least the labrids taken in the study area were not dominated by genera with long larval stage durations. Assuming my generic identifications are correct, the Hawaiian species of the two most abundant labrids, *Labrid S* (*Cheilinus?*) and *Labrid B* (*Pseudojuloides?*) have much shorter larval stage durations than those of other tentatively identified genera such as *Thalassoma*, *Gymnolepis*, and *Xyrichtys* (Victor 1986b). In contrast, available age data on pomacentrids (Thresher et al. 1989; Wellington and Victor 1989) indicate that Hawaiian species of the most frequently taken genera—*Chromis*, *Stegastes*, and *Plectroglyphidodon*—tend to have longer larval stage durations than do the infrequently taken *Dascyllus* and *Abudefduf*.

Taxa with unique pelagic "prejuvenile" stages (acanthurids, chaetodontids) or whose larvae possess long spines (e.g., *Symphysanodon*) or other apparent modifications for pelagic existence were abundant in the present samples but were far outnumbered by labrids, parapercids, gobiids, and mullids, none of which show obvious special modifications for pelagic existence. The most abundant serranid larvae, *Luzonichthys earlei*, was relatively nondescript and had less developed spines than most other serranid larvae. While it is possible that taxa whose larvae are large, long-lived, or modified for pelagic existence will better survive dispersal offshore, occurrence and abundance in offshore waters are not well predicted by larval size, duration, or morphology.

Most of the larvae from this study were of taxa which spawn pelagic eggs as adults, and the three most frequently taken families (labrids, parapercids, serranids) are pelagic spawners. Predominance of larvae of pelagic spawners was not, however, overwhelming. The demersally spawning gobiids were fourth in number of specimens, and six other demersally spawning families (Microdesmidae, Eleotridae, Apogonidae, Pomacentridae, Blenniidae, Schindleriidae) were among the top 20 families taken. The observed dominance of pelagic spawners does not seem surprising given that most families of inshore Hawaiian fishes are pelagic spawners. Leis and Miller (1976) reported a similar
dominance by larvae of pelagic spawners in offshore waters of Hawaii and contrasted this with evidence of dominance by larvae of demersal spawners in inshore coastal waters. They concluded from this, without comparison of inshore and offshore densities, that larvae of pelagic spawners tend as a group to be more abundant in offshore waters and those of demersal spawners more abundant close to shore.

Comparison of the results of the present study with those of Leis (1978, 1982) from inshore waters off the same coast of Oahu indicate that not only are the conclusions reached by Leis and Miller (1976) not supported, but also that their proposed general differences in dispersal patterns between larvae of demersal and pelagic spawners are questionable. Leis's (1978, 1982) data show that dominance by larvae of demersal spawners in inshore waters is due to few species—primarily a tripterygiid, a schindleriid, and a gobiid. Their densities were much higher than those of any taxon taken offshore in the present study. Larvae of pelagic spawners were absent or very rarely taken; however, so were larvae of most demersally spawning taxa taken in the present study. Leis and Miller (1976) noted that larvae of certain demersal spawners (salarine blennies and *Chromis*) were apparent exceptions to their proposed trend. In fact, the few species of demersal spawners which dominate inshore are apparently the exceptions. Smith et al. (1987) report that inshore areas adjacent to deep water in the Caribbean are dominated by "clupeids, blennioids, and gobioids." Although the number of species involved is not given, it appears that high abundances of just a few types of larval fishes may characterize inshore waters in other areas bathymetrically similar to Hawaii.

Furthermore, Leis's results—like those of other studies of ichthyoplankton in inshore Hawaiian waters—were based on plankton tows which filtered only a few hundred m³ per sample. Even if larvae of pelagic spawners and the "missing" types of demersal spawners had been present inshore at densities 10-100 x those observed offshore, only an occasional capture would be expected by such small volume samples. While small volume samples are adequate to show that certain taxa are much more abundant inshore than offshore, inshore waters must be sampled with procedures comparable to the BB or IK tows used in the present study in order to determine if any larval forms or sizes are ever more abundant offshore than inshore.

If, as hypothesized above, the occasional and often coincident high catches of certain taxa in offshore waters were due to recent movement of surface waters, then some of the taxa taken offshore must occur somewhere else at considerably higher densities than usually observed in these samples. As mentioned above, *Schindleria* and certain goby larvae are known to routinely occur at considerably higher densities within a few km of shore. (Preliminary analyses of samples recently collected off windward Oahu indicates that certain other taxa such as *Lutjanus* and holocentrids are also more abundant closer to shore.) If densities of more taxa prove to be higher somewhere between the location of the present study and shore, it may mean that nearshore larvae which occur more than a few km offshore are normally a minor and perhaps inconsequential fraction of total potential recruits to island populations and are of consequence only for zoogeographic dispersal.

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**Citations**


