Temporal and spatial variation in length of larval life and size at settlement of the Hawaiian amphidromous goby _Lentipes concolor_

R. L. Radtke*‡, R. A. Kinzie III† and D. J. Shafer†¶

*Hawaii Institute of Geophysics and Planetology, School of Ocean and Earth Science and Technology, University of Hawai‘i, Honolulu, Hawai‘i 96822, U.S.A. and †Department of Zoology, University of Hawai‘i, Honolulu, Hawai‘i 96822, U.S.A.

(Received 8 August 2000, Accepted 30 June 2001)

Larvae of the Hawaiian amphidromous goby _Lentipes concolor_ settled after a mean length of larval life (LLL) of 86.2 ± 8.5 days (n=236, range=63–106 days) at a mean size of 16.0 ± 0.7 mm _L_T_ (n=154, range=14.1–17.9 mm). Mean LLL for _L. concolor_ was about twice that typically reported for tropical marine gobiids. Variation in LLL (CV=10%) and size at settlement (CV=4%) were low, and comparable to that for marine gobiids. LLL and _L_T_ were weakly positively correlated (Pearson’s correlation coefficient _r_=0.50, _P_<0.0001). Larvae settled after shorter planktonic lives and at smaller sizes during months with warmer ocean temperatures. Inter-island variation in LLL did not support a dominant south-east to north-west larval drift, following the dominant south-east to north-west flow of prevailing currents in the Archipelago. Instead, recruits on Maui Island, centrally located in the archipelago, had shorter LLL than recruits to upstream Hawai‘i and downstream Kaua‘i islands. These findings have important implications for understanding the complex life history dynamics of amphidromous fishes as well as their management.

Key words: Gobiidae; larval life history; recruitment; retrospective analysis; otoliths.

INTRODUCTION

Most demersal marine fishes have complex life cycles featuring a pelagic larval stage followed by settlement to a benthic reproductive stage. Patchy distributions of food, predators and suitable substrata for settlement, contribute to high larval mortality and recruitment stochasticity (Sale, 1980; Caley _et al._, 1996; Steele, 1997). Two variable aspects of fish early life history that may be closely linked to success of an individual recruit are length of larval life (LLL) and size at settlement. Length of larval life and size at settlement vary both within and among species (Victor, 1986a; Thresher _et al._, 1989; Wellington & Victor, 1989; Cowen, 1991; Victor, 1991; McCormick, 1994; Shafer, 1998), although size at settlement appears to be a more conservative character within a species. Variations in LLL and size at settlement have implications for larval mortality (Ricker, 1975) and post-settlement advantages (Doherty, 1982, 1983; Hunte & Côté, 1989).

‡Author to whom correspondence should be addressed. Tel.: +1 808 956 7498; fax: +1 808 956 9516; email: radtke@hawaii.edu

¶Present Address: School of Ocean and Earth Science and Technology, University of Hawai‘i, Honolulu, Hawai‘i 96822, U.S.A.
Benefits associated with an extensive pelagic stage include: avoidance of benthic predators (Strathmann, 1985, 1986), access to prey sources which do not overlap with those of conspecific adults, and increased growth prior to settlement (Doherty et al., 1985; Strathmann, 1990). Two groups of tropical fishes appear to have especially long LLL. First, Hawaiian marine fishes with pelagic larval stages may have longer LLL than conspecifics elsewhere in the Pacific (Victor, 1986a; Thresher et al., 1989), although information on the LLL of reef fishes in Hawai‘i is sparse. Second, the marine larvae of freshwater fish with amphidromous life history patterns appear to have longer LLL than other marine species (Radtke et al., 1988; Bell et al., 1995). Longer LLL in amphidromous fishes may be related to the length of time required to locate discrete freshwater settlement sites (Radtke et al., 1988). Among the longest LLL on record for tropical species with marine larvae, are those reported for the Hawaiian amphidromous gobies Awaous guamensis Valenciennes and Stenogobius hawaiiensis Watson (Radtke et al., 1998), though sample sizes in that study were small. Larger sample sizes might provide greater insights into the larval life histories of Hawaiian amphidromous fishes.

The spatial and temporal variation in LLL and size at settlement for a large sample of Lentipes concolor (Gill), an endemic Hawaiian amphidromous goby (Maciolek, 1977) were investigated. The amphidromous life history of L. concolor has been described in Kinzie (1990, 1997). Length of larvae life and size at settlement of L. concolor recruits collected on three islands (Kaua‘i, Maui and Hawai‘i) at different times of the year from 1992 to 1996 were measured to determine whether the magnitude and variability in LLL of L. concolor corroborated preliminary findings of extraordinary long LLL in Hawaiian amphidromous fishes.

**MATERIALS AND METHODS**

Recently recruited L. concolor (n=236), ranging in size from 14-1 to 20-5 mm total length ($L_T$) were collected from the mouths of Hawaiian streams from October 1992 to May 1996. Fish were collected from Hakalau and Nanue streams on Hawai‘i, located at the south-eastern end of the archipelago, from Waialohe Pond (the mouths of Pā‘ina‘au and Palauhulu Streams) on Maui, located in the centre of the Hawaiian chain; and from Wainiha and Hanakapi‘ai Streams on Kaua‘i, the northernmost of the main islands (Fig. 1). Because collections were made opportunistically, it was not possible to expend equal effort at all times of the year resulting in unequal sampling of seasons on different islands. Special efforts to increase sample sizes of recruits during months with warmer sea surface temperatures (August to November) on Kaua‘i were unsuccessful, possibly reflecting recruitment seasonality (Chong, 1996).

Recruits were preserved in buffered alcohol. $L_T$ and standard length ($L_S$) were measured from rehydrated fish, and otoliths were dissected and prepared for analysis according to standard procedures (Shafer, 2000). Daily increments are deposited in sagittae of well-fed juvenile L. concolor (unpubl. data). A prominent check mark was present towards the edge of sagittae in most juveniles collected from locations upstream from the ocean (Fig. 2), and was assumed to have formed during the settlement transition from oceanic to freshwater environments (Radtke & Kinzie, 1996). Length of larval life was estimated by counting increments from the sagitta core to the settlement mark or to the sagitta margin in otoliths of new recruits.

Size at settlement was only measured for fish determined to have just settled (i.e. fish recruiting within the past 24 h). Small individuals captured at or near the stream mouth,
and lacking a settlement mark in their otoliths, were judged to have just settled. Size at settlement could not be back-calculated from older individuals due to allometric somatic-otolith scaling, which resulted in larger sample sizes for estimations of length of larval life (Table I) than size at settlement (Table II).

Sea surface temperature varies on multiple temporal and spatial scales in the Hawaiian Islands. No direct estimates of surface temperature (SST) history were made for recruits in this study because no information was available on pelagic locations of larvae of this species in the Archipelago. Instead, larvae were grouped according to whether their larval life occurred during warm or cool ocean temperatures (Shafer, 1998). Two SST regimes can be distinguished in Hawai‘i: one with warmer temperatures, typically reaching maxima around October, and the other with cooler temperatures, typically reaching minima around March (K. Bigelow & C. Boggs, unpubl. data). Recruits collected during March and April were assigned to the ‘cool SST’ season, and recruits collected during September, October and November were assigned to the ‘warm SST’ season.

RESULTS

Length of larval life for L. concolor ranged from 63 to 106 days (mean ± s.d., 84.9 ± 8.4 days; Table I). There were significant differences in LLL among islands (ANOVA, $F=12.78$, $P<0.0001$) and between warm and cool water seasons (ANOVA, $F=32.78$, $P<0.0001$) (Table III). Maui recruits had shorter LLL than those to Hawai‘i and Kaua‘i, which had similar LLL (Bonferroni Simultaneous Tests, Table III). Lentipes concolor had shorter LLL during times
associated with warmer sea surface temperatures (Table III). There was little interaction between island and season in the ANOVA model ($F=2.76, P=0.07$).

Size at settlement ranged from 13.5 to 17.9 mm $L_T$ (mean 16.0 ± 0.71 mm, Table II). There was no difference in size at settlement among islands (ANOVA, $F=0.01$, $P>0.98$), but *L. concolor* settled at smaller sizes during months with warmer sea surface temperatures (ANOVA, $F=23.53$, $P<0.0001$) (Table IV). Interaction between season and island in the ANOVA model was slight (ANOVA, $F=2.93$, $P>0.06$, Table IV). Size at settlement was positively correlated with LLL (Pearson’s correlation coefficient $r=0.50$, $P<0.0001$, Fig. 3).

Table I. Length of larval life for *Lentipes concolor* collected from streams on the islands of Hawai‘i, Maui and Kaua‘i. Sample size ($n$), means, ranges and coefficient of variation (CV) are presented for all fish collected and for sub-sets of fish collected during times associated with cool sea surface temperatures (March to April) and warm sea surface temperatures (September to November)

<table>
<thead>
<tr>
<th>Island</th>
<th>Total (Jan.–Dec.)</th>
<th>Cool SST (Mar.–Apr.)</th>
<th>Warm SST ( Sep.–Nov.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$n$</td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
<td>Hawai‘i</td>
<td>91</td>
<td>88.3</td>
<td>(69–106)</td>
</tr>
<tr>
<td>Maui</td>
<td>99</td>
<td>80.7</td>
<td>(63–100)</td>
</tr>
<tr>
<td>Kaua‘i</td>
<td>46</td>
<td>87.3</td>
<td>(65–102)</td>
</tr>
<tr>
<td>Totals</td>
<td>236</td>
<td>84.9</td>
<td>(63–106)</td>
</tr>
</tbody>
</table>

Fig. 2. Settlement mark (see arrow) in the sagitta from a 16.5 mm $L_T$ *L. concolor*. Scale bar=25 μm.
The mean LLL for \textit{L. concolor} (84.9 ± 8.4 days) is substantially longer than the 30–50 days typically reported for small coral reef fishes (Brothers et al., 1983; Victor, 1986a; Wellington & Victor, 1989; Wilson & McCormick, 1999), and the 20–50 days typically reported for marine gobies (Brothers et al., 1983; Sponaugle & Cowen, 1994; Shafer, 1998). The Caribbean goby \textit{Gnatholepus thompsoni} Jordan has the longest LLL of all tropical marine gobies examined to date, with bimodal means of 60.0 and 86.7 days and a coefficient of variation of 22.4\% (Sponaugle & Cowen, 1994). The longer of the two modes of LLL in \textit{G. thompsoni} was suggested to result from delayed metamorphosis. The mean LLL for \textit{L. concolor} was similar to that reported for two amphidromous gobies in the West Indies (83.4 days for \textit{Sicydium punctatum} Perugia and 87.7 days for \textit{Sicydium antillarium} Ogilvie-Grant, Bell et al., 1995), which like \textit{L. concolor}, are

### Table II

Size at settlement (\(L_T\)) for \textit{Lentipes concolor} collected from streams on the islands of Hawai‘i, Maui, and Kaua‘i. Sample size (\(n\)), mean, range, and coefficient of variation (CV) are presented for all fish collected and for subsets of fish collected during times associated with cool sea surface temperatures (March to April) and warm sea surface temperatures (September to November).

<table>
<thead>
<tr>
<th>Island</th>
<th>(n)</th>
<th>(L_T) (mm)</th>
<th>(T) (Jan.–Dec.)</th>
<th>(T) (Cool SST Mar.–May)</th>
<th>(T) (Warm SST Sep.–Nov.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Range</td>
<td>CV</td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
<td>Hawai‘i</td>
<td>38</td>
<td>15.7</td>
<td>14.1–17.3</td>
<td>0.04</td>
<td>15.3</td>
</tr>
<tr>
<td>Maui</td>
<td>85</td>
<td>16.0</td>
<td>15.5–17.2</td>
<td>0.04</td>
<td>16.5</td>
</tr>
<tr>
<td>Kaua‘i</td>
<td>31</td>
<td>16.2</td>
<td>14.0–17.9</td>
<td>0.05</td>
<td>16.4</td>
</tr>
<tr>
<td>Totals</td>
<td>154</td>
<td>16.0</td>
<td>13.5–17.9</td>
<td>0.04</td>
<td>16.4</td>
</tr>
</tbody>
</table>

### Table III

General linear model ANOVA of effect of island (Kaua‘i, Maui, Hawai‘i) and season (cool or warm) on length of larval life of \textit{Lentipes concolor}.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>MS</th>
<th>(F)</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Island</td>
<td>2</td>
<td>606.1</td>
<td>12.78</td>
<td>0.0001</td>
</tr>
<tr>
<td>Season</td>
<td>1</td>
<td>1554.2</td>
<td>32.78</td>
<td>0.0001</td>
</tr>
<tr>
<td>Interaction</td>
<td>2</td>
<td>130.8</td>
<td>2.76</td>
<td>0.068</td>
</tr>
<tr>
<td>Error</td>
<td>116</td>
<td>47.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>121</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Bonferroni simultaneous tests

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Difference of means</th>
<th>s.e. of difference</th>
<th>(T)</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kaua‘i-Maui</td>
<td>-5.283</td>
<td>1.721</td>
<td>-3.071</td>
<td>0.008</td>
</tr>
<tr>
<td>Kaua‘i-Hawai‘i</td>
<td>3.685</td>
<td>2.046</td>
<td>1.801</td>
<td>0.223</td>
</tr>
<tr>
<td>Maui-Hawai‘i</td>
<td>8.968</td>
<td>1.855</td>
<td>4.833</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

### Discussion

The mean LLL for \textit{L. concolor} (84.9 ± 8.4 days) is substantially longer than the 30–50 days typically reported for small coral reef fishes (Brothers et al., 1983; Victor, 1986a; Wellington & Victor, 1989; Wilson & McCormick, 1999), and the 20–50 days typically reported for marine gobies (Brothers et al., 1983; Sponaugle & Cowen, 1994; Shafer, 1998). The Caribbean goby \textit{Gnatholepus thompsoni} Jordan has the longest LLL of all tropical marine gobies examined to date, with bimodal means of 60.0 and 86.7 days and a coefficient of variation of 22.4\% (Sponaugle & Cowen, 1994). The longer of the two modes of LLL in \textit{G. thompsoni} was suggested to result from delayed metamorphosis. The mean LLL for \textit{L. concolor} was similar to that reported for two amphidromous gobies in the West Indies (83.4 days for \textit{Sicydium punctatum} Perugia and 87.7 days for \textit{Sicydium antillarium} Ogilvie-Grant, Bell et al., 1995), which like \textit{L. concolor}, are
sicydine species. LLL was reported to range between 35 and 186 days for six species of amphidromous gobies in Taiwan, though sample sizes for five of the six species ranged between 1 and 2 fish (Shen et al., 1998). Interestingly, the maximum LLL for *L. concolor* is much shorter than the mean LLL reported for two non-sicydine Hawaiian amphidromous gobies, *A. guamensis* (161 days, *n*=8) and *S. hawaiiensis* (135 days, *n*=15) (Radtke et al., 1988), which may reflect phylogenetic differences. Results from this study, together with results from previous work, suggest that amphidromous gobies, in general, may have longer LLL than marine gobies. Longer LLL may be related to the amphidromous lifestyle, including the developmental complexities required to complete the marine-freshwater transition, and the length of time required to locate isolated freshwater settlement sites.

Variation in LLL of *L. concolor* (CV=10%) was not significantly greater than that typically reported for tropical reef fishes [CVs ranging from 6·9 to 23·7%].

### Table IV. General linear model ANOVA of effect of island (Kaua‘i, Maui, Hawai‘i) and season (cool or warm) on size at settlement of *Lentipes concolor*

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>Seq SS</th>
<th>Adj SS</th>
<th>Adj MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Island</td>
<td>2</td>
<td>3·7943</td>
<td>0·0103</td>
<td>0·0052</td>
<td>0·01</td>
<td>0·986</td>
</tr>
<tr>
<td>Season</td>
<td>1</td>
<td>9·1776</td>
<td>8·4822</td>
<td>8·4822</td>
<td>23·53</td>
<td>0·0001</td>
</tr>
<tr>
<td>Interaction</td>
<td>2</td>
<td>2·1156</td>
<td>2·1156</td>
<td>1·0578</td>
<td>2·93</td>
<td>0·060</td>
</tr>
<tr>
<td>Error</td>
<td>71</td>
<td>25·5995</td>
<td>25·5995</td>
<td>0·3606</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>76</td>
<td>40·6870</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 3. Correlation between size at settlement (*Lₜ*) and length of larval life (LLL) for *Lentipes concolor* collected from streams on Kaua‘i (□) Maui (○), and Hawai‘i (△). Pearson’s correlation coefficient *r*=0·50 for all data; *r*=0·61 for fish collected on Kaua‘i; *r*=0·62 for Maui; *r*=0·37 for Hawai‘i.
(Cowen 1991, Robertson 1992, Wilson & McCormick 1999). The CV of LLL for *L. concolor* was also not greater than that for marine gobies [22.4% for *G. thompsoni* and 9.4% for *Coryphopterus glaucofraenum* Gill (Sponaugle & Cowen, 1994); 14.5% for *Bathygobius coalitus* Bennett (Shafer, 1998)]. Low variation in LLL reported for two other Hawaiian amphidromous gobies (*A. guamensis*, CV=3.5%; and *S. hawaiiensis*, CV=6.8%) was thought to be due to the small sample sizes examined in that study (Radtke et al., 1988); but the CV of LLL for *L. concolor* is also small, despite a much larger sample size.

Variation in LLL may result from various environmental factors including temperature (Bell et al., 1995; McCormick & Molony, 1995; Shafer, 1998), food availability (Jones, 1986; Cushing, 1990), and local current patterns (Lobel & Robinson, 1986, 1988). For *L. concolor*, seasonal patterns of shorter LLL during months with warmer sea surface temperatures were consistent across years. Inverse relationships between LLL and sea surface temperature have been reported for the tropical goatfish *Upeneus tragula* Richardson on the Great Barrier Reef, Australia (McCormick & Molony, 1995) and the tropical marine goby *B. coalitus* in Hawai‘i (Shafer, 1998).

Although currents surrounding the main Hawaiian Islands are highly variable in their direction and speed, on average, currents move from south-east to north-west, with eddies forming on the leeward sides of islands, especially on Maui (Qiu et al., 1997) and Hawai‘i (Lobel & Robinson, 1986). The extent of larval exchange among spawning populations of *L. concolor* is unknown, but it is enough to result in genetic homogeneity among the main islands (Zink, 1991).

If a substantial proportion of *L. concolor* larvae are frequently entrained in this westward current, then recruits to the island of Hawai‘i, at the southern end of the main Hawaiian Islands, would be expected to have shorter and less variable LLL (since recruits could have originated from Hawai‘i); whereas recruits to Kaua‘i, at the northern end of the main Hawaiian Islands, would be expected to have longer and more variable LLL (since recruits would most likely have originated from streams ranging from Hawai‘i to Kaua‘i). Instead, LLL for *L. concolor* recruits to Kaua‘i and Hawai‘i did not differ from each other. Only Maui, central in the island chain, differed by having a mean LLL c. 1 week shorter. It is possible that eddies surrounding Maui could result in greater retention and shorter LLL for *L. concolor*. Lobel (1997) compared the LLL of the damselfish *Plectroglyphidodon imparipennis* Vaillant & Sauvage from the island of Hawai‘i and Johnston Atoll, south-west of the main Hawaiian Islands. Recruits on Hawai‘i and Johnston Atoll had similar LLL, suggesting that recruits to Midway were probably spawned locally, and not the product of spawning on the main Hawaiian Islands.

Multiple factors make the detection of a larval source-sink relationship among the main Hawaiian Islands difficult with a retrospective otolith-based approach. Detection of limited down-current movement of larvae may be hindered by the overwhelming dilution of the larval supply by locally spawned larvae. The majority of successful *L. concolor* recruits may not disperse far from local coastlines. This possibility is supported by recent findings that dispersal of marine larval among local open populations may not be as common as originally proposed in early models (Jones et al., 1999; Swearer et al., 1999). Furthermore, larval gobiids are more commonly found in nearshore waters (Leis, 1982;
Kobayashi, 1987). Mesoscale circulation features around islands (Lobel & Robinson, 1986), especially in the lee of the larger islands, and small-scale local physical differences among freshwater-marine interfaces may contribute to high intra-island variability in LLL of recruits. Although sample sizes in this study are large compared with similar studies on coral reef fishes, complex factors underlying the temporal and spatial variability in LLL may demand even larger sample sizes, or more discriminating methods to resolve questions about larval dispersal and recruitment patterns.

*Lentipes concolor* demonstrated low variation in size at settlement, which may reflect declining larval growth rates during late larval stages (Victor, 1986b; Fowler & Short, 1996). Size at settlement was weakly positively correlated with LLL, which may be common among other reef species (Victor, 1986b; Shafer, 1998). However, the relationship may sometimes be complicated (Bell et al., 1995). Variation in size at metamorphosis may have important consequences for post-settlement survival (Kaplan, 1980; Miller et al., 1988; Semlitsch et al., 1988).

In conclusion, LLL of *L. concolor* was similar to that of other sicydine amphidromous gobies (Bell et al., 1995), but shorter than the long LLL reported for two other Hawaiian amphidromous species (Radtke et al., 1988). The recruits of *L. concolor* were smaller and younger at settlement during months with warmer sea surface temperatures, and appeared to be youngest in streams on Maui. Patterns of LLL among islands did not support a substantial larval drift among the main Hawaiian Islands. If local recruitment of Hawaii’s amphidromous gobies is predominately derived from local spawning effort, then this has important implications for management of amphidromous species in Hawai‘i. Specifically, persistence of populations on each island may require successful spawning, larval development, and recruitment on each island.

Today, many Hawaiian streams are modified, particularly at their mouths. This could prevent newly hatched amphidromous larvae from reaching the ocean from streams where adults currently exist, and reduce the availability of suitable settlement sites on an island. Such a bottleneck in the life history *L. concolor* may contribute to observations of declining numbers of this species (Devick et al., 1995).

Thanks are due to C. Chong, and S. Hau for field collections. This manuscript was improved by comments from K. Cole, J. Frederick and two anonymous reviewers. This study was funded in part by National Science Foundation grants DEB-93-22618, OCE-98-13649, and OPP-98-13708. This is Hawai‘i Institute of Geophysics and Planetology contribution No. 1170 and SOEST contribution No. 5833.

**References**


