



# Estuaries as Nurseries for the Jacks *Caranx ignobilis* and *Caranx melampygus* (Carangidae) in Hawaii

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Estuaries provide juvenile nursery habitat for many species of fish that inhabit marine environments as adults. In Hawaii, some juvenile *Caranx ignobilis* and *Caranx melampygus* occupy estuaries opportunistically before moving to nearshore ocean habitats. This study examined the extent and nature of estuarine habitat available in the lower Hanalei River of Kauai, the relative abundance and distribution of jacks in the estuary, and their diets. Salinity measurements indicated that the upstream extent of saltwater ranged from the mouth to nearly 5 km upriver and was strongly influenced by the variable river discharge. Juvenile jacks between 80 and 310 mm FL were observed on underwater transects over the full range of mixohaline conditions. Hand-operated seine collections produced overall catch rates of ~0.64 fish/haul for each of these species. The two jacks ate much the same spectrum of food items. *C. ignobilis* was somewhat more piscivorous than *C. melampygus*, as determined by measures of frequency of predation and number and bulk of prey. Data for length at age, incorporating daily otolith increment counts from these estuarine juveniles and previous counts from non-estuarine specimens, were fitted to a lifetime von Bertalanffy growth model. The results greatly extended the age range of the model and suggested that growth rates were not much different between estuarine and non-estuarine fish.

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## Introduction

Large jacks of the genus *Caranx* (Carangidae) are predatory fishes that play an important role in the ecology of tropical and subtropical neritic marine environments. Jacks represent an important fishery resource throughout the tropics. In Hawaiian waters, *Caranx ignobilis* (Forsskal) and *Caranx melampygus* (Cuvier & Valenciennes) are two of the most common *Caranx* species. Adults and larger juveniles support a moderate commercial fishery (1998 catch of 5000 kg, \$14 400 landed value, HDLNR, 2000) and a popular recreational fishery of much higher overall estimated economic value (Gaffney & Associates, 2000).

Adults are found in almost all nearshore habitats, including rocky shores, reefs and embayments. Juveniles inhabit protected environments such as backreef areas, sand flats, and lagoons. They also occur in estuaries, where their role as a component of the ichthyofauna is poorly understood. Utilization of estuarine habitat by juvenile jacks appears opportunistic and variable in spatial extent and duration. Neither

*C. ignobilis* nor *C. melampygus* is estuarine-dependent using the definition of Blaber *et al.* (1989) because viable populations occur in regions where there are no estuaries. Although jacks inhabit estuaries throughout the tropics, little research on juvenile fish faunas has been done in estuaries where *C. ignobilis* and *C. melampygus* are found. Previous studies have examined diets, distribution and abundance, but not age and growth of estuarine juveniles.

Of the approximately 360 perennial streams in Hawaii, about 20 form stream mouth estuaries (Maciolek, 1981; Maciolek & Timbol, 1981). Most Hawaiian streams are small and flow over steep topography. They usually enter the ocean by flowing over or through wave-formed sand or rock berms. These geological characteristics, combined with the typically rapid changes in stream discharge, have limited the development of stable inland reaches where freshwater is regularly influenced by seawater.

There have been few directed studies of the ichthyofauna of these Hawaiian estuaries. The physical, hydrographic, and some biological characteristics of the mangrove estuary at the confluence of Heeia

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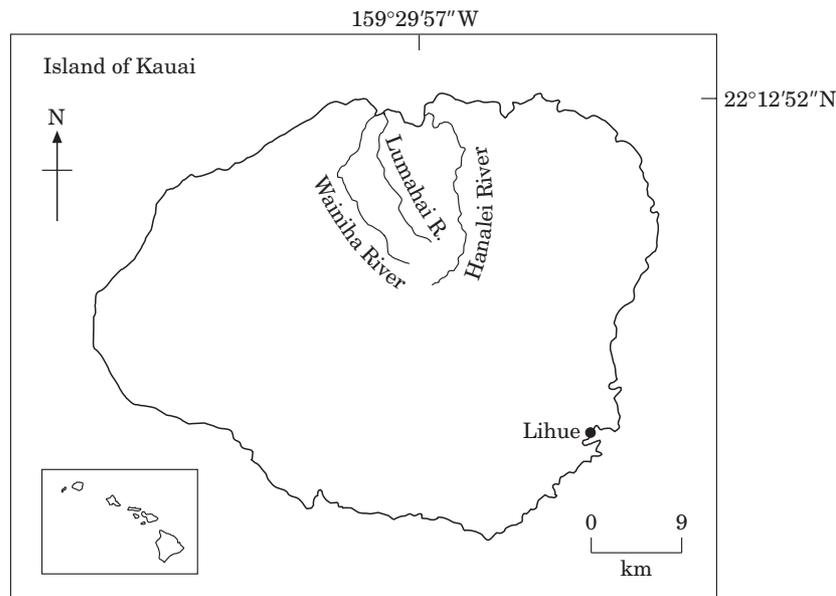


FIGURE 1. Island of Kauai in Hawaii (inset). Latitude and longitude of the mouth of the estuary of the Hanalei River (north shore) are shown.

Stream and Kaneohe Bay, Oahu were studied by Walsh (1967). However, no *Caranx* species were reported there. Kahana estuary, also on the island of Oahu, was the focus of research that described the physical characteristics of the estuary and trophic relationships of the macrofauna (Timbol, pers. comm.; Maciolek, 1981; Maciolek & Timbol, 1981). The abundance of *C. ignobilis* and *C. melampygyus* reported from Kahana estuary was low (only six individuals collected), although subsequent work has shown that their populations are large enough to support recreational fishing (Archer *et al.*, 1980; pers. obs.). Our research on the north shore of Kauai (of which this work is a part) has documented consistent occurrence of juvenile *C. ignobilis* and *C. melampygyus* in the river mouth estuaries of Hanalei, Wainiha, and Lumahai rivers (Harrison *et al.*, 1991).

The purpose of the present study was to examine the role of juvenile *C. ignobilis* and *C. melampygyus* in the Hanalei river estuary as part of a transient juvenile fish assemblage that makes use of the estuary as a nursery. The approach was to secure a better understanding of the environmental biology of these two carangids by analysing life history characteristics and habitat use. This was accomplished by: (1) defining the extent and dynamics of the estuarine habitat; (2) estimating population densities; (3) observing spatial and temporal distribution of juvenile jacks in the estuary; (4) analysing diets of *C. ignobilis* and *C. melampygyus* and examining overlap of their predation on specific prey groups; and (5) estimating age and

determining growth parameters of estuarine *C. ignobilis* and *C. melampygyus* and comparing them with growth characteristics for non-estuarine juveniles and sub-adults.

## Methods

### Description of habitat

The Hanalei River and its estuary lie on the north shore of the island of Kauai (Figure 1). The lower river and estuary meander through a low-lying flat floodplain and discharge into the east side of Hanalei Bay. The river is about 27 km long, and its headwaters receive intermittent but often heavy precipitation. (Mean annual rainfall on nearby Mt. Waialeale is 1016 cm/yr.) Long-term mean discharge is  $6.145 \text{ m}^3/\text{s}$  (217 cfs), although there is high variation throughout the year (Timbol, 1986).

Between March 1989 and October 1990, field work was performed in the estuary at approximately 2-week intervals. Aerial photographs were used to map habitat types. Habitat variables (cover density, substrate composition, etc.) were recorded by direct underwater visual observation. Locations regarding stations and physical/chemical habitat variables (e.g. the extent of saltwater intrusion) are expressed in terms of 'river metre', the distance in metres upriver from the mouth of the estuary (Figure 2).

Salinity profiles were recorded from the surface to the bottom at 0.5-m depth intervals using a YSI

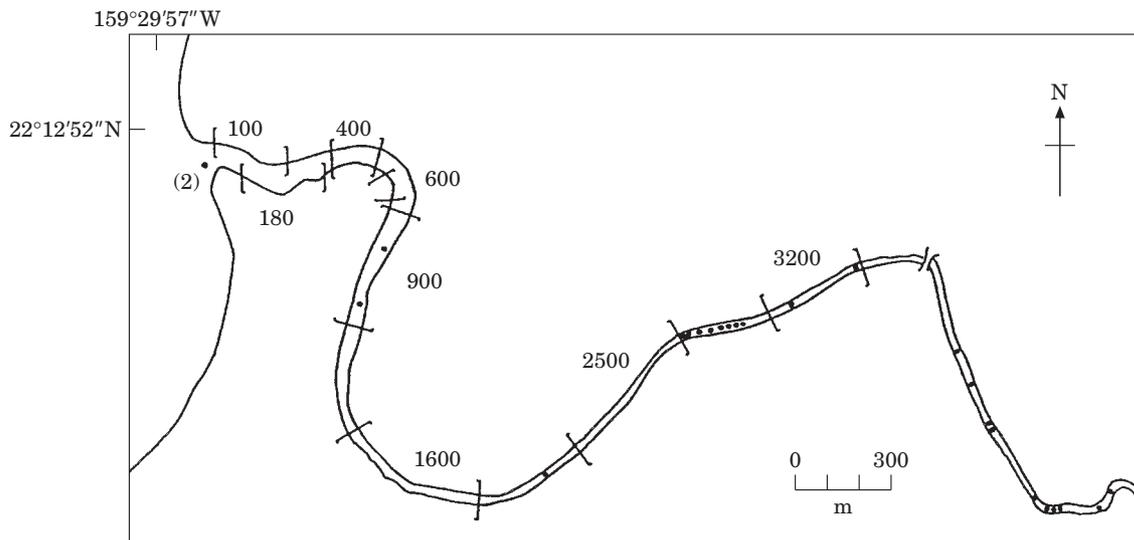


FIGURE 2. Estuarine portion of the Hanalei River, Kauai, Hawaii. Distances shown along the course of the estuary are measured in metres from the mouth, and mark the midpoints of study sites (enclosed in brackets [ ]) for underwater fish observations (Sites 400, 900, 1600, 2500 and 3200) and seining for fish collection (Sites 100, 180 and 600). Dots within the river represent 25 'head of tide' measurements made on 23 days between March 1989 and October 1990. Two separate occasions, marked (2) at the river mouth, indicate measurements when all water in the river was fresh.

Model 33 salinity-conductivity-temperature (SCT) meter. Particular care was taken to locate the 'head of tide'—the maximum upstream point of detectable salinity (+0.5)—on as many days and under as many different river discharge conditions as feasible. Discharge data were obtained from the U.S. Geological Survey gauging station No.16103000, located at river km 7.9 (22°11'31"N 159°27'57"W), at 11 m elevation on the river. Tidal height was obtained from published tide charts and adjusted both for regional and local (estuarine) time differences. Relationships between tidal height, river discharge and head of tide were examined using linear least squares regression.

#### *Abundance and distribution*

Juvenile jacks were collected primarily with a beach seine 31 m × 1.8 m with 6.4 mm square heavy delta mesh. Additional collections were made using a similar seine ~9 m long and a gill net 31 m × 2.2 m with 13 mm square monofilament mesh (used as a seine). Two similar, unvegetated banks suitable for seining were located near the estuary mouth (river metre 100 and 180) and upstream near river metre 600 (Figure 2).

Direct, systematic, underwater observations were carried out in five sites centred at river metre 400, 900, 1600, 2500 and 3200 (Figure 2). Linear transects 100 to 200 m long were established within each site parallel to the bank. Observations were made

by two snorkellers swimming timed, standardized surveys on these transects. Numbers and sizes of jacks observed were recorded.

#### *Analysis of gut contents*

Specimens used for gut content analysis came from collections with the 31 m beach seine and occasionally from collections with the other two nets, spear or hook-and-line. All jacks collected were immediately put on ice in the field and frozen soon afterward. Collections were made between 09:00 and 17:00h.

Contents of the entire gastrointestinal tract were identified to the lowest feasible taxon. Procedures followed were similar to those described by Hyslop (1980) and Parrish *et al.* (1985). Identifiable prey items were enumerated and liquid volume displacement was measured. For prey items that had undergone partial digestion, estimates of total original volume were made by comparison with whole individuals of similar size.

Three quantitative measures were taken for each prey category in the diet. The numerical percent (%N) is the number of individuals of a prey category divided by the total number of all prey individuals in the sample. The volume percent (%V) is the volume of a prey category divided by the total volume of all prey in the sample. The frequency percent (%F) is the number of guts containing a prey category divided by the total number of guts containing any prey in

the sample. These measures were combined to form an index of relative importance (IRI), where  $IRI = \%F(\%N + \%V)$  (Pinkas *et al.*, 1971). The IRI for each prey category was expressed as a percent of the sum of IRI values of all categories, i.e. as %IRI.

Overlap of diets was computed between the two *Caranx* species and between size groups within each species, using the simplified Morisita-Horn  $C_H$  formula (Krebs, 1999):

$$C_H = \frac{2 \sum_{i=1}^n p_{ij} p_{ik}}{\sum_{i=1}^n p_{ij}^2 + \sum_{i=1}^n p_{ik}^2}$$

where  $n$  is the number of prey categories, and  $p_{ij}$  and  $p_{ik}$  are the %IRI for the  $i$ th prey category for predator groups  $j$  and  $k$ .

Percent frequency (%F) was used to examine the amount and type of inorganic material in the guts that contained prey. Different types of sand (e.g. basaltic or calcareous) were characterized visually under magnification. This extraneous material in the guts is a probable indicator of spatial foraging patterns.

#### Age and growth

Sudekum *et al.* (1991) validated experimentally that calcareous increments in the otoliths of *C. melampygus* were deposited daily. We examined otoliths from a range of sizes of both *Caranx* species found in the estuary. The left sagitta was removed, washed and dried in preparation for analysis. Otoliths were cast in resin blocks and ground with fine sandpaper until the desired plane was exposed. This exposed section was highly polished with 0.3  $\mu$ m alumina paste, etched for 2–4 min with 8% ethylene diamine tetraacetate (EDTA), desiccated, vacuum coated with gold, and examined under a scanning electron microscope (Brothers, 1987). Sequential series of photomicrographs providing full coverage from the otolith core to the margin were assembled and growth increments enumerated.

These age data were pooled with and compared to data from non-estuarine jacks from the Northwestern Hawaiian Islands (NWHI) (Sudekum *et al.*, 1991). The NWHI jacks, because of their geographic isolation and the local geography, could never have been in an estuarine environment. The data were fitted to the von Bertalanffy growth equation (Ricker, 1975):

$$l_t = L_\infty [1 - e^{-K(t-t_0)}],$$

where:

$l_t$  = length at age  $t$ ;  $L_\infty$  = theoretical maximum length;  $K$  = a constant indicating the rate of change in length;  $t_0$  = theoretical age at 0 length.

To determine whether the growth data of the jacks in Hanalei estuary could be incorporated into a larger growth model, for each species, the parameter estimates for the pooled data were compared to the parameter estimates of the NWHI jacks alone.

## Results

### Habitat description

For most of the length of the estuary (76%), the banks were lined with thickets of hau (*Hibiscus tiliaceus*) and California grass (*Brachiaria mutica*). For most of the remaining length, banks were bare sand/gravel or lined with trees such as the false kamani (*Terminalia catappa*).

In most places, banks were steep to nearly vertical, water depths throughout the system were mostly 1 to 3 m, and substrate was composed of silt, sand, and gravel. In areas of sand and gravel above river metre 600, basaltic material of terrigenous origin was most abundant; farther downstream (river metre 600 to the mouth), the dominant sand and gravel was of reef-derived, calcareous material. Bottom cover (defined as recessed areas in brush, grass, or in the substrate) occurred primarily along the banks rather than in the open stream bed between them. Some bottom cover was available in the stream bed in a relatively small area of dead coral near the estuary mouth, between river metre 200 and 600. Snorkel transects for visual observation were established along large percentages of each type of habitat (Figure 2).

Head of tide was determined and salinity profiles taken in the estuary a total of 25 times on 23 days between March 1989 and October 1990 (Figure 2). The longitudinal extent of saltwater in the estuary was highly variable, ranging from not present on two occasions (i.e. river water was fresh all the way to the mouth) to a maximum measured intrusion at river metre 4830. Twenty-nine percent of the head of tide observations were found between river metre 2600 and 3000. Water of measurable salinity reached or exceeded river metre 3000 70% of the time (Table 1).

Vertical salinity and temperature profiles typically showed marked gradients between the overlying cold, freshwater layer and the warm, partially mixed saltwater below. Isopleth curves generated from a longitudinal series of vertical profiles demonstrated the 'salt wedge' characteristic of saltwater intrusion into mixohaline reaches (Figure 3). The tip of the salt

TABLE 1. Percent of all time that head of tide reached or exceeded upstream distance in the Hanalei River estuary on 23 days between March 1989 and October 1990. On two occasions, the head of tide was at the river mouth (i.e. all water in the river was fresh)

Distance of head of tide above river mouth	Percent of time
0 m	100%
700 m	90%
2000 m	80%
3000 m	70%
4000 m	30%
5000 m	0%

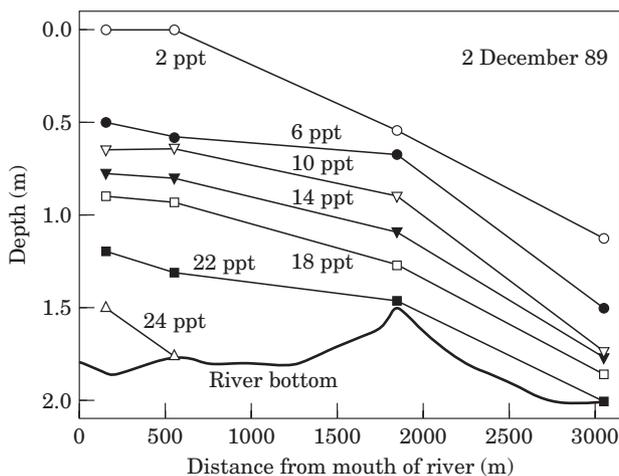


FIGURE 3. Plot of salinity isopleths derived from a longitudinal series of vertical salinity profiles measured during typical flow conditions (98 cfs discharge, head of tide at river metre 3080, 2 December 1989). Bathymetry of the river bottom is approximate.

wedge represents the head of tide, which changed its longitudinal position dramatically with time.

The upstream extent of head of tide in the estuary was more dependent on discharge than on tidal height. A linear regression was performed on the position of head of tide (river metre) and the  $\log_e$  2-day averaged discharge defined as the arithmetic mean of the discharge for the two previous days (Figure 4). At the long-term gauged mean discharge of 217 cfs, the head of tide would be expected to be at about river metre 2700 by this relationship. At discharges of 1600 cfs or higher, head of tide would be expected to occur at or near the mouth of the estuary. An attempt was made to include the effect of tidal height in this model of the intrusion of saltwater into the estuary. A significant linear regression relationship could not be demonstrated for the position of head of

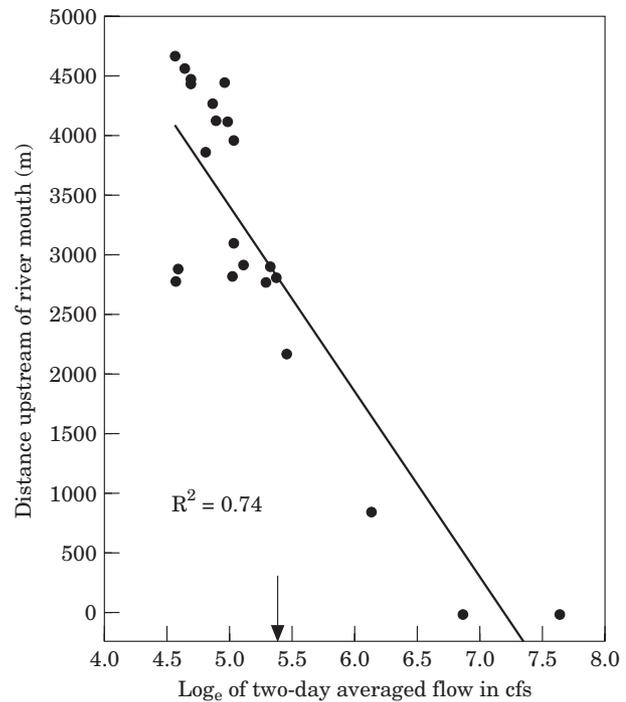


FIGURE 4. Linear least squares regression relationship between position of head of tide and  $\log_e$  of river discharge. The two lowest points (zero distance upstream) represent two occasions when all water in the river was fresh. Mean annual discharge is indicated by arrow.

tide as a function of tidal height with discharge or of tidal height alone.

#### Abundance and distribution

Ninety-eight *C. ignobilis* and 82 *C. melampygus* were collected by beach seining (primarily with the 31-m seine) in 160 hauls between May 1989 and October 1990. They were collected in 26.3% and 16.3% of all hauls respectively. The size range of *C. ignobilis* was 51 to 168 mm FL. *Caranx melampygus* sizes were from 54 to 177 mm (Figure 5). Morphometric relationships are given in Table 2.

Seine hauls were standardized on a catch per unit effort (CPUE) basis for comparisons of relative abundance or density, with a single seine haul used as a unit of effort. For the 31-m seine (used for 76% of all hauls), the overall CPUE values (all sites combined) were 0.63 and 0.64 fish per seine haul for the two jack species. Catch per unit effort for these two species was low but similar (0.17 and 0.20 fish per seine haul) at the upriver collection site (river metre 600), and somewhat higher and similar (0.78 and 0.79) at the lower river sites (river metre 100 and 180). In a 17-month time series, CPUE of juveniles of both

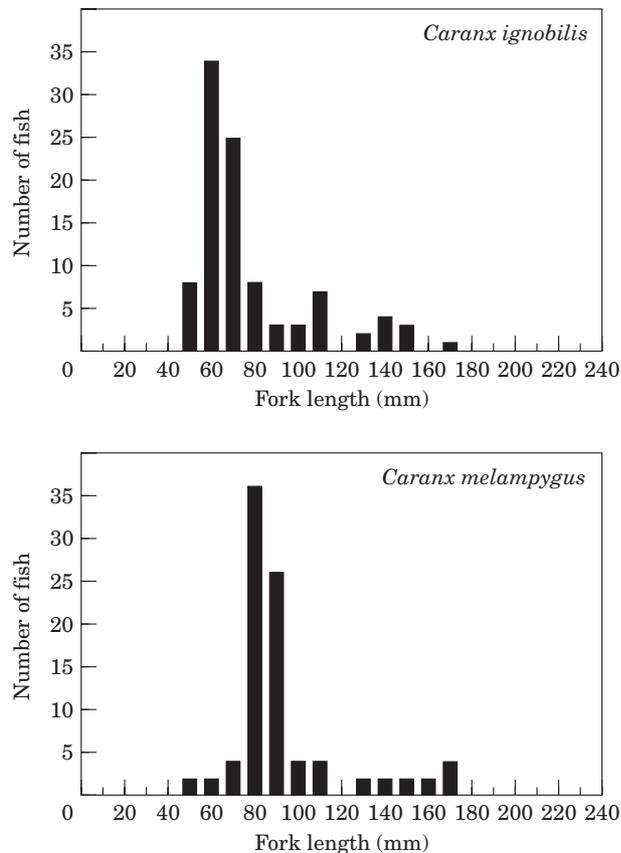


FIGURE 5. Size distributions of 98 *Caranx ignobilis* (51–168 mm FL) and 82 *Caranx melampygyus* (54–177 mm FL) collected by beach seine from the Hanalei estuary.

species was generally low and variable except for a late summer/autumn peak in 1990 (Figure 6).

From a total of 62 visual censuses (an overall effort of 46 observation hours), the *Caranx* species (combined) were observed at all stations except the farthest upstream station (i.e. over river metres  $\sim 300$ –3000). This portion of the river was mixohaline (below the head of tide)  $\sim 70\%$  of the time in our measurements (Table 1). Sightings (and especially identification to

species) of these highly mobile carangids were limited by high turbidity and resultant poor visibility in these estuarine waters. Our best visual index of abundance of all *Caranx* over this full range of the river was a mean of  $\sim 0.8$  individuals censused per hour over all transects. Only about 20% of the individuals were identified to species. The density of carangids sighted did not seem greatly different over this length of the river (range of means of the four stations  $\sim 0.79$ – $1.4$  individuals/h, with no clear spatial trend). Based on the small samples of fish identified to species, the best estimate of the index for each of the two *Caranx* species over this range of stations was  $\sim 0.08$  individuals/h. The absolute values are not meaningful, but the result suggests (in agreement with the seining results) that the abundance of the two species is similar. The size range of jacks censused visually was 80 to 130 mm FL, except for one individual of 310 mm and one of 400 mm FL.

#### Analysis of gut contents

Of 106 *C. ignobilis* guts examined, 83 (78%) had contents that were identifiable to some taxonomic level (Table 3). These fish ranged from 50 to 177 mm FL. Fish were a frequently observed prey group in the samples (65 %F). When fish as a group were considered separately (underlined values), the fish in 94 %F of the predators were not identifiable to any lower taxonomic level, resulting in low %F, %N, %V and % of summed IRI values for individual fish taxa. However, the great majority of unidentified fish remains appeared to be mugilids or *Kuhlia sandvicensis*. Distinguishing between these two taxa when partially digested was usually not possible. At small sizes, their scales and bones digested quickly. Otoliths were frequently found, but they too were partially dissolved and did not aid in distinguishing between these prey groups. Of predators containing identified fish prey, 9%F had eaten gobioids, but only one prey individual

TABLE 2. Relationships determined by regression among standard length (SL), fork length (FL), and total length (TL) in millimetres and whole body wet weight (W) in grams for *Caranx ignobilis* (50 to 177 mm SL) and *Caranx melampygyus* (53 to 165 mm SL)

<i>Caranx ignobilis</i>			<i>Caranx melampygyus</i>		
Relationship	R <sup>2</sup>	Sample size (n)	Relationship	R <sup>2</sup>	Sample size (n)
$W = 1.64 \times 10^{-5}(SL)^{3.09}$	0.99	39	$W = 1.35 \times 10^{-5}(SL)^{3.11}$	0.96	44
$SL = 0.943(FL) - 1.4$	0.99	39	$SL = 0.938(FL) - 0.404$	0.99	44
$SL = 0.778(TL) + 2.5$	0.99	39	$SL = 0.753(TL) + 5.6$	0.99	44
$TL = 1.211(FL) - 5.0$	0.99	39	$TL = 1.242(FL) - 7.6$	0.99	44

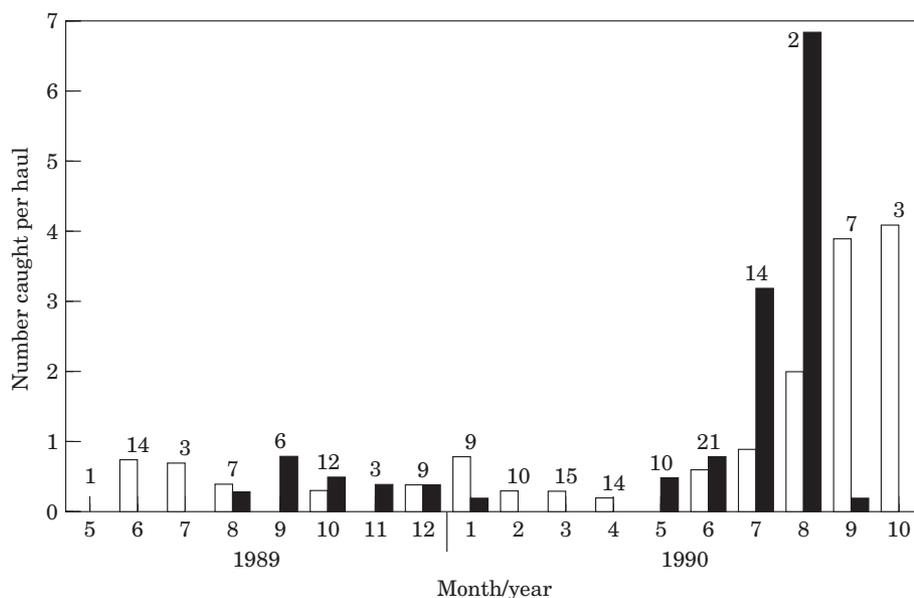


FIGURE 6. Time series of monthly mean catch per unit effort by beach seine collections of *Caranx ignobilis* and *Caranx melampygus* from the Hanalei estuary. Total number of hauls made during a month is indicated at each monthly interval. □ *C. ignobilis*; ■ *C. melampygus*.

TABLE 3. Summary of gut content analysis of 83 *Caranx ignobilis* specimens. At the highest systematic level of analysis, the prey groups and table values are in bold. The next level of analysis is of those table values not italicized or in parentheses (); 'Fish (pooled)' represents all fish taxa combined, analysed at the same level as the major invertebrate subgroups (shown in lower case). Values in italics refer to analysis performed only with prey fish (invertebrates excluded). Values in parentheses are of minor taxa that were not treated as separate groups in analysis at higher levels

	Frequency %	Numerical %	Volume %	% of Summed IRI
<b>FISH</b>	<b>65.06</b>	<b>12.57</b>	<b>96.63</b>	<b>52.49</b>
Fish (pooled)	65.06	12.57	96.63	99.74
Kuhliidae ( <i>Kuhlia sandwicensis</i> )	3.70	1.28	1.84	0.07
Bothidae ( <i>Bothus mancus</i> )	1.85	0.64	2.39	0.03
Mugilidae	3.70	1.28	1.30	0.06
Gobioids	9.26	8.97	5.85	0.82
( <i>Eleotris sandwicensis</i> )	(1.85)	(0.64)	(0.24)	(0.01)
Unidentified fish	94.44	87.82	88.62	99.01
<b>CRUSTACEANS</b>	<b>71.08</b>	<b>87.11</b>	<b>3.33</b>	<b>47.50</b>
Amphipoda	3.61	10.64	0.14	0.29
Tanaidacea	30.12	30.46	0.06	6.49
Isopoda (Flabellifera)	36.14	38.92	0.33	10.48
Shrimp	22.89	2.82	0.31	0.53
Stomatopoda	1.20	0.08	1.16	0.01
Copepoda	2.41	2.82	<0.01	0.05
Crabs	1.20	0.16	1.02	0.01
Unidentified crustaceans	10.84	1.13	0.21	0.11
<b>INSECTS AND SPIDERS</b>	<b>3.61</b>	<b>0.32</b>	<b>0.02</b>	<b>0.01</b>
Trichoptera	2.41	0.24	0.02	<0.01
Araneidea ( <i>Gasteracantha</i> sp.)	1.20	0.08	<0.01	<0.01

(*Eleotris sandwicensis*) was identifiable to species. Only two predator individuals (4 %F) had eaten identifiable *K. sandwicensis*, and two had eaten identifiable mugilids.

Crustaceans were found in 71 %F of the guts with prey. Most important of these were isopods (36 %F), shrimp (23 %F), and tanaids (30 %F). Amphipods and copepods were of less importance (4 %F and

Table 4. Summary of gut content analysis of 83 *Caranx melampygus* specimens. At the highest systematic level of analysis, the prey groups and table values are in bold. The next level of analysis is of those table values not italicized or in parentheses (); 'Fish (pooled)' represents all fish taxa combined, analysed at the same level as the major invertebrate subgroups (shown in lower case). Values in italics refer to analysis performed only with prey fish (invertebrates excluded)

	Frequency %	Numerical %	Volume %	% of Summed IRI
<b>FISH</b>	<b>43·37</b>	<b>3·23</b>	<b>95·06</b>	<b>32·89</b>
Fish (pooled)	43·37	3·23	95·06	99·09
Kuhliidae ( <i>Kuhlia sandwicensis</i> )	2·78	0·76	1·10	0·03
Gobioids	13·89	10·61	5·68	1·26
Unidentified fish	97·22	88·64	93·23	98·71
<b>CRUSTACEANS</b>	<b>85·54</b>	<b>96·77</b>	<b>4·93</b>	<b>67·11</b>
Amphipoda	6·02	3·57	0·49	0·19
Tanaidacea	53·01	69·78	0·19	28·62
Isopoda (Flabellifera)	57·83	21·90	1·02	10·23
Shrimp	28·92	1·10	1·22	0·52
Copepoda	2·41	0·17	<0·01	<0·01
Crabs	2·41	0·07	0·98	0·02
Portunidae	1·20	0·02	0·88	0·01
Unidentified crustaceans	6·02	0·15	0·15	0·01

2 %F, respectively). Insects and spiders were of minor importance. Most of the guts containing prey appeared rather full, and none contained visible parasites except one (67 mm SL) that contained a single acanthocephalan.

Ninety *C. melampygus* guts were analysed (53 to 165 mm FL), and 83 (92%) contained identifiable prey items. Fish made up 43 %F of the diet (Table 4), and most of these prey could not be identified. Of predators containing identified fish prey, 14% ate gobioids—none identifiable to lower levels. Crustaceans were in 86 %F of the guts containing prey; most frequent were isopods (58 %F), tanaids (53 %F), and shrimp (29 %F).

The numerical percents and frequency percents for total crustaceans in the diets of both *C. ignobilis* and *C. melampygus* were high, but the volume percents were very low, reflecting primarily the very small size and large numbers of the tanaids, isopods and amphipods. The resulting %IRI values for fish as a group and crustaceans as a group in *C. ignobilis* were similar; for *C. melampygus*, %IRI for crustaceans was considerably larger than that for fish. Since this result is largely due to the very much greater number of tiny crustacean prey, and since a large percentage of both jacks contained fish as very high percentages of their volume of food, the dominance of fish in trophic support of both these carangids is probably greater than the IRI values suggest.

The overall diet overlap of *C. ignobilis* and *C. melampygus*, compared using %IRI, was expressed by a  $C_H$  of 0·93. High values of overlap were also obtained with three other common overlap indices:

Pianka's, percentage overlap, and Horn's (Krebs, 1999). The fraction of guts containing fish was not significantly different between the two *Caranx* species ( $\chi^2=0\cdot05$ ,  $df=1$ ,  $P<0\cdot81$ ). However, the higher %F, %N, %V and %IRI values suggest that *C. ignobilis* (52 %IRI) is somewhat more piscivorous than *C. melampygus* (33 %IRI). The overlap calculated between 'large' (over 90 mm FL,  $n=20$ ) and 'small' (less than 90 mm FL,  $n=65$ ) *C. ignobilis* was high ( $C_H=0\cdot92$ ). The overlap between the same size subgroups (over 90 mm FL,  $n=38$ ; less than 90 mm FL,  $n=45$ ) of *C. melampygus* was comparable ( $C_H=0\cdot90$ ). The fraction of guts containing fish as prey was not significantly different between size groups for *C. ignobilis* ( $\chi^2=0\cdot33$ ,  $df=1$ ,  $P<0\cdot57$ ) or between size groups of *C. melampygus* ( $\chi^2=0\cdot18$ ,  $df=1$ ,  $P<0\cdot67$ ).

Prey diversity was low, with 11 major prey groups in the diet of *C. ignobilis* and 8 in the diet of *C. melampygus*. The total number of prey organisms for some of the minor prey groups (insects, spiders, stomatopods, crabs) was low, in some cases only a few individuals. This resulted in low accuracy in describing the quantitative contribution to the diet by these minor groups.

Inorganic matter was found in 30% of the *C. ignobilis* guts and 58% of the *C. melampygus* guts. Of these, *C. melampygus* had a higher frequency of basaltic sand (37 %F) than did *C. ignobilis* (15 %F). The sand was probably consumed incidentally while foraging for benthic prey, in contrast to taking prey from higher in the water column. Most sand in the upriver portions of the estuary (above river metre 600) is basaltic; in the reach below this, the primary sand size

TABLE 5. Estimated ages of juvenile jacks based on examination of daily growth increments in otoliths

<i>Caranx melampygus</i>			<i>Caranx ignobilis</i>		
SL (mm)	Age in:		SL (mm)	Age in:	
	Days	Years		Days	Years
70	100	0.27	60	94	0.26
77	88	0.24	62	82	0.23
85	92	0.25	66	82	0.23
100	118	0.32	72	87	0.24
107	91	0.25	82	89	0.24
133	203	0.55	104	160	0.44
			111	130	0.36
			136	126	0.35
			142	122	0.33
			152	258	0.71

sediment is reef-derived calcareous material. The occurrence of these two sand types in the river bed and in the guts of the two species is consistent with the occurrence of the food items in the guts, and with direct underwater observations. *C. melampygus* appears to forage on benthic organisms more frequently than does *C. ignobilis*, and possibly more often in areas farther up the estuary.

#### Age and growth

Length and weight data for a sample of each species were fitted by regression to power functions (Table 2). The exponents of these functions indicate that growth is nearly isometric. Simple linear functions were also fitted by regression to relate standard length (SL), fork length (FL), and total length (TL) (Table 2). For each of the four functions, the parameters estimated for the two species are very similar and reflect the morphological similarity of juveniles of the two species.

The daily growth increments of otoliths from 10 *C. ignobilis* and 6 *C. melampygus* were examined by SEM for age estimation (Table 5). This limited range of sizes could not be used alone to produce a growth model for the full range of sizes attainable by the species. The Hanalei estuary data were pooled with age estimates for fish from the NWHI (Sudekum *et al.*, 1991).

The pooled data sets were fitted to the von Bertalanffy growth equation, and the results were compared with parameter estimates based on NWHI data alone (Table 6). For both species, the pooled sample size was greatly increased and the lower end of the size range was extended considerably. For the

growth curves of both species, the parameter estimates for the growth coefficient  $K$  and for  $t_0$  decreased, and the estimates for  $L_\infty$ , the asymptotic maximum length, increased (Figures 7 and 8).

For each species, the von Bertalanffy growth equation was also fitted with a data set weighted so that the numbers of observations were approximately equal in each portion of the lifespan where there were data. Estimated growth parameters ( $L_\infty$ ,  $K$ ,  $t_0$ ) were not substantially different from those obtained with unweighted data. Despite the disproportionately large numbers of observations for small individuals in the pooled data sets (Figures 7 and 8), the von Bertalanffy growth equation fitted to unweighted data appears to adequately describe growth characteristics for all sizes attained by both species.

## Discussion

#### Habitat description

In Kahana estuary (Oahu), which shares many geomorphological and hydrological characteristics with Hanalei, Timbol (pers. comm.) reported a salinity and temperature regime similar to that of Hanalei. Based on limited measurements of dissolved oxygen (DO) in Hanalei estuary and extensive measurements in Kahana estuary, it appears that in both estuaries, low DO conditions rarely if ever limit distribution of the macrofauna. Less extensive limnological studies (Archer, 1981; Harrison *et al.*, 1991) indicated that two other estuaries, Wainiha and Lumahai, located on the north shore of Kauai close to Hanalei, had broadly similar physical characteristics, but lower discharge.

TABLE 6. Estimated parameters and sample characteristics for the von Bertalanffy growth model for *C. ignobilis* and *C. melampygyus* from two collections: the Hanalei estuary and the Northwestern Hawaiian Islands (NWHI). Columns 1 and 3 are based on pooled data from Hanalei and the NWHI; columns 2 and 4 are based on data from the NWHI only. (NWHI data from Sudekum *et al.*, 1991)

	<i>C. ignobilis</i> (pooled)	<i>C. ignobilis</i> NWHI only)	<i>C. melampygyus</i> (pooled)	<i>C. melampygyus</i> (NWHI only)
$L_{\infty}$ (asymptotic SL)	2129 mm	1838 mm	973 mm	897 mm
K	0.082/yr	0.111/yr	0.194/yr	0.233/yr
$t_0$	-0.173 yr	0.097 yr	-0.196 yr	-0.044 yr
$R^2$	0.9832	0.9766	0.9628	0.9344
n (sample size)	20	10	20	14
Range of SL used	60–1180 mm	106–1180 mm	70–660 mm	122–660 mm
Range of estimated ages	0.24–9.27 yr	0.75–9.27 yr	0.23–5.90 yr	0.51–5.90 yr

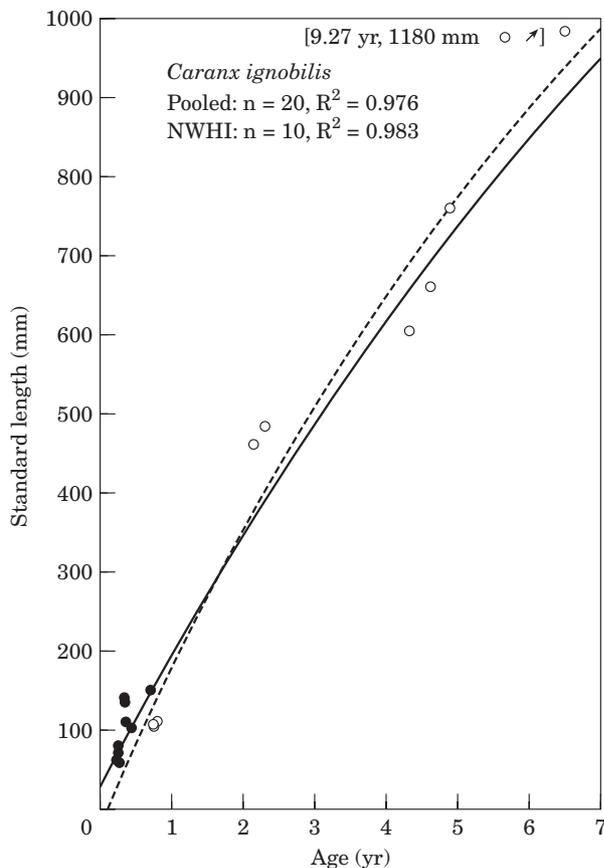


FIGURE 7. Growth data and von Bertalanffy growth curves derived for *Caranx ignobilis*. See Tables 5 and 6 for details. --- NWHI; — Pooled; ○ NWHI; ● Hanalei.

Maciolek (1981) commented that the vertical tidal range in Hawaiian marine waters is small and the 'physiochemical features of Hawaiian estuaries are primarily dependent upon stream discharge relative to basin morphometry'. Thus,

Hawaiian estuaries are fundamentally different from systems where tidal influence is strong, e.g. in many temperate, continental regions (Glen, 1979; Jay & Smith, 1988; Dyer, 1989).

#### Abundance and distribution

In Kahana estuary, Maciolek and Timbol (1981) reported a total catch of six individuals of '*Caranx* sp.', and Archer *et al.* (1980) reported *Caranx ignobilis* as 'common' near the mouth of the estuary but absent farther upstream. Harrison *et al.* (1991), using the same timed underwater census protocol and personnel as in the present study, reported densities of 0.54 and 1.2 fish/h for unidentified *Caranx* sp. in Wainiha and Lumahai estuaries, respectively. The relative abundances of *C. ignobilis* and *C. melampygyus* in Hanalei are well below those of many juvenile marine fishes that inhabit the estuary. However, the juvenile jacks are the largest piscivores that are common throughout the estuary.

*Caranx ignobilis* was described as an abundant temporary juvenile inhabitant of northern Australian mangrove creek habitat (Blaber, 1986). Blaber and Milton (1990) reported that *C. ignobilis* and *C. melampygyus* co-occurred in comparable abundance in mangrove estuaries of the Solomon Islands. In estuaries of Natal, South Africa, Blaber and Cyrus (1983) described *C. ignobilis* as 'uncommon but widespread' throughout the seven geographically distinct systems under study, and found *C. melampygyus* the most abundant of five carangids in a single estuary. *Caranx ignobilis* was found throughout most euryhaline situations (salinity 0–38) and throughout a wider turbidity range. *Caranx melampygyus* was found only in water of high salinity and in systems with lower turbidity. In

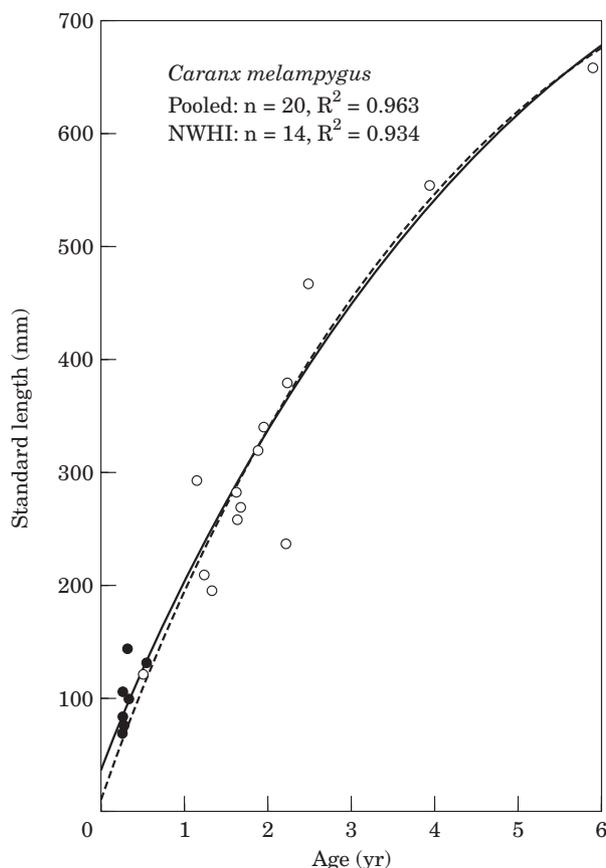


FIGURE 8. Growth data and von Bertalanffy growth curves derived for *Caranx melampygius*. See Tables 5 and 6 for details. --- NWHI; — Pooled; ○ NWHI; ● Hanalei.

the Hanalei system, the two species occur in similar relative abundance in habitats having the full range of salinity from 0 to 35.

#### Analysis of gut contents

When the diets of predator groups *j* and *k* are completely distinct, overlap as measured by  $C_H$  is 0; when the proportions of prey categories are identical,  $C_H$  is 1 (Simpson, 1949). This measure of overlap is most rigorous when  $p_{ij}$  and  $p_{ik}$  are large. The index also depends upon the assumption that the food resources are taken from the same habitat for both predator groups (Horn, 1966).

Langton (1982) suggested that  $C_H$  values of 0–0.29 be considered ‘low’ overlap, 0.30–0.59 ‘medium’ overlap, and >0.60 ‘high’ overlap. By these criteria, the value of  $C_H=0.93$  resulting from calculations of diet overlap between all *C. ignobilis* and *C. melampygius* is indicative of high overlap. The overlap indices between ‘large’ and ‘small’ juvenile *C. ignobilis* ( $C_H=0.92$ ) and between similar subgroups of *C.*

*melampygius* ( $C_H=0.90$ ) both indicated high overlap, and it is unlikely that a major dietary shift occurs for either species during growth through the size ranges that were collected in the estuary.

In Kahana estuary on Oahu, Maciolek (1981) determined that 47% of the diet of a sample of six ‘*Caranx* sp.’ individuals (77 to 108 mm SL, probably *C. melampygius*) was composed of fish (gobiids, mugilids, and *Kuhlia*) and that 53% was composed of benthic crustaceans (especially palaemonid and penaeid shrimps). Although the diets were quantified using a protocol different from this study, the results are similar to those of *C. melampygius* from Hanalei. However, the small sample size and uncertainty of species identification make the Kahana results difficult to interpret.

Diets of adult *C. ignobilis* from the NWHI (Sudekum *et al.*, 1991) consisted largely of fish (90% IRI), and the diets of *C. melampygius* even more so (99% IRI). *Caranx melampygius* larger than 350 mm SL showed a significant increase in piscivory, with a decrease in the proportion of crustaceans consumed. It seems that this change to more piscivorous habits occurs at about the largest size that these species are found in the Hanalei estuary.

Blaber and Cyrus (1983) reported the diets of 33 juvenile (40 to 199 mm SL) *C. ignobilis* from South Africa and found that the highest frequency percent of prey taxa were crustaceans. Small penaeid and mysid shrimps were the most frequently consumed prey groups (found in 42% and 21% of the guts, respectively). Small gobiids were the most frequently (15%) observed prey fish in the samples. Thirty five subadult estuarine *C. ignobilis* (200 to 550 mm SL) showed a distinct dietary shift from small crustaceans to fish, with mysids completely absent in the diet of the fish of subadult size. Of 158 *C. melampygius* juveniles (40 to 169 mm SL) examined in the same study, most had also consumed small crustaceans (penaeids 41%, mysids 61%). The 20 subadults examined (170 to 270 mm SL), like *C. ignobilis*, exhibited a trend toward greater piscivory, with gobiids, centropomids, and atherinids occurring in greater frequencies in the diet with increasing size. Like both species of juvenile jacks in Natal, most small *C. ignobilis* in a sample from northern Australia (Blaber & Blaber, 1980) consumed crustaceans, especially small penaeids (in 86% of the sample).

Based on %F alone, the results for the juveniles in these locations do not seem greatly different from our findings in Hanalei for fish of the same general size group, although %F of fish at Hanalei may be somewhat higher. In light of our results with all the diet measures, a more complete analysis of the diets from

these other locations, including %N and especially %V, might lead to more meaningful comparisons with our findings. The finding of increasing piscivory as these jacks mature from juveniles to subadults is consistent with our results here, combined with our earlier results in the NWHI (Sudekum *et al.*, 1991).

#### *Age and growth*

The age and length data for *C. ignobilis* and *C. melampygyus* indicate that the estuary is commonly occupied by juveniles between the ages of 0.2 and 0.7 years. It is not known whether residence in the estuarine system is continuous, or if there is recurrent in- and out-migration. Adults seem to be uncommon in the estuary.

Estimated ages of juvenile jacks from Hanalei were in close agreement with the lower range of age estimates from the smaller of the jacks from the NWHI. Combining the data from the two studies considerably extended the size and age range for the von Bertalanffy growth model for both the jack species (Table 6, Figures 7 and 8). The pooled data set could be fitted well to the von Bertalanffy growth model, and the parameters thus estimated are not greatly different from those based on the NWHI data alone.

No direct, rigorous comparisons could be made between the growth rates of jacks aged from the two locales because both data sets were small and there was little overlap in the juvenile size range. However, the data do not suggest a difference in growth rates between estuarine and NWHI fish. If increased prey availability were a primary factor in determining estuarine residence, then it would be reasonable to expect higher growth rates from the fish taken from the estuary (de Decker & Bennett, 1985).

#### *Value of estuarine nursery habitat*

No information is available on the abundance of invertebrate prey in the Hanalei estuary, but the availability of fish prey seems high. Small juvenile stages of several fish species (e.g. kuhliids, mugilids) that are known prey of these jacks were abundant in our surveys of reaches where the jacks were abundant (Harrison *et al.*, 1991) and occurred in our diet studies (Tables 3 and 4).

Although these jacks can tolerate salinities well below full seawater values, our visual censuses and study of the salinity distribution in the estuary indicate that they are absent or uncommon in reaches of the lower river that are usually fully fresh or very low in salinity. We found them only in areas that are downstream of the head of tide >70% of the time. Since

observations and feeding results (e.g. sediment in gut samples) suggest strong demersal associations, they may occur almost to the head of tide by remaining near bottom (in the salt wedge). All collections by seining (our most quantitative method) were mixohaline 90% of the time (Table 1), i.e. on all occasions measured except during or shortly after major freshets. However, the markedly lower CPUE by seine at river metre 600 than at river metres 100 and 180, together with patterns of salinity distribution such as shown in Figure 3, suggest that the *Caranx* species are less abundant farther upriver in regimes of lower salinity.

Other factors, both biological and physical, may be important in determining the extent of estuarine use by *C. ignobilis* and *C. melampygyus*. Blaber and Blaber (1980) examined various correlations between estuarine use by juvenile marine fish and biological and physical conditions found in a large Australian subtropical estuary. They found that increased prey availability, refuge from agitated offshore waters, and increased turbidity were more highly correlated with estuarine occupancy than were decreased salinity or refuge from potential predators. Shelter from mechanical stress, especially turbulence from waves along the shoreline, may be less important for these jacks than for many estuarine species. Both jacks are commonly found in high energy, wave exposed, marine environments as juveniles and adults. The estuary may be a physically stressful environment because of its unpredictable flooding and frequent changes in salinity. Circumstantial evidence suggests that predation pressure on both jack species is much reduced in Hanalei estuary compared to adjacent coastal waters. Few aquatic or terrestrial predators are found to co-occur with the jacks in the estuary. This may be largely because of the lower and more variable salinity environment. The higher turbidity of the estuarine waters provides additional refuge from predation pressure. Juvenile marine fish have been shown to prefer turbid estuarine conditions (Blaber & Blaber, 1980; Cyrus & Blaber, 1987a, b) and to avoid clear water.

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