

Abstract.—The large jack species *Caranx ignobilis* and *Caranx melampygus* were collected from the nearly pristine shallow waters of the atolls, reefs, and shoals of the North-western Hawaiian Islands. Both species were aged by counting daily otolith increments and validating frequency of otolith deposition by marking captive fish with tetracycline. Growth for each species was well described by a von Bertalanffy relationship. Measured growth of captive *C. melampygus* was also in agreement. Gravid fish of both species were found only in April–November; peak spawning season for both was about May–August. Reproduction began at ~350 mm SL (~2 years old) in *C. melampygus* and at ~600 mm SL (~3½ years old) in *C. ignobilis*. Fecundity of female *C. melampygus* varied approximately as the 1.7 power of body weight. Both species were >90% piscivorous, as judged from combined volume and number of prey and incidence of predation. Crustaceans and cephalopods comprised several percent of the diet of *C. ignobilis*; both groups were present but less important in *C. melampygus*. Both jack species ate gastropods in trace amounts. The overall diet of the two species showed moderate overlap: “Pianka’s” index of overlap, $A_{yz} = 0.42$. The rate of food consumption for captive *C. melampygus* was used to estimate the respiratory metabolic coefficient, which in turn was used to estimate respiratory demands for all size-classes of both species. The von Bertalanffy model predicted growth energy, and reproductive energy was estimated from values of the gonadosomatic index. These energy terms were combined to calculate the food consumption required to sustain all size-classes appearing in local catch data. This distribution can be represented by a composite individual for each species consuming a little less than 50 kg/year (*C. melampygus*) and about 150 kg/year (*C. ignobilis*). Rough population estimates indicated that at one well-studied atoll, the two species populations combined may eat over 30,000 metric tons of prey per year. These results suggest a quantitatively important trophic role for these top-level carangid predators.

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Life History and Ecology of Large Jacks in Undisturbed, Shallow, Oceanic Communities*

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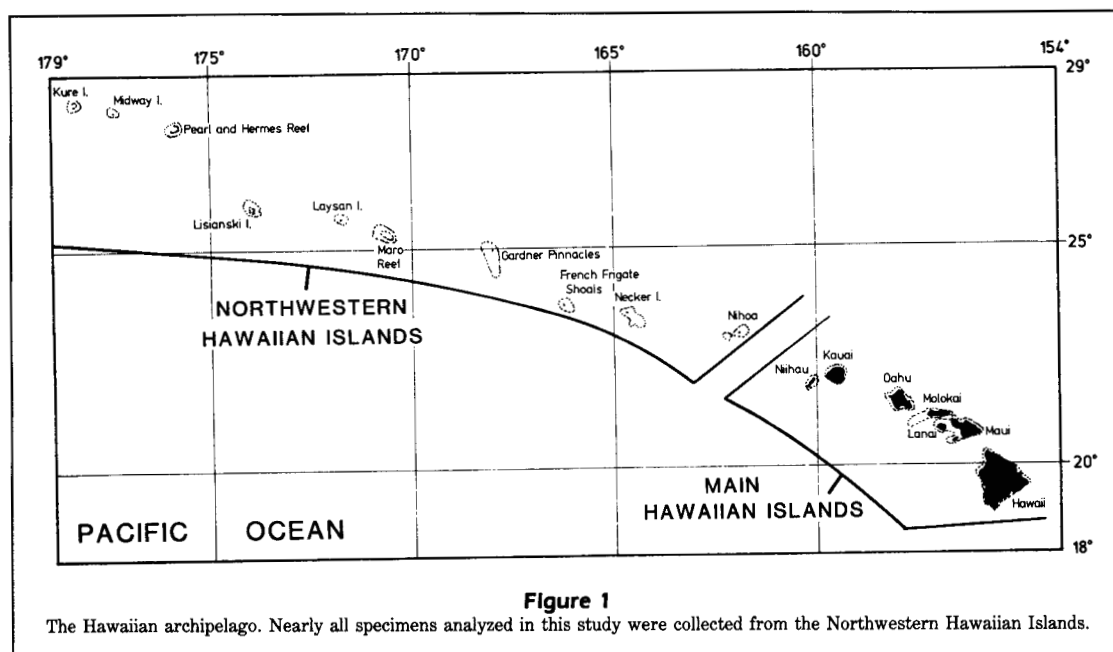
Large jacks (family Carangidae) are widely distributed in tropical and subtropical waters and are highly prized in local fisheries wherever they occur. Where their populations have not been depleted by fishing, these large, active predators are often abundant, and they are probably important in the ecology of nearshore communities. In particular, *Caranx ignobilis* (Forsk.) and *C. melampygus* (Cuvier and Valenciennes) are large carnivores that occur commonly throughout much of the tropical Indo-Pacific. These fast, wide-ranging species occupy the entire water column, but their habitats appear to be mostly demersal. They seem to maintain important ties with the demersal fish and benthic fauna of shallow coastal areas, islands, atolls, and isolated shoals.

In Hawaii, these two species are commonly the most abundant of the large, shallow-water, demersal jacks.

Large jacks, and these *Caranx* species in particular, have long been important food and market fishes in Hawaii (Cobb 1905, Hamamoto 1928, Titcomb 1972). Heavy commercial and recreational fishing pressure has developed, especially in the last several decades (Gosline and Brock 1960, Ralston and Polovina 1982, Ralston 1984, Ralston and Kawamoto 1988, Hawaii DLNR 1989), and stocks in the main, inhabited islands are certainly considerably depressed (Shomura 1987).

Despite their widespread occurrence and importance in fisheries, the species biology and ecology of most jacks have been inadequately studied, and little information is available to guide decisions for fishery management. For species such as *C. ignobilis* and *C. melampygus*, which combine large size, high natural abundance, and aggressive feeding habits, the predatory effects on the demersal fauna might be expected to be significant. Therefore, study of the species biology and ecology of these jacks is important both for manage-

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ment of their fisheries and for understanding the ecology of the communities in which they occur.

The uninhabited Northwestern Hawaiian Islands (NWHI) (Fig. 1) offered a particularly appropriate study area because of their size, isolation, and almost pristine biotic communities. Their ecology and natural resources were the subject of a 5-year, multi-agency study (Grigg and Pfund 1980, Grigg and Tanoue 1984), which included major trophic work on shallow-water communities by the Hawaii Cooperative Fishery Research Unit (e.g., DeCrosta et al. 1984, Sorden 1984, Parrish et al. 1985, Norris and Parrish 1988). The present study was done in conjunction with this larger program. Results from these relatively undisturbed carangid populations in the NWHI are also relevant for other populations of large jacks and for management of exploited jack populations.

Materials and methods

Collection Information

Specimens of one or both species were collected from French Frigate Shoals (FFS), Maro Reef, Midway Islands, Pearl and Hermes Reef, Lisianski Island, and Necker Island (Fig. 1). Samples were obtained by a wide variety of methods, including handlining, trolling,

casting, longlining, and spearing by divers using SCUBA. All jacks came from water less than 30m deep. In atoll waters, they were taken both inside and outside the barrier reefs. Collections were made irregularly between September 1978 and March 1983, including all months of the year except February (*C. melampygyus*) and February and December (*C. ignobilis*). A little over half of all specimens were taken in fall (September–November). Night collections were logistically difficult and largely unproductive. Therefore, there is a daytime bias in the sampling that may have influenced dietary results. The unpreserved fish were weighed whole, and the standard (SL), fork (FL), and total (TL) lengths were measured to the nearest millimeter. Guts of all specimens were injected with formalin in the field and/or frozen promptly. Data were taken on a total of 154 *C. melampygyus* and 120 *C. ignobilis*.

Age and growth

For a selected group of specimens covering a wide range of sizes of both species, age was estimated by counting short-period increments of carbonate deposition in otoliths (Radtke 1987). The fish were decapitated along a boundary represented by the edge of the operculum. A sagittal cut was then made through the midline of the head and the cranial cavity exposed. The

Table 1

Relationships determined by regression among standard (SL), fork (FL), and total (TL) lengths in millimeters and whole wet body weight (W) in grams for *Caranx melampygus* and *Caranx ignobilis*.

<i>Caranx melampygus</i>			<i>Caranx ignobilis</i>		
Functional relationship	Square of correlation coefficient (r^2)	Sample size (n)	Functional relationship	Square of correlation coefficient (r^2)	Sample size (n)
$W = 2.86 \times 10^{-5} (SL)^{2.974}$	0.99	149	$W = 2.30 \times 10^{-5} (SL)^{2.977}$	0.98	118
$SL = 0.929FL + 1.5$	0.99	141	$SL = 0.924FL + 6.0$	0.99	107
$SL = 0.878TL - 17.4$	0.99	140	$SL = 0.855TL - 17.5$	0.98	107
$TL = 1.052FL + 24.3$	0.99	140	$TL = 1.070FL + 35.7$	0.99	107

sagittae were clearly evident in this dissection. Otoliths were removed from each side of the cranial cavity, cleaned, washed, stored in glycerol, then dried at 60°C for 24 hours, and weighed. Right and left otoliths were segregated.

Whole sagittae were embedded in epoxy casting resin and serially sectioned with a low-speed jewelers' saw. Sections 300 μ m thick were attached to scanning electron microscope (SEM) viewing stubs with 5-min epoxy and polished with 0.3 μ m alumina paste. The polished sections were etched for 1–20 minutes with 6% ethylene diamine tetraacetate (EDTA) with pH adjusted to 8 with sodium hydroxide. The otolith sections were washed in water, dried, coated with gold, and viewed in an SEM at various magnifications.

A sample of five right sagittae were sectioned in different planes as described by Radtke (1987) to determine that the optimum plane for enumerating increments was the transverse frontal plane. With this technique, we believe that no increments were lost in the chosen plane. Smallest increments were counted with the SEM on sections in this plane of the left sagittae of all specimens used for age determination. Increments were counted from sequential SEM images of the otolith surface, starting at the origin (center) and moving to the otolith margin at the rostrum (anterior). With this methodology, the area read for ageing was consistent for all individuals analyzed. On the assumption that one increment equals one day's growth (Pannella 1971 and 1974), the data were fitted to the von Bertalanffy growth equation (Fabens 1965).

A marking study using tetracycline was undertaken to validate the assumption of daily periodicity of otolith increments. Live carangids were collected from Kaneohe Bay, Hawaii by commercial fishermen using bait nets. Six juvenile *C. melampygus* (197–338 mm SL) and four juvenile *C. ignobilis* (113–225 mm SL) were acclimated for 1 month in a tank of flowing seawater

5.5 m in diameter by 0.6 m deep, exposed to natural sunlight. After 1 month, the fish were measured and given an intraperitoneal injection of 27.5 mg/kg wet body weight of oxytetracycline. To reduce trauma to the fish, they were not weighed at the time of the injections, but their weights were estimated from length-weight relationships derived from wild-caught fish (Table 1). The fish were fed *ad libitum* on a diet of raw herring until recapture, when they were sacrificed. Five *C. melampygus* were sampled after 55 days, the sixth *C. melampygus* and the four *C. ignobilis* after 137 days. Upon recapture, all fish were weighed and standard, fork, and total lengths were measured.

Sagittae from all experimental fish were removed, cleaned, dried, and mounted in clear casting resin. Sections were made both perpendicular and parallel to the rostral axis of the otolith. The sections counted were in a transverse frontal plane, much the same as those prepared for the SEM and as described by Radtke (1987). Sections were polished with 400-grit Carborundum wet-dry sandpaper, mounted on glass slides, and viewed at 300 \times under a binocular microscope with an ultraviolet light source. The number of increments between the fluorescent mark and the outside edge of the otolith was counted and compared with the number of days that the fish was alive after injection.

Reproduction

Sex ratio, spawning season, and size at first reproduction (SFR) were estimated for both species. Gonads were visually examined and classified as male, female, immature, or unknown. These classifications were based on the size, color, morphology, and texture of the gonadal tissue. Gonads from 70 *C. melampygus* and 10 *C. ignobilis* were removed, wet weighed to the nearest gram, and kept frozen for later, more detailed analysis.

Spawning season was estimated by visual examination of gonads and classification of the mature gonads as either developing or gravid (Kesteven 1960). Months were noted in which there was a significant increase in the number of gravid fish collected relative to the number of mature fish with developing gonads. Spawning season was also estimated by using the gonadosomatic index (GSI):

$$\text{GSI} = (\text{gonad wet weight/whole body wet weight}) \times 100.$$

The GSI for each mature individual was plotted against the date of capture. The spawning season was defined as the period of the year during which a significant proportion of the fish had high GSI values.

To determine the SFR, all fish taken during the spawning season were put into size-classes based on standard length (50 mm SL classes for *C. melampygus* and 100 mm classes for *C. ignobilis*). The number and percent of individuals with gravid gonads in each size-class was determined. As body size increased, at sexual maturity the percent of fish with gravid gonads rose sharply. The lower limit of the size-class in which 50% gravid gonads was reached was taken as the SFR. The SFR was transformed to an age at first reproduction by using the length-age relation from the von Bertalanffy growth equation.

Ovaries from gravid females captured during the peak of the spawning season were used to estimate fecundity, which is defined here as the estimated number of mature ova in the gonad of a spawning female at one time (Everhart and Youngs 1981). Three 2g aliquots from various parts of each ovary were combined and placed in Gilson's fluid (Simpson 1951). This solution hardens and liberates the eggs and breaks down the ovarian tissue. The egg masses were left in this fluid for 2 weeks, then washed with water and the ovarian tissue removed. Subsamples were obtained by using van Dalsen's (1977) technique as modified slightly by Everson (1984). Each ovary sample was brought up to 500 mL with water and mixed with a magnetic stirrer. When a homogeneous mixture was obtained, three 5 mL aliquots were drawn. All ova more than 0.4 mm in diameter in each 5 mL subsample were counted using a binocular dissecting microscope. A fecundity estimate, F , was calculated from the formula

$$F = ((N_1 + N_2 + N_3)/3) \times (500/5) \times (G/S)$$

where N_1, N_2, N_3 = the number of mature ova in each subsample,
 G = total gonad weight,

S = weight of the gonad sample placed in the Gilson's fluid.

Diet

Contents were removed from preserved guts and all prey identified to the lowest taxa possible. The number of individuals and volume of each taxon were noted, as well as the length, weight, and extent of digestion. Many fish in advanced states of digestion were identified by using reference collections of Hawaiian fish scales (Sylvester 1969) and skeletons. Whole prey lengths and volumes were approximated in many cases by comparison of the dimensions of recognizable parts with reference specimens of common Hawaiian reef fishes. The index of relative importance (IRI) was calculated, as defined by Pinkas et al. (1971),

$$\text{IRI} = (\text{numerical \%} + \text{volume \%}) \times \text{frequency \%},$$

where, for each predator species,

numerical % = (number of individuals of one prey category divided by total number of prey individuals found in all the guts) \times 100,

volume % = (volume of one prey category divided by total volume of all prey found in the guts) \times 100,

frequency % = (number of guts containing prey of one category divided by total number of guts that contained any identifiable prey items) \times 100.

A measure of dietary overlap between *C. melampygus* and *C. ignobilis* was provided by the index of overlap, A_{yz} (Pianka 1973). The value of the index varies from 1 when diets are identical with respect to proportional IRI composition to 0 when diets are distinct. We calculated the index using the formula

$$A_{yz} = \left(\sum_i p_{iy} p_{iz} \right) / \left(\sum_i p_{iy}^2 \sum_i p_{iz}^2 \right)^{1/2},$$

where p_{iy} and p_{iz} are the proportions of the total IRI represented by the i th prey category for predator species y and predator species z , respectively.

The effect of individual predator size on the diet of *C. melampygus* was assessed by comparing the occurrence of prey items found in the guts of sexually immature and mature fish.

Energy budget and population consumption

Ingestion rates were measured in captivity. A group of six *C. melampygyus* and a group of four *C. ignobilis* were held in separate sections of a tank of flowing seawater 5.5 m in diameter and 0.6 m deep. Standard, fork, and total lengths were measured for all fish, and then they were allowed to acclimate to the tank for 1 month while being fed raw herring at least once a day. Uneaten food was removed and the weight consumed was calculated for each feeding. Maximum feeding rates were estimated by feeding *ad libitum* at least three times daily during several intensive feeding periods that ranged between 4 and 10 consecutive days each. The fish used in this experiment were not the same individuals used in the tetracycline marking experiment.

Age-specific rations (rates of food consumption) of the two jack species in the wild and annual consumption by their total populations were estimated by using the measured ration in captivity for specimens of one size, together with results obtained by the preceding procedures for growth, reproductive output, and length-weight relationship. Data for the captive specimens were used in the basic energy budget model for fish (Mann 1965 and 1969, Parrish 1975) to obtain the respiratory metabolic rate, Q ,

$$kC = Q + S + G$$

where k = ration assimilation coefficient, representing the fraction of the ingested ration available for utilization in metabolic processes,

C = ration, or rate of food consumption,

Q = rate of respiratory metabolism,

S = rate of production of reproductive material,

G = growth rate.

For the captive fish, ration (C) was measured. Growth (G) was both measured and estimated from the von Bertalanffy model. The value of $k = 0.8$ (Winberg 1956:209, Mann 1967 and 1969) was adopted. Since the fish were prereproductive, the reproductive term (S) was absent. The respiratory metabolic coefficient (α) was estimated from the relationship

$$Q = \alpha W^\gamma,$$

using the calculated Q , the weight (W) of experimental fish, and $\gamma = 0.8$ as a reasonable approximation for

most fishes (Winberg 1956:149, Mann 1965 and 1969, Paloheimo and Dickie 1965 and 1966). This coefficient was then used in the original model to calculate Q for fish of any weight, W . No experimental results were available to estimate α directly for *C. ignobilis*. In view of the other similarities with *C. melampygyus* and the high probability of strong metabolic similarities, the value of α for *C. melampygyus* was also used for *C. ignobilis*. The corresponding growth rate for any weight was derived from the von Bertalanffy model (computing age corresponding to weight from the model directly and evaluating the first derivative of the model at that weight). For fish larger than the SFR, the maximum observed GSI was used with the body weight to estimate the rate of production of reproductive material (S). With all three terms on the right side of the model computed, ration (C) was readily determined for fish of any size.

The size-frequency distribution of the wild population of each species was estimated by pooling length and weight data for all specimens collected in this study with data compiled by the Hawaii Division of Aquatic Resources and the National Marine Fisheries Service: in total, some 253 specimens of *C. melampygyus* and 802 of *C. ignobilis*. Weight-class increments of 200 g were used for *C. melampygyus* and 500 g for *C. ignobilis*. The fraction in each size-class was multiplied by the appropriate computed ration, and the results were summed to estimate an individual ration representative of the population as a whole. This ration of the representative individual, multiplied by the population size for any area, provides an estimate of consumption rate by the entire population.

Population sizes for both species were estimated for one of the the major study areas, French Frigate Shoals (FFS), using two methods. First, sightings of the species made during 56 visual underwater transect censuses in a variety of shallow-water habitats were pooled. For a crude population estimate, for such wide-ranging species, the distribution of these censuses over the various habitat types was taken as representative of all the habitats occupied by these fishes. Each sighting was expressed as the number of fish seen per unit area. Estimates of the total submerged area of FFS of less than about 20 m depth (the apparent prime depth range of these species locally) were based on data from Atkinson and Grigg (1984), Agegian (1985), and J.J. Polovina (NMFS Honolulu Lab., Southwest Fish. Sci. Cent., pers. commun.). The product of this area and the population density estimates from the visual census provided rough estimates of the total populations of both jack species at FFS.

A second population estimate was based on the assumption that the density of the almost unexploited jack populations at FFS must be higher than the

population density indicated by the highest catches on record for other parts of the archipelago where fishing is significant. Data from the highest catches reported (Cobb 1905) were used directly where species were identified in the catch statistics. Where species were reported pooled in the statistics, they were separated by making the assumption that both species of interest occurred as the same percentage of all shallow-water, demersal, large jacks in 1900—the year in which the data of Cobb (1905) were collected—as in 1981–86 (when catch data were available by species). The catches of the two species in 1900, thus reconstructed, were converted to densities using the summed area (Agegian 1985) within these species' habitat depth range around the main, inhabited Hawaiian islands where the 1900 statistics were obtained. These densities provide a lower limit to estimates of the FFS population densities.

The products of jack population estimates with the respective ratios of the representative individual for each species produced estimates for total population consumption (or predation pressure), including all prey consumed. The predation pressure on each prey category was obtained by multiplying these total consumptions by the volume percent (as a decimal fraction) for that prey category.

Results

Age and growth

The relationship between whole wet body weight (W) and standard length (SL) was described for both species by performing a log-linear power function regression on these two variables (Table 1). For both species, weight is approximately a cubic function of standard length, indicating nearly isometric growth. The similarity in parameter estimates (Table 1) is consistent with the morphological similarity of these two species. Linear regressions were performed to permit conversion between standard, fork, and total lengths (Table 1).

Otolith growth increments from 14 *C. melampygyus* and 10 *C. ignobilis* (Table 2) were counted with the aid of SEM (Fig. 2) to estimate age (Appendix A). Assuming that increments were deposited daily, the data were fitted to the von Bertalanffy growth equation (Fig. 3) for fish SL , l_t (in millimeters), as a function of age, t (in years),

Table 2
Parameters of the von Bertalanffy growth model for *Caranx melampygyus* and *Caranx ignobilis* and summary of data used for the regressions.

	<i>Caranx melampygyus</i>	<i>Caranx ignobilis</i>
L_{∞} (asymptotic SL)	897 mm	1838 mm
W_{∞} * (asymptotic whole wet weight)	17,313 g	120,139 g
K	0.233/year	0.111/year
t_0	-0.044 year	0.097 year
r^2 [correlation coefficient] ²	0.99	0.99
n (sample size)	14	10
Range of SL used	122–660 mm	106–1180 mm
Range of estimated ages	0.51–5.90 year	0.75–9.27 year

* Based on standard length-weight relationships from Table 1.

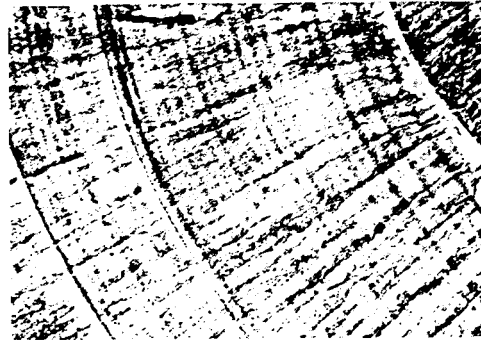
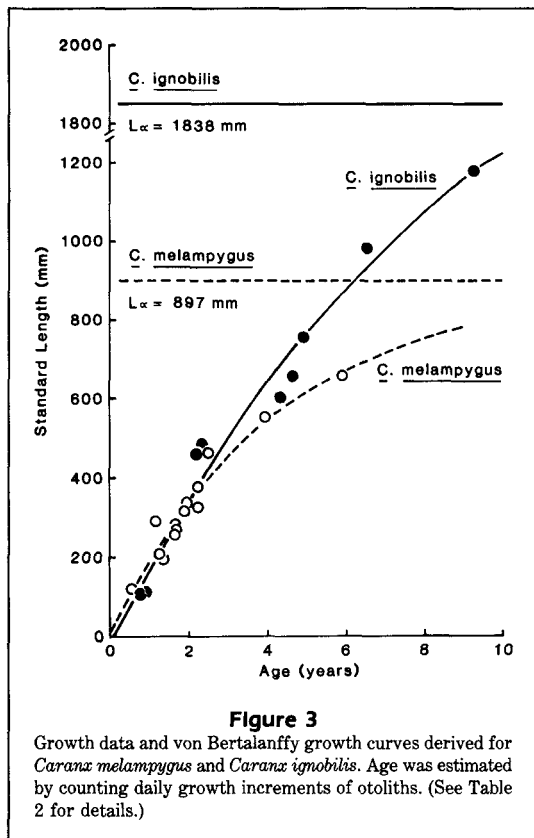


Figure 2
Scanning electron micrograph of a sagitta from *Caranx melampygyus*.

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

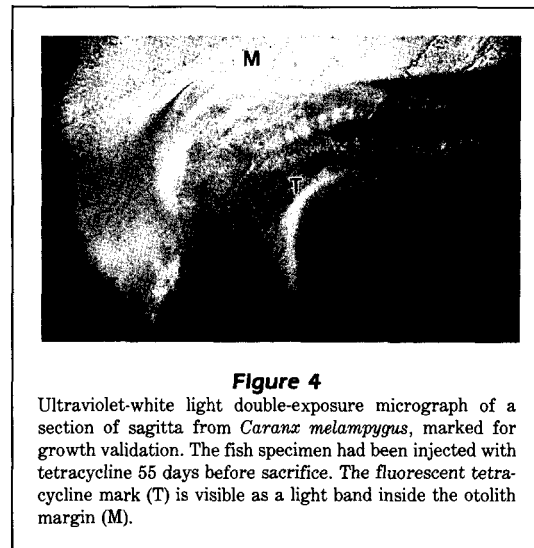
The estimates for the parameters are shown in Table 2.

The accretion rate of otolith growth increments was measured in *C. melampygyus* using six tetracycline-marked animals, held 55 days after injection. A discrete fluorescent line was discernible in all six subjects (Fig. 4), although marginal increments (developed peripheral to the line) were evident in only five. Three thin replicate sections were made from the sagittae of each, and marginal increments were enumerated, although one of the five specimens produced only two satisfactory preparations.



The 14 counts yielded a pooled mean of 51.6 marginal increments (range 47–62, SD 4.31) and a 95% confidence interval of 49.1–54.1 increments. One-way analysis of variance, however, showed that significant differences existed among the five fish in mean increment count (F 4.61, df 4, 9, P 0.027). Furthermore, variation in marginal increment deposition within specimens (s^2 8.80) was comparable to that between specimens (s^2 10.59). When mean counts of the five individual fish were compared, the 95% confidence interval for the population mean was 47.0–56.1 marginal increments. The number of days since injection (55) falls within this interval, and in general the marginal counts are reasonably close to this number.

During the maximum feeding-rate experiment, the six specimens of *C. melampygus* increased from an average standard length of 174 mm (range 166–185 mm) to 239 mm (range 225–252 mm) over a period of 161 days. This represents an average growth rate of 0.40 mm/day. An instantaneous growth rate of 0.45 mm/day (1.02 g/day) was calculated for “wild” fish

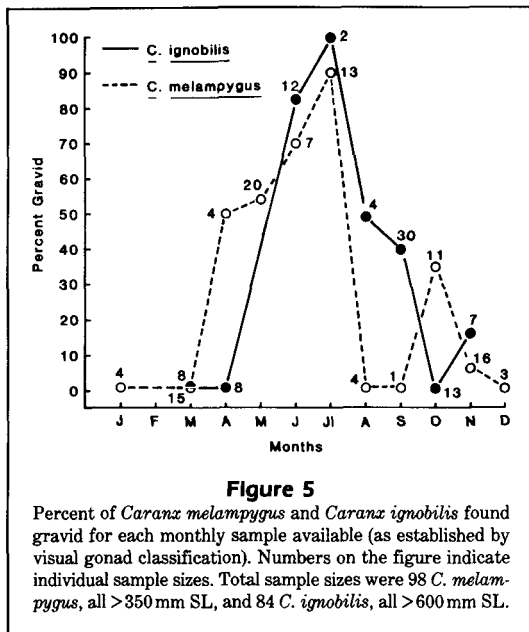


within the same size range by using the von Bertalanffy growth curve.

Reproduction

Sex was determined in 119 specimens of *C. melampygus* and 110 specimens of *C. ignobilis*. In both species, the sex ratio of the samples, M:F, was slightly skewed toward females: 1:1.48 for *C. melampygus* (χ^2 4.45, df 1, P 0.04) and 1:1.39 for *C. ignobilis* (χ^2 2.95, df 1, P 0.08).

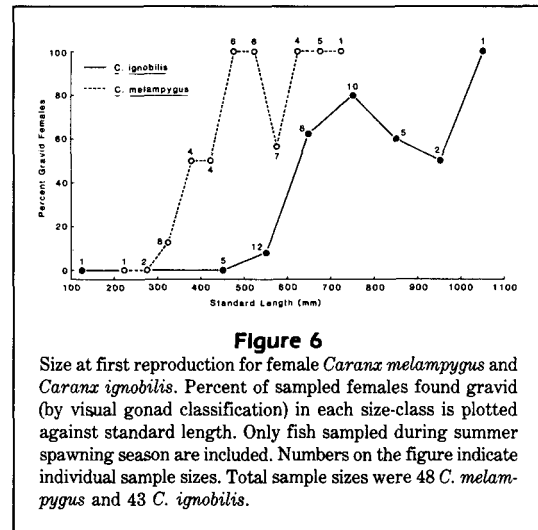
Using morphological criteria, gonads from 152 *C. melampygus* and 124 *C. ignobilis* were visually classified into one of three reproductive stages (immature, developing, or gravid). To test the accuracy of this visual technique, gonadosomatic indices from 62 *C. melampygus* were compared with the reproductive stages assigned visually for each fish. A two-way factorial analysis of variance, with stage (immature, developing, or gravid) and sex (male or female) as classification variables and log-transformed GSI as the dependent variable, showed that stage (F 44.34, df 2, 52, P < 0.0001), but not sex (F 0.95, df 1, 52, P 0.334) affected gonadosomatic index. The interaction term was insignificant (F 1.69, df 2, 52, P 0.194). Mean values of the untransformed GSI's for the three stages of reproductive condition were 0.16%, 0.42%, and 4.54%, respectively. Sidak t -tests (SAS 1985) revealed that all three means were significantly different from one another. Thus, the two methods of establishing reproductive condition show a high degree of concord-



ance. Visual gonad stage was the variable we used most often for determining spawning season and SFR.

Of 98 mature *C. melampygyus* (>350 mm SL) compared by visual gonad classification, gravid individuals were found from April to November (Fig. 5). In May, June, and July more than half the individuals were gravid. Results from April, August, and September are questionable because sample sizes were small. The GSI's were also plotted against the month of capture to determine spawning season for *C. melampygyus*, with consistent results. Again June and July were the peak months, but there were no gonad samples from which GSI's could be calculated in April or May. A peak in reproductive condition was also visually observed in gonads of mature (>600 mm SL) *C. ignobilis* in summer (Fig. 5). No animals of mature age were caught in December, January, or February, but only 1 of the 36 taken from October to April was gravid.

Among 48 female *C. melampygyus* caught during spawning season (April to October), first reproduction (based on visual gonad classification) appeared to occur between the 325 mm and 375 mm length-classes. In this size range, the percent of gravid individuals increased sharply from 12% to 50%, and at least 50% of all larger females were gravid during these months (Fig. 6). For 43 female *C. ignobilis* caught from May to October, there was a sharp increase from 8% to 62% gravid between the 550 mm and 650 mm length-classes (Fig.



6), and all larger length-classes had a higher incidence of gravid females. Thus, it appears that female *C. melampygyus* reach sexual maturity at about 350 mm SL, and female *C. ignobilis* at about 600 mm SL.

Fecundity was estimated for *C. melampygyus* from ovaries of 11 gravid females caught in July. The estimated fecundity ranged from 49,700 mature ova for a fish of 760 g (328 mm SL) to 4,270,000 for one of 6490 g (640 mm SL) (Appendix B). A log-linear power function regression was performed in which fecundity, F, in number of eggs, was compared with total wet body weight, W, in grams, and SL, in millimeters. The regression equations are:

$$F = 0.923 W^{1.694}, \quad (r^2 0.84),$$

$$F = 2.286 \times 10^{-9} (SL)^{5.359}, \quad (r^2 0.80).$$

Diet

Of 118 guts of *C. ignobilis* examined, 68.6% contained identifiable prey items, which were subjected to qualitative and quantitative analysis (Table 3). Of the *C. ignobilis* guts with identifiable prey items, 80.3% contained the remains of fishes. Parrotfish (Scaridae) were the most important identified family of fish in the diet, occurring in 13.6% of the guts that contained prey. Carangids, most notably the opelu *Decapterus macarellus*, were identified in 8.6% of the guts, and wrasses (Labridae) and bigeyes (Priacanthidae) each occurred in 6.2%. Eels (Anguilliformes: Muraenidae, Congridae,

Table 3

Summary of stomach content analysis for *Caranx ignobilis* based on 81 specimens containing prey identifiable to some taxonomic level. At the highest systematic level of analysis, unidentified fish were included in the total number of prey individuals. (In addition, only numerical and frequency percents were calculated for unidentified fish, as shown within parentheses.) Unidentified fish were not included in the totals used to calculate volume percent nor in any analysis at lower systematic levels. Percentages for a few identifiable species appear within brackets []; no IRI was calculated at this level. All values not underlined or enclosed were used together as a single level for analysis.

Prey item	Numerical %	Volume %	Frequency %	% of summed IRI
Fish	<u>69.1</u>	<u>73.1</u>	<u>80.3</u>	<u>90.2</u>
Scaridae	13.4	13.4	13.6	23.0
Carangidae	5.2	4.5	8.6	5.3
<i>Decapterus macarellus</i>	[2.2]	[2.3]	[3.7]	
Labridae	3.7	15.6	6.2	7.5
Priacanthidae	3.7	6.8	6.2	4.1
Muraenidae	6.0	4.9	6.2	4.3
Congridae	6.0	5.1	6.2	4.3
Unidentified eels	4.5	4.7	4.9	2.9
Mullidae	2.2	8.6	2.5	1.7
<i>Parupeneus cyclostomus</i>	[0.8]	[8.2]	[1.2]	
Pomacentridae	3.0	0.9	3.7	0.9
Ostraciidae	3.0	1.7	4.9	1.4
Monacanthidae	5.2	0.9	2.5	1.0
Acanthuridae	2.2	2.6	1.2	0.4
Holocentridae	0.8	2.9	1.2	0.3
Ophiidiidae (<i>Brotula multibarbata</i>)	0.8	0.5	1.2	0.1
Unidentified fish	(24.2)	—	(44.4)	—
Crustaceans	<u>12.9</u>	<u>11.0</u>	<u>17.3</u>	<u>3.3</u>
Palinurid lobsters	3.0	10.5	3.7	3.2
Unidentified crustaceans (incl. 1 portunid crab)	14.2	0.6	13.6	12.6
Cephalopods	<u>17.4</u>	<u>15.9</u>	<u>24.7</u>	<u>6.5</u>
Squid	10.5	2.8	9.9	8.3
Octopus	11.2	12.5	12.4	18.4
Unidentified cephalopods	1.5	0.6	2.5	0.3
Gastropods (<i>Bittium parcum</i>)	<u>0.6</u>	—	<u>1.2</u>	<0.05

and unidentified) were found in 14.8% of the guts, cephalopods in 24.7%, and crustaceans (including lobsters, crabs, and shrimp) in 17.3%.

Of 147 guts of *C. melampygus* examined, 85.0% contained identifiable prey items (Table 4), and 96.0% of these contained the remains of fish. The wrasses (Labridae), goatfish (Mullidae), filefish (Monacanthidae), damselfish (Pomacentridae), parrotfish (Scaridae), and bigeyes (Priacanthidae) were the most important families of fishes in the diet of *C. melampygus*. Eels and cephalopods made negligible contributions. Crustaceans of many diverse groups were found in 19.2% of the guts with identifiable prey items, but they accounted for less than 1% of total prey volume. Palinurid lobsters were absent.

Comparison of the diets of the two length categories of *C. melampygus* showed only one significant difference. Crustaceans were found in 17 of 42 guts from fish of the smaller length category (<350 mm SL), but in only 7 of 107 guts from the larger length category (>350 mm SL). This indicates a statistically significant (χ^2 21.5, df 1, $P < 0.001$) change in the diet of *C. melampygus* with size.

The Pianka (1973) index of overlap, used to measure the degree of similarity in the diets of the two carangids, was calculated from the proportional IRI representation (% of summed IRI) for each prey group found in the two species. The value of A_{yz} was 0.42.

Maximum feeding rates were determined for six captive juvenile *C. melampygus*. These fish started at a mean weight of 124.5 g, and during the course of the

Table 4

Summary of stomach content analysis for *Caranx melampygus* based on 125 specimens containing prey identifiable to some taxonomic level. At the highest systematic level of analysis, unidentified fish were included in the total number of prey individuals. (In addition, only numerical and frequency percents were calculated for unidentified fish, as shown within parentheses.) Unidentified fish were not included in the totals used to calculate volume percent. No unidentified animals from any major taxonomic group were used in any analysis at lower systematic levels. Percentages for some identifiable genera and species appear within brackets []; no IRI was calculated at this level. All values not underlined or enclosed (except Caridea) were used together as a single level for analysis.

	Numerical %	Volume %	Frequency %	% of summed IRI
Fish	<u>85.4</u>	<u>98.7</u>	<u>96.0</u>	<u>98.66</u>
Labridae	18.1	13.0	23.2	36.4
<i>Bodianus bilunulatus</i>	[0.5]	[1.0]	[0.8]	
<i>Thalassoma</i> spp.	[3.8]	[2.8]	[4.8]	
<i>Xyrichtys</i> spp.	[1.9]	[1.7]	[1.6]	
Mullidae	7.1	17.7	12.0	15.0
<i>Parupeneus multifasciatus</i>	[1.9]	[8.0]	[3.2]	
<i>P. cyclostomus</i>	[0.5]	[3.5]	[0.8]	
Monacanthidae (<i>Pervagor</i> spp.)	13.3	7.4	12.0	12.5
Scaridae	6.2	19.0	8.0	10.2
Pomacentridae	7.1	9.4	10.4	8.7
<i>Stegastes fasciolatus</i>	[1.0]	[0.7]	[1.6]	
<i>Chromis</i> spp.	[2.4]	[5.0]	[2.4]	
Priacanthidae	5.2	16.0	6.4	6.8
Acanthuridae	2.9	6.7	4.0	1.9
<i>Acanthurus nigroris</i>	[0.5]	[4.9]	[0.8]	
<i>Naso unicornis</i>	[1.0]	[0.4]	[0.8]	
Synodontidae	2.9	2.0	4.8	1.2
Holocentridae	2.9	1.2	3.2	0.7
<i>Flammeo sammara</i>	[0.5]	[0.5]	[0.8]	
Belontiidae	1.0	3.7	1.6	0.4
Kyphosidae	1.4	0.4	2.4	0.2
Pomacanthidae (<i>Centropyge potteri</i>)	1.0	0.8	1.6	0.15
Blenniidae	3.3	0.1	0.8	0.14
Ophichthidae	1.0	0.2	1.6	0.1
Muraenidae	0.5	0.5	0.8	0.04
Unidentified eels	0.5	0.2	0.8	0.03
Gobiidae	1.0	—	0.8	>0.04
Tetraodontidae	1.0	0.1	0.8	0.04
Scorpaenidae	0.5	0.2	0.8	0.03
Bothidae	0.5	—	0.8	>0.02
Unidentified flatfish	0.5	0.1	0.8	0.02
Unidentified fish	(34.8)	—	(44.0)	—
Crustaceans	<u>11.2</u>	<u>0.9</u>	<u>19.2</u>	<u>1.3</u>
Shrimp	9.0	0.4	9.6	4.6
Caridea (incl. <i>Alpheus</i> , <i>Saron</i> and <i>Rhynchocinetes</i> spp.)	2.9	0.14	4.8	
Crabs (incl. Portunidae and other Brachyura)	1.9	0.14	3.2	0.3
Stomatopods	2.4	0.14	3.2	0.4
<i>Pseudosquilla ciliata</i>	[1.4]	[0.06]	[1.6]	
<i>Pseudosquilla oculata</i>	[1.0]	[0.08]	[1.6]	
Isopods	0.5	—	0.8	>0.02
Cephalopods	<u>0.6</u>	<u>0.4</u>	<u>1.6</u>	<u>0.01</u>
Octopus	0.5	0.4	0.8	0.04
Gastropods (incl. <i>Bittium impendens</i> , <i>Vitricithna marmorata</i> , and <i>Modulus tectum</i>)	<u>2.8</u>	—	<u>2.4</u>	<u>>0.04</u>

161-day experiment, grew to a mean weight of 302.5 g. All fish survived and appeared healthy throughout the course of the feeding experiment. Four intensive feeding periods of 6, 6, 4, and 5 days duration resulted in an average daily food consumption rate of 0.084 g food per gram of fish. Three *C. ignobilis* specimens of about 500 g each were used in a similar experiment. Three intensive feeding periods with these fish resulted in an average daily food consumption rate of about 0.05 g food per gram of fish. However, this estimate is probably low because these experimental fish seemed to be in poor health during confinement.

Energy budget and population consumption

Based on the captive feeding experiments with *C. melampygus*, an estimate of $\alpha = 0.19 \text{g}^{0.2}/\text{day}$ (at about 24°C) was derived and used for all energy budget calculations for both species. Estimates of all major components of the energy budget were calculated for the 38 weight-classes of *C. melampygus* (ranging from 200 to 10,000 g) and the 71 weight-classes of *C. ignobilis* (ranging from 500 to 41,000 g) represented in the size-frequency database. Table 5 contains selected

Table 5

Computed major components of an estimated energy budget for *Caranx melampygus* and *Caranx ignobilis* in the Northwestern Hawaiian Islands. Values are selected for various sizes within the full range of the size distribution (26 additional size-classes for *C. melampygus* and 55 for *C. ignobilis* are not shown). All energy rates are expressed in equivalent grams of fish tissue.

1	2	3	4	5	6	7	8	9
Weight class (g)	SL (mm)	Age (yr)	Growth rate, G (g/day)	Respiratory metabolic rate, Q (g/day)	Reproductive production rate, S (g/day)	Individual ration, C (g/day)	Fraction of population	Proportional ration of weight class* (g/year)
<i>Caranx melampygus</i>								
200	200	1.05	1.29	13.17	0	18.08	0.057	375
1000	344	2.06	3.01	47.72	0	63.42	0.053	1223
1200	366	2.23	3.26	55.22	0.33	73.52	0.041	1091
2000	434	2.83	4.01	83.09	0.55	109.57	0.024	975
3000	498	3.47	4.56	114.93	0.82	150.39	0.016	892
4000	548	4.05	4.85	144.68	1.09	188.28	0.041	2794
5000	591	4.61	4.97	172.95	1.37	224.12	0.0081	665
6000	628	5.16	4.97	200.11	1.64	258.40	0.0041	383
7000	662	5.71	4.86	226.38	1.92	291.45	0.0041	432
8200	698	6.40	4.63	256.92	2.25	329.75	0.012	1468
9000	720	6.89	4.43	276.79	2.46	354.60	0.0041	526
10000	746	7.53	4.12	301.13	2.74	384.98	0.0041	571
Total (including weight classes not shown) = ration of individual representative of population =								47,815
<i>Caranx ignobilis</i>								
1000	367	2.10	3.82	47.72	0	64.44	0.019	447
2000	458	2.68	5.75	83.09	0	111.06	0.037	1490
3000	521	3.10	7.24	114.93	0	152.72	0.058	3250
4000	571	3.45	8.47	144.68	0	191.44	0.018	1240
5000	613	3.75	9.53	172.95	1.37	229.82	0.014	1169
6000	650	4.03	10.47	200.11	1.64	265.29	0.011	1104
7000	682	4.28	11.31	226.38	1.92	299.51	0.024	2632
8000	712	4.51	12.07	251.90	2.19	332.70	0.032	3848
9000	739	4.73	12.76	276.79	2.46	365.02	0.030	4053
10000	764	4.94	13.40	301.13	2.74	396.59	0.027	3853
15000	870	5.87	15.93	416.51	4.11	545.69	0.021	4291
20000	953	6.69	17.71	524.30	5.48	684.35	0.011	2849
25000	1024	7.43	18.98	626.77	6.85	815.74	0.011	3396
30000	1085	8.14	19.87	725.19	8.22	941.60	0.0025	871
35000	1140	8.81	20.47	820.37	9.59	1063.03	0.0013	492
41000	1198	9.61	20.87	931.07	11.23	1203.97	0.0013	557
Total (including weight classes not shown) = ration of individual representative of population =								150,686
* Product of Columns 7 and 8, adjusted to annual basis.								

Table 6

Annual consumption (ration) of entire estimated populations of *Caranx melampygus* and *C. ignobilis* at French Frigate Shoals (FFS) and predation on major prey categories.

Estimated total population at FFS	Ration of individual representative of population* (kg/yr)	Breakdown by prey category**			Total consumption by population (t/yr)
		Prey category	Volume % (from Tables 3 and 4)	Consumption of prey category (t/yr)	
<i>Caranx melampygus</i> 230,000	47.82				11,000
		Fish	98.7	10,854	
		Crustaceans	0.9	99	
		Cephalopods	0.4	44	
<i>Caranx ignobilis</i> 130,000	150.69				19,600
		Fish	73.1	14,320	
		Crustaceans	11.0	2,155	
		Cephalopods	15.9	3,115	
Both species combined 360,000					30,600
		Fish		25,174	
		Crustaceans		2,254	
		Cephalopods		3,159	

* From Table 5
** Volume percent for gastropod prey was not measured; amounts were negligible compared with the other three categories.

values covering the full range of sizes, with energy rate terms expressed in fish tissue gram equivalents. Age and standard length were computed from the von Bertalanffy model, and energy components were calculated as described in the Methods section. Entries within a row in Columns 1-7 are all raw, unweighted values for an individual of a particular weight-class. Thus, Column 7 contains the estimated ration of a weight-class. In Column 9, this value is weighted by the fraction (Column 8) which that weight-class contributes to the total population. Thus, for *C. melampygus* the sum of all 38 "proportional ration" values such as the examples in Column 9 constitutes the ration of a hypothetical individual representative of the entire population, i.e., 47.82 kg/year of prey. Similarly, for *C. ignobilis* the sum of all 71 "proportional ration" values provides the annual ration of such a representative individual, i.e., 150.69 kg/year.

The best estimates of species populations for FFS that our census data permit are about 230,000 *C. melampygus* and 130,000 *C. ignobilis* (Table 6). Combined with the estimate of annual ration of the representative individual of each species, these values produce estimates of total annual consumption of about 11,000 metric tons (t)/year by *C. melampygus* (about 22 t/year per km² of prime habitat), and about 19,600 t/year by *C. ignobilis* (about 39.2 t/year per km²). Table 6 shows the annual amount eaten of each major prey category, based on results in Tables 3 and 4.

Discussion

Age and growth

Length-weight data for these species have been previously reported. Seki (1986a) reported a power function regression based on 124 *C. ignobilis* specimens caught in the Northwestern Hawaiian Islands, ranging in FL from 207 to 1330 mm. Applying the FL-SL relationship of Table 1 to his result produced the expression,

$$W = 3.44 \times 10^{-5} (SL - 6.0)^{2.913}$$

Over the range of sizes collected in both studies, predictions of W from this relationship and that of Table 1 (based on 118 NWHI specimens) agree within about 7% at worst, and for a large majority of the specimens they agree within 2-5%. Their predictions are most divergent (over 8.5%) as L_{∞} is approached.

Seki (1986b) also reported an expression for FL versus weight based on only 24 specimens of *C. melampygus*, 93-710 mm FL. Applying the FL-SL relation of Table 1 to this result produced the expression,

$$W = 3.0053 \times 10^{-5} (SL - 1.5)^{2.941}$$

The agreement between predictions of this expression and those of Table 1 (based on 149 NWHI specimens)

is much poorer. Over the range collected in both studies, the relationship from Seki predicts W values 14.5–17% lower than our estimates; near L_{∞} , the difference is almost 18%. The larger difference compared with that for *C. ignobilis* may be due to the small sample size for one *C. melampygus* regression.

Williams (1965) also fitted a length-weight expression based on 75 *C. melampygus* specimens from east Africa. Converted to common units (SL in millimeters, W in grams), his relationship is

$$W = 1.4173 \times 10^{-5} SL^{3.066}.$$

Over the range of sizes occurring in both studies, this expression predicts weights 10–17% lower than ours and closer to those of Seki (1986b). Near L_{∞} it is within 8% of our estimates, and for our smallest specimens its estimates are about 27% lower. The large differences between predictions of Williams' model and ours may reflect a difference in body proportions or in large-scale "condition factor" between this species in the NWHI and east Africa. Or the result may simply be an artifact of sampling. Williams (1965) commented that in his sample, males were probably larger on average and more variable in weight than females. The ratio of males to females was much larger in his sample than in ours.

Uchiyama et al. (1984) fitted length-weight data for *Seriola dumerili* and *Pseudocaranx dentex* from the NWHI to power functions. For all four of these large, closely related species, the data fit a power function model well and the parameter values are similar.

Uchiyama and Tagami (1984) reported a preliminary von Bertalanffy growth equation for *Seriola dumerili* based on counts of daily otolith increments up to about 2 years of age (well below the inflection point of the von Bertalanffy weight curve). These results show a faster initial increase in size early in life in *S. dumerili* than in either *Caranx* species. The K values for both *Caranx* species fall well within the range of common values for many large fishes.

For both *Caranx* species, our counts of otolith growth increments made with an SEM gave estimates of age that could be fitted well to the von Bertalanffy age-length model. The daily nature of increment deposition was partly validated for *C. melampygus* by the tetracycline marking experiment. Caution must be used in extrapolating the one-to-one correspondence to fish larger than those used in the validation experiment. Recent work has shown that growth increments in the otoliths of older fish may be deposited at intervals greater than one day (Pannella 1971, Wild and Foreman 1980, Ralston and Miyamoto 1983). If so, age would be underestimated and growth rate would be overestimated.

The close agreement between the growth rate measured for captive *C. melampygus* fed *ad libitum* and the natural rate estimated from the von Bertalanffy growth curve may be fortuitous. There are a number of aspects of the captive situation that might be expected to create disparity between these results. Even though the fish were fed at least daily to satiation, the confined tank environment and human disturbance may have affected their behavior or health and slowed their growth. These fish are wide-ranging active predators, and the laboratory tank provides an unnatural environment for feeding and metabolism. A limitation of the captive feeding study was that only young, fast-growing, sexually immature specimens were available. It is not clear that the growth pattern or metabolic parameters estimated from these experiments are fully applicable over the life span of the fish. Relative growth and ingestion rates are high at younger ages, and otolith ring deposition is more likely to be daily. It would be useful, but technically difficult, to perform these experiments with large adults.

The von Bertalanffy relationship obtained for *C. ignobilis* predicts a value of $SL_{\infty} = 1838$ mm, and (by use of our length-weight regression) $W_{\infty} = 120.14$ kg. By comparison, the largest *C. ignobilis* specimens reported caught in Hawaii (with length estimates based on our regression) are 86.71 kg (1648 mm), 81.49 kg (1613 mm), and two specimens of 68.10 kg reported as measuring about 1524 mm and 1626 mm FL, respectively (about 1417 mm and 1512 mm SL, on the basis of our regressions) (Chuck Johnston, Editor, Hawaii Fishing News, Honolulu, pers. commun.). All these reports are from the main, inhabited Hawaiian islands and reflect recent conditions, following several decades of heavy fishing pressure on the species. Larger specimens may occur in the relatively unfished NWHI, where stocks are in near virgin condition and sampling has been sparse.

For *C. melampygus*, the predicted $SL_{\infty} = 897$ mm and $W_{\infty} = 17.31$ kg. Catch records from the fishery are not well documented. However, there are reliable reports of a *C. melampygus* caught on Oahu that weighed just over 19 kg and one caught on Lanai that weighed about 13.6 kg (Peter Dunn-Rankin, Univ. Hawaii, Honolulu, pers. commun.). The largest specimen for which we found documented record was one of our own: $SL = 760$ mm, $W = 10.00$ kg. From sizable collections by the Hawaii Division of Aquatic Resources and by the National Marine Fisheries Service, the largest specimens reported (with length estimates based on our regression) were 8.20 kg (698 mm) and 6.40 kg (642 mm), respectively. For both these jack species, the values of L_{∞} and W_{∞} derived from our size-age data are close to or somewhat greater than reported values.

Reproduction

The sex ratios for both species were skewed slightly toward females. The deviation from unity was not highly significant, and the difference may be merely a sampling artifact. Off the coast of east Africa, Williams (1965) reported overall sex ratios significantly biased toward males for both *C. melampygyus* (M:F 1.68:1, *N* 78) and *C. ignobilis* (M:F 2.01:1, *N* 323). Males also predominated in an earlier series of collections there (Williams 1956). Off Zanzibar Island (east Africa) during the summer spawning season, he reported encountering shoals of "ripe and running" *C. ignobilis* composed almost entirely of males. He also sampled shoals where only females were caught and suggested that the sexes segregate in the prespawning period. Our catch data indicate that disproportionate numbers of gravid females were taken from large schools during summer. This behavior suggests that spawning by *C. ignobilis* is not a random process, but is coordinated in space and time. Whether or not large numbers of males and females aggregate to spawn is unknown, but seems likely.

Based on the data in Figure 5, it appears that both species spawn primarily in summer. However, the paucity of quantitative gonad data (e.g., GSI's) makes it difficult to present a complete picture of the annual reproductive cycle for either species. A review of the spawning patterns of Hawaiian fishes by Walsh (1987) suggested that most Hawaiian reef fishes spawn primarily during summer.

Based on the condition of gonads examined in the field, Williams (1956, 1965) concluded that spawning of *C. ignobilis* off east Africa (1°S–10°S lat.) occurs from July to March, peaking in November to March (the austral summer). He reached no conclusions about seasonality of spawning in *C. melampygyus*, but he documented ripe gonads throughout the austral spring and summer (September to March).

Based on visual underwater observations of spawning behavior between Cebu and Bohol in the Philippines (10°N lat.), von Westernhagen (1974) concluded that the main spawning season of *C. ignobilis* was December and January, with a lesser peak in June. "Limited but noticeable" behavioral spawning activity was reported throughout the year for a group of carangid species that included *C. ignobilis*, but it is not clear in what months *C. ignobilis* specifically was observed spawning. This seasonal trend based on observed behavior at low northern latitudes differs from the trend indicated at higher latitudes by our examination of gonads. Von Westernhagen also found that gonads of dissected specimens were always only partly ripe, suggesting serial spawning over a prolonged seasonal period.

In our study, female *C. melampygyus* became sexually mature at about 350 mm SL, which is about 39% of L_{∞} . The calculated age of a 350 mm *C. melampygyus* is close to 2 years. Female *C. ignobilis* mature at about 600 mm SL, about 33% of L_{∞} , at an estimated age of about 3½ years.

Williams (1965) estimated that the onset of sexual maturity in *C. melampygyus* in east Africa occurred at about 30–40 cm (apparently SL). The basis of this estimate is not clear, but it agrees well with our results for the NWHI. In southern Africa, van der Elst (1981) indicated that maturity in this species occurred at 40 cm FL (source of information not stated). From plots of standard length and weight frequency of more than 330 *C. ignobilis*, Williams (1965) surmised that maturity was reached between 54 and 61 cm (apparently SL), and between about 3 and 5 kg. Both this length and weight estimate are consistent with our results. Van der Elst (1981) stated that "sexual maturity coincides with a fork length of 60 cm and an age of approximately 3 years."

Fecundity in our study was estimated only for *C. melampygyus*. The equation relating fecundity to weight suggests a strongly nonlinear increase in fecundity with increasing body weight. *Carama melampygyus* appears to be a highly fecund species with a profligate reproductive pattern common to many pelagic marine fishes.

Diet

The diet of *C. ignobilis* contained a considerable diversity of fish types and invertebrates (Table 3). The perciform and tetraodontiform fishes were very important, but eels, crustaceans, and cephalopods were also significant in numbers and volume. The large number of reef fishes suggests that *C. ignobilis* spends much of its time foraging over shallow-water reef habitats, but the presence of squid and the schooling carangid *Decapterus macarellus* indicates exploitation of more open-water habitats as well. Diet results of Williams (1965) from east Africa also indicate feeding at all levels in the water column and probably over a variety of substrates. The presence in the diet of nocturnally active species such as eels, lobsters, and octopus suggests at least partly nocturnal feeding habits. Okamoto and Kawamoto (1980) concluded that *C. ignobilis* "appeared to be primarily a night feeder" in the NWHI. Van der Elst (1981) characterized this species in southern Africa as "more active during the day, especially at dusk and dawn."

C. melampygyus appears to be more dependent on diurnally active, shallow-water reef fishes (Table 4). The labrids, mullids, pomacentrids, scarids, and monacanthids, which made up over 80% of its diet (percent

of summed IRI), are among the more common reef fishes in the NWHI (Parrish et al. 1985). No deep-water or pelagic species were represented in the diet, which suggests that *C. melampygus* associates closely with shallow-water reefs. The relatively low incidence of nocturnally active prey items suggests that this species is primarily a diurnal or crepuscular feeder. Based on their studies in the NWHI, Okamoto and Kawamoto (1980) also believed that it feeds mostly diurnally. On Hawaii Island, Hobson (1974) concluded that it probably feeds most often during early morning and late afternoon. In southern Africa, van der Elst (1981) stated that "while most active during early morning and late afternoon, it also hunts at night."

Little information is available on the diets of these two *Caranx* species in Hawaii or elsewhere. Okamoto and Kawamoto (1980) made the following brief, summary report, based on examination of the guts of 104 *C. ignobilis* and 27 *C. melampygus* from the NWHI: "Stomach contents of (*C. ignobilis*) . . . included spiny and slipper lobsters, shrimps, portunid crabs, octopuses (*Octopus cyanea* and *Octopus ornatus*), eels, cornetfish, squirrelfishes (family Holocentridae), and surgeonfishes. The omilu (*C. melampygus*) on the other hand, was primarily a diurnal fish feeder with piha (*Spratelloides delicatulus*) comprising the bulk of its diet." Small, incidental collections of *C. melampygus* guts at South Kona (Hobson 1974, five specimens with prey) and South Kohala (Parrish, unpubl. data, three specimens with prey) on the west coast of Hawaii Island contained fishes, shrimp, stomatopods, and mysids.

Only fishes (including the serranid *Anthias* and a carangid) were found in the guts of four *C. melampygus* examined by Randall (1955) from the Gilbert Islands and two specimens examined by Hiatt and Strasburg (1960) from the Marshall Islands. Randall (1980) also reported on fish prey in the guts of 44 specimens of *C. melampygus* from the Marshall Islands, Hawaiian Islands, Line Islands, Marcus Island, Solomon Islands, and the Red Sea. Prey groups included eels, Caracanthidae, Serranidae (*Anthias* spp.), Priacanthidae, Carangidae, Caesionidae, Mullidae, Pomacentridae, Cirrhitidae, Labridae, Gobiidae, Acanthuridae, and squid. He also found food in the guts of seven specimens of *C. ignobilis* from the Marshall Islands, Line Islands, Hawaiian Islands, Pitcairn Group, and the Marquesas (Randall 1980). Prey included Scorpaenidae, Scaridae, and Acanthuridae.

Off east Africa, Williams (1956, 1965) reported only the percent of *C. ignobilis* specimens that contained each prey category (frequency percent) from 170 specimens that contained identifiable prey. His results included eels (0–2%), Synodontidae (0–1%), Plotosidae (0–1%), Belonidae (*Tylosurus* sp.) (1–2%), *Atherina* sp. (1–2%), Carangidae (0–2.5%), Leiognathidae (0–1%),

Sphyraenidae (0–1%), Scaridae (2.5–6%), *Siganus* sp. (1–2%), Monacanthidae (0–1%), Tetraodontidae (0–1%), shrimp (0–2%), stomatopods (including *Squilla* sp.) (6–10%), and cephalopods (including squid) (2.5–4%). Including many unidentified prey groups, 79–84% of *C. ignobilis* contained fish, and at least 12% contained crustaceans. Similar analysis of 89 *C. melampygus* specimens containing prey (Williams 1956, 1965) indicated the following frequency percent for prey categories: Holocentridae (0–3%), Scorpaenidae (0–2%), *Caesio* spp. (2–13%), Lutjanidae (including *Lutjanus* sp.) (2–3%), Mullidae (0–2%), Labridae (0–2%), Scaridae (5–7%), and stomatopods (0–2%). Altogether, 97–100% of these specimens contained fish (many unidentified).

Based on all available results, the diets of both *Caranx* species appear to be strongly dominated by fishes; *C. melampygus* was considerably more limited to fishes in our study. Both jacks ate a wide variety of species and ecological types of fishes. In both, the labrids, scarids, mullids, and priacanthids were among the most important prey, and pomacentrids and monacanthids were at least moderately abundant. All these families except monacanthids were reported in the earlier studies of the diet of *C. melampygus*.

Scarids occurred more widely and abundantly in the diets than any other fish family. This result may be biased by the ease of identifying scarid dental plates among digested fish remains. No scarids could be identified to lower taxa. Scarids may be somewhat more important to *C. ignobilis*. Labrids were important by all measures in our study (especially for *C. melampygus*) but less prominent in the reports of others. Eels were rather widely reported in the diets of both species. At least two eel families were represented in each species in our studies (a total of three eel families). Their considerable abundance in *C. ignobilis* suggests frequent, active feeding close around reef structures or other substrates that provide good cover. Seven *C. ignobilis* individuals in our study contained more than one eel each; one contained both a muraenid and a congrid eel.

Monacanthids probably are taken commonly by these jacks when monacanthid densities are normal. However, the heavy consumption indicated by our data is probably a result of an unusual population explosion of the filefish *Pervagor pilosoma* that occurred during the course of the study. The monacanthids in *C. ignobilis* were not further identifiable, but 24 of 28 monacanthid individuals in *C. melampygus* were identified as *P. pilosoma* and the other four as the genus *Pervagor*. Fourteen of the 15 incidents of predation (involving 27 of 28 prey individuals) occurred between late June 1982 and late March 1983 (when field work ended). These incidents began with the first sizable collections of jacks after the surge in the filefish

population was initially observed in visual censuses. Census counts of *P. spilosoma* remained high to the end of the study. This temporal pattern of predation and prey abundance appears to offer an example of opportunistic feeding on sporadically abundant prey. The much higher incidence of *P. spilosoma* in *C. melampygyus* appears to reflect the specific locations and timing of sampling relative to the filefish population surge.

Potts (1980) analyzed the predatory behavior of *C. melampygyus* at Aldabra Atoll (Indian Ocean). His observations indicated that this species sometimes forages in small groups, but that it is most often found singly or in pairs. Major (1978), who conducted an investigation of the predator-prey interactions of a captive group of juvenile *C. ignobilis* in Kaneohe Bay, Hawaii, showed that there are advantages to group hunting of schooling fish. *Caranx* species are known to form interspecific feeding associations with large labrids and other predatory species such as sharks, barracuda, sting rays, and eagle rays (Potts 1980). *C. melampygyus* sometimes follow species that disturb the substrate, causing small fishes and crustaceans to be flushed out and exposed (Hobson 1974; pers. observ.). Some of the small crustaceans and gastropods found in the guts of *C. melampygyus* may have been taken in this way.

Potts described *C. melampygyus* as a diurnally active predator that increased hunting activity at dawn and dusk, when small midwater planktivorous fishes are moving to or from the shelter of the reef. These observations are generally consistent with our analysis of the feeding habits of this species in Hawaii. However, nocturnal fishes and crustaceans occurred in some of our samples, and planktivorous fishes did not dominate the diet.

The total incidence of benthic invertebrate prey in our specimens was considerable: 43% (frequency) for *C. ignobilis* and 22% for *C. melampygyus* (including all cephalopods). *Caranx ignobilis* is one of the few fishes known to consume large, fully adult lobsters (Gooding 1985). Lobsters occurred in about 4% of the specimens, composing over 10% of the diet by volume in our study (Table 3). Okamoto and Kawamoto (1980) also reported this interaction, and Gooding (1985) observed such predation in the field. Lobsters are large, long-lived invertebrates that appear to be situated high in the benthic trophic system. This is one of several links that suggests that these large, abundant *Caranx* species, with their high rates of food consumption, are particularly important apex predators (Table 6).

Large crustaceans occur rather widely in the diets reported for *C. ignobilis* and *C. melampygyus* (Williams 1956 and 1965, Hobson 1974, Okamoto and Kawamoto 1980, Parrish unpubl. data). In our study, the frequency

of occurrence and numerical percent of crustaceans in the diet were sizable, but the low volumes for groups other than lobsters suggest that their dietary role is quantitatively minor (Tables 3 and 4). Many crustaceans could not be identified to low taxonomic level, but the major groups found in these *Caranx* species appear to be among those most common in the diets of a wide range of other carnivorous, demersal fish species in the NWHI, e.g., shrimp, crabs, and stomatopods (Parrish et al. 1985). All these major groups have also been reported in other diet studies of these jacks.

The higher incidence of crustaceans in smaller individuals of *C. melampygyus* in our study was not obviously related to characteristics of the habitat or social structure. Fish of many sizes (larger and smaller than 350 mm SL) overlapped broadly among habitats, both in our collections of specimens and in many field observations. Benthic sampling in the NWHI suggested that large crustaceans were widely available in most of these types of habitats. No direct evidence is available to confirm the basis of this size difference in diet of *C. melampygyus*; it may reflect changing food preference with age and the ability of larger individuals to capture larger fish as prey. (All the crustaceans found in *C. melampygyus* specimens of all sizes could probably have been captured easily by even the smallest of the specimens.)

In our study, *C. ignobilis* consumed both the benthic/demersal octopus and the more pelagic squid in quantities (Table 3) that suggest that this trophic interaction is ecologically important to predator and prey populations. Only two specimens of *C. melampygyus* contained cephalopods. There have been occasional previous reports of cephalopods in these jack species (Williams 1956, Okamoto and Kawamoto 1980, Randall 1980).

There was a relatively low overlap of specific diet items between *C. ignobilis* and *C. melampygyus* (index $A_{yz} = 0.42$), indicating some separation of feeding niches of these two sympatric congeners. Morphologically, they are very similar, but a mature *C. ignobilis* is considerably larger than a mature *C. melampygyus*. This difference in body size probably accounts for the occurrence or higher incidence of larger prey individuals and some larger species (e.g., lobsters, octopus) in *C. ignobilis*.

Energy budget and population consumption

Preliminary energy budget calculations and estimates of food consumption were made for jack populations primarily for their ecological interest. Clearly, the estimates of energy budget terms are crude and may be of limited value from a physiological perspective.

Measured ration of fish feeding *ad libitum* while swimming actively in a relatively undisturbed captive environment was used as an estimate of the natural, long-term, average ration of fish in the wild. If feeding were not reduced by trauma or behavioral effects of captivity, such feeding should provide an estimate of maximum natural ration, given superabundant, easily accessible food. Since the measured growth rate in captivity closely approximated the growth rate estimated for wild fish by the von Bertalanffy model, it may be that the effects of captivity depressed the *ad libitum* feeding activity from the maximum rate, to approach the natural, long-term, average rate. In any case, there is no clear direction of bias and no obvious way to improve the estimate of natural ration.

For the parameters k and γ , there seem to be no data specifically for these jacks or for closely related species. Published values for a considerable number of rather large, active, perciform fishes are similar to those chosen in this study (about 0.8 for both parameters) (e.g., Winberg 1956). The value of k chosen affects the entire calculation of captive α and subsequently of C for all weight-classes. The value of γ affects the entire calculation of captive α , but affects only one term (the largest) in the subsequent calculation of C . For each of these parameters, because it occurs in the calculation of captive α and subsequently of C , the effects of any inaccuracy in the choice of the value tend to cancel.

Use of a single value of α for all sizes of fish introduces another assumption. In previous work, this coefficient has often been treated as constant over a considerable range of sizes (Winberg 1956). However, for most species, α has not been determined for large sample sizes or large size ranges. A rather extreme range of sizes is included in the present calculations. No adequate measurements were available to produce a direct estimate of α for *C. ignobilis*. The use in its place of the α calculated for *C. melampygus* represents an approximation, and thus the estimated components of the energy budget for *C. ignobilis* may be less reliable. However, the similarity of α values presented by Winberg (1956) for a wide variety of less closely related species suggests that the approximation used is acceptable. Temperatures in the seawater feeding tanks were close to normal sea temperatures throughout the year, and therefore no correction of α for temperature seemed necessary. (The full annual range of tank and sea temperatures was small.)

The quality of the estimate of growth rate depends upon the quality of the fitted von Bertalanffy model as a descriptor of actual growth. Both regressions were good fits, and t_0 and L_∞ values were realistic. The use of dW/dt , evaluated for each chosen weight-class, is probably the best estimate of growth rate available from the von Bertalanffy model.

The estimate of reproductive output is crude, but little else is available. Since whole body weights were used in the von Bertalanffy model regressions, at least part of the reproductive energy may be viewed as included in the growth rate term, G (on some sort of average basis across all specimens and seasons). However, since the development of reproductive products is seasonal, it seemed reasonable to add a term representing the weight of a fully developed gonad to represent additional annual reproductive energy demand. The effects from both these terms may somewhat overestimate reproductive demand. However, multiple clutches may be developed over the course of a year, so the gonad weight alone may underestimate the actual reproductive energy.

As in all such energy budgets for active animals beyond the early juvenile stages, the respiratory metabolism term, Q , was dominant (see Table 5). The growth term, G , was never more than 10% of Q for the size-classes calculated here, and the reproductive term, S , was always substantially less than G . Therefore, factors affecting the accuracy of the components of Q (e.g., assumptions about the parameters α and γ) produce the greatest effects on the total estimate of the ration, C .

Components of the basic energy budget derived in this study, e.g., growth parameters (L_∞ , W_∞ , K , and t_0), maximum GSI, and α , should be similar in other tropical and subtropical localities where these species occur. The value of α (and corresponding metabolism and ration) can be readily adjusted for other temperatures by using Krogh's (1959) "normal curve" or corresponding mathematical functions (e.g., Winberg 1956:32, Ursin 1967:2396).

The estimate of population consumption in the specific case of FFS was of particular interest because of the extensive community trophic work done there. A mathematical trophic model of the shallow marine ecosystem there has been produced (Polovina 1984), with the biota lumped into a dozen large trophic compartments. Jacks (especially these two *Caranx* species) are major members of one of the top trophic-level compartments. Comparison of our numbers for consumption with those from the model suggests that these jacks provide an even more important trophic path than the large-scale model predicts.

The census methodology used to produce the population estimates in Table 6 was not designed to adequately census such wide-ranging, highly mobile species, and these estimates must be considered rough. They probably represent maximum estimates. No method was found to check them directly. Extrapolation of the catch data for the year 1900 from the main Hawaiian islands produced an estimated "catch" for FFS of about 44 *C. melampygus*/km² and 26 *C. ignobilis*/km².

This is an order of magnitude lower than the visual census estimates of full populations of 460/km² and 260/km², respectively. There is no basis for estimating accurately what fraction of the standing stock of either species was caught in 1900. However, there is no evidence that the fishery was immediately depleted, so it seems likely that the standing stock was several times the annual catch for each species. It seems reasonable that the actual present stock sizes at FFS are not much greater than the figures in Table 6, and they are probably not less than a third of those estimated figures.

Based on our study, it is clear that populations of these two species combined eat at least a few thousand metric tons annually at this medium size atoll (about 500 km² in area to a depth of about 20 m). From an ecological perspective, this must represent one of the most important top-level trophic paths in this system (and probably in many others). The estimated combined predation pressure (Table 6) by these two jacks exceeds the combined estimate for the three dominant shark species in the same system (DeCrosta et al. 1984) by a factor of about 40. This source of mortality should be considered in any quantitative examination of the population ecology of the prey groups, particularly fish, large crustaceans, and cephalopods. The diet composition results in Tables 3 and 4 permit such analysis at lower systematic levels as well.

The information now available about these two important jacks provides an outline of their life history and trophic ecology. Both species are moderately fast growing, attain large size, and live at least several years. Both mature at relatively large size (a major consideration in fishery management), have apparent high fecundity, and may reproduce for at least 4–6 years, with a pronounced seasonal spawning cycle. These jacks are highly piscivorous, but show considerable quantitative separation in their specific diets. *Caranx melampygus* is more dependent on fishes, whereas *C. ignobilis* has a more varied diet that includes large crustaceans and cephalopods. Both species have high metabolic demands and correspondingly high rates of food consumption. Large populations of these species may impose considerable predation mortality on benthic/demersal communities, particularly on fishes. These jacks are potentially of interest in many shallow-water tropical environments because of their role in community ecology as well as in local fisheries.

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Appendix A

Numbers of increments visible by scanning electron microscopy in the otoliths of various size specimens of *Caranx melampygus* and *Caranx ignobilis*, and corresponding estimated ages of specimens (assuming daily deposition of increments).

<i>Caranx melampygus</i>			<i>Caranx ignobilis</i>		
Length of fish (mm SL)	No. of otolith increments	Estimated age (yr)	Length of fish (mm SL)	No. of otolith increments	Estimated age (yr)
122	186	0.510	106	274	0.751
196	486	1.332	109	276	0.756
210	458	1.255	113	293	0.803
259	598	1.638	462	793	2.173
270	612	1.677	485	846	2.318
283	596	1.633	606	1580	4.329
294	423	1.159	660	1690	4.630
320	687	1.882	760	1793	4.912
328	812	2.225	985	2387	6.540
341	710	1.945	1180	3384	9.271
380	813	2.227			
468	904	2.477			
555	1435	3.932			
660	2154	5.901			

Appendix B

Estimated batch fecundity for 11 gravid female specimens of *Caranx melampygus* of various sizes.

Length of fish (mm SL)	Whole wet weight of fish (g)	Whole wet weight of ovary (g)	Est. no. of eggs in ovary
328	760	14.1	49,700
465	1985	46	284,000
502	2590	78.5	774,000
503	2724	133	987,000
514	3667	182	888,000
520	3807	224	2,600,000
596	5167	292	1,690,000
617	5650	210	1,020,000
640	6490	440	4,270,000
649	6615	223	1,540,000
654	6220	249	2,220,000