

# The abundance of juvenile yellowtail (*Seriola quinqueradiata*) near the Kuroshio: the roles of drifting seaweed and regional hydrography

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## ABSTRACT

We assess the effect of drifting seaweed (*Sargassum* sp.) biomass, geography and hydrography on juvenile yellowtail (*Seriola quinqueradiata*) abundance variation off the southeast coast of Japan, near the Kuroshio Current. The amount of drifting seaweed mats progressively increased northeastward into the cooler, coastal waters. Frontal structure indexed using a station-to-station  $\Delta$ SST did not explain spatial variation in the seaweed mat distribution, although the western extent of the Kuroshio Current appeared to act as a boundary. Juvenile yellowtail constituted 51–62% of the fish collected in association with drifting seaweed mats in April 1996 and 1997 and 29% in June 1996. The abundance of juvenile yellowtail was positively correlated with seaweed biomass. The geographic distribution of juvenile yellowtail associated with drifting mats varied among sampling periods, being more southwesterly in April and more northeasterly in June. Simple multiple regression models based on seaweed biomass and geographic distribution (latitude) explained between 35% and 43% of the variation in juvenile yellowtail abundance in spring. Associations with spatial and temporal variations in hydrographic conditions did not contribute to explained variation in

a meaningful manner. The results presented here indicate that, off the southeast coast of Japan during April, yellowtail juveniles are likely to be most abundant when seaweed biomass is high, occur offshore, and are bounded by the western extent of the Kuroshio Current near the 19–20°C SST isotherm.

**Key words:** abundance distribution model, drifting seaweed, juvenile yellowtail, Kuroshio, *Sargassum*, *Seriola quinqueradiata*

## INTRODUCTION

Drifting seaweed increases the complexity of the pelagic environment and provides habitat in the open ocean that is comparable to that of littoral vegetation in coastal environments (Gorelova and Fedoryako, 1986; Kingsford, 1995). Seaweed mats provide food and refuge for some species (Shaffer *et al.*, 1995) and likely represent a dispersal agent for a variety of marine organisms (Kingsford, 1992; Ingolfsson, 1995; Shaffer *et al.*, 1995). Over 70 species of fish from 30 families are documented as being associated with drifting seaweed, particularly during their early life history (Uchida and Shojima, 1958; Shojima and Ueki, 1964; Ida *et al.*, 1967; Mitchell and Hunter, 1970; Kingsford and Choat, 1985; Safran and Omori, 1990; Kingsford, 1992, 1995).

Juvenile yellowtail (*Seriola quinqueradiata*) is frequently associated with drifting seaweed off the coast of western Japan. Yellowtail spawning grounds in the East China Sea and the coastal waters of southwestern Japan are at the southern end of the yellowtail distribution (Fig. 1; Mitani, 1960; Murayama, 1991; Uehara *et al.*, 1998), and spawning typically occurs during the northern winter and spring (Ochiai and Tanaka, 1986). Larvae are postulated to be transported to the waters around Japan by the two regionally dominant and warm currents (Ochiai and Tanaka, 1986): the Tsushima Warm Current that flows from the East China Sea to the Japan Sea and the Kuroshio Current that flows northeast along the southeast coast of Japan into the western Pacific Ocean (Fig. 1). Juvenile

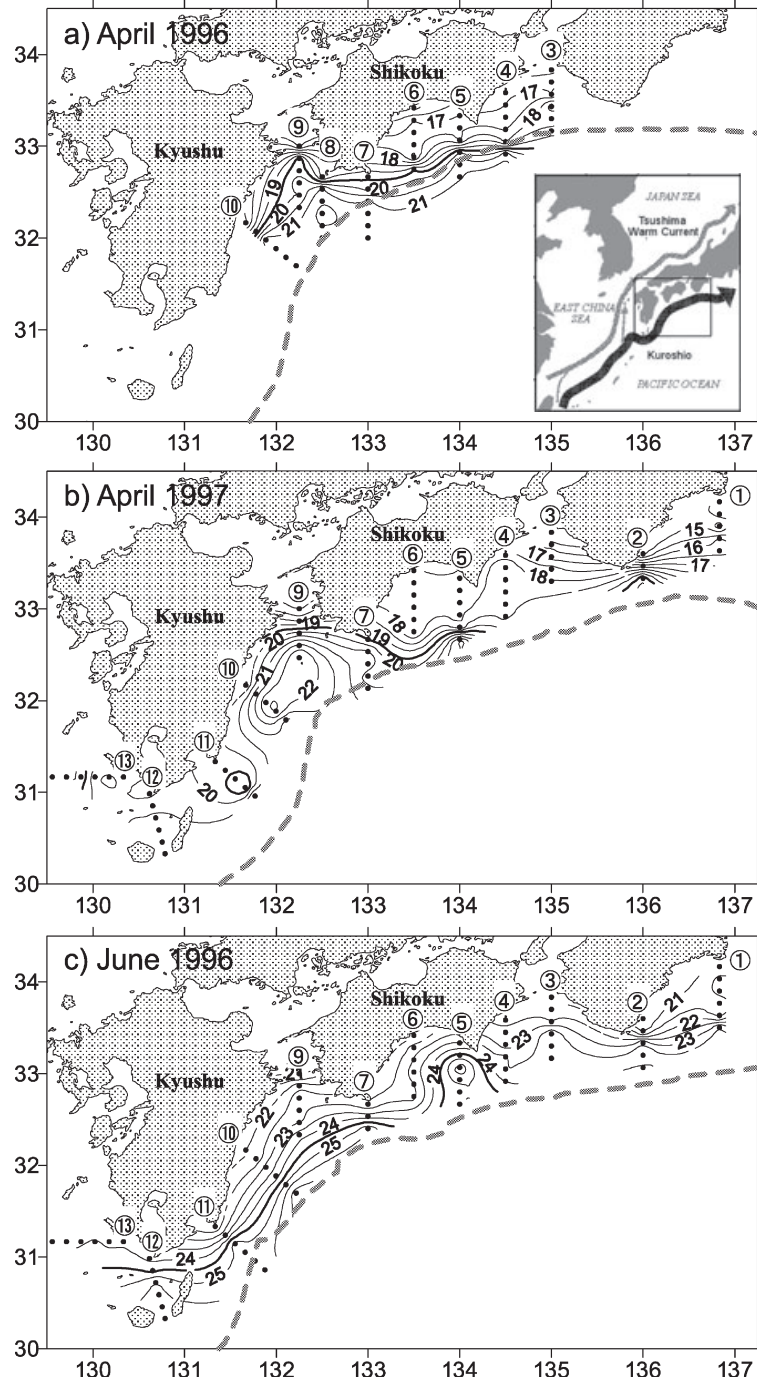
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**Figure 1.** Charts of western Japan off the Pacific coasts of the Islands of Kyushu and Shikoku showing numbered sampling transects (circled number), station locations (solid symbols), and sea-surface temperature isotherms (0.5°C increments) constructed using measurements at each transect station in: (a) April 1996; (b) 1997; and (c) June 1996. The 19–20°C isotherms indicate the approximate western boundary of the Kuroshio Current in April and the 24–25°C isotherms indicate the approximate boundary in June (highlighted in bold at 19.5 and 24.5°C, respectively). Dashed lines indicate the synoptic location of the Kuroshio Current axis during the study periods (Japan Coast Guard, 1996a,b, 1997). The inset in panel (a) illustrates the geographic location of the study in relation to the East China Sea, the Pacific Ocean, the Japan Sea and the regionally dominant Kuroshio and the Tsushima Warm Current (adapted from Isobe, 2000).



yellowtail aggregate around drifting mats of seaweed (primarily *Sargassum* species near Japan; Yoshida, 1963; Ohno, 1984) during spring and early summer (Ochiai and Tanaka, 1986), and it is at this time Japanese fishermen concentrate on the mats to collect juvenile yellowtail for use as aquaculture seed stock and for grow-out. In recent years the Japanese annual total allowable catch of yellowtail juveniles associated with seaweed mats was in the order of 40 million individual fish (Kataoka, 1993).

Four decades ago, Mitani (1965a,b,c, 1968) used an aerial survey of seaweed mats to assess the abundance of seaweed-associated yellowtail juveniles. The focus was on a fast and efficient assessment of the mats that relied on an assumed relationship between the abundance of the seaweed and the abundance of juvenile yellowtail. In the early 1980s, Hanaoka *et al.* (1984) estimated the abundance of seaweed-associated yellowtail juveniles off the southeast coast of Japan using an aerial survey of seaweed mats and the commercial fishery catch data. However, there remains little quantitative information that relates juvenile abundance to unit seaweed biomass and addresses the influence of hydrographic conditions on the association between the seaweeds and the juveniles. Here, we report on a study conducted in the coastal Pacific off the southeast coast of Japan during 1996 and 1997 to quantify the geographic distribution of the association and the influence of the local hydrography therein. We address two working hypotheses: (1) the abundance of seaweed mats should be related to the regional hydrography (for example, concentrated in frontal regions along the western boundary of the Kuroshio); and (2) the abundance of juvenile yellowtail should be a positive function of seaweed biomass. We develop a multiple regression model to explain juvenile yellowtail abundance variation in relation to geography, hydrography, and seaweed biomass and then test the model.

## MATERIALS AND METHODS

### Surveys

Three oceanographic surveys were conducted off the southeast coast of Japan during 17–27 April and 11–28 June 1996, and 8–28 April 1997. Each survey involved data collection along a series of transects each ~74 km long and oriented normal to the coast and the main axis of the Kuroshio (Fig. 1). Eight transects were surveyed in April 1996, and 12 were surveyed in June 1996 and in April 1997. We collected hydrographic data during daylight at fixed stations along each

transect, made visual estimates of seaweed mat abundance and seaweed mat area, and collected seaweed and associated fish samples.

Hydrographic data were collected along each transect at fixed stations arranged at ~15 km intervals (Fig. 1). This procedure provided approximately six stations per transect unless reduced due to weather conditions or time limitations. Sea surface temperature (SST) was recorded at each station using a bucket and thermometer.

Along each transect, observers on each side of the vessel counted seaweed mats within 20 m of the vessel and estimated mat surface areas (those nominally >100 cm<sup>2</sup>). The 20-m-wide swath was estimated using the geometry of the foredeck breadth and the alignment of deck fixtures on the vessel. The mats were typically <1 m<sup>2</sup> (though infrequently >3 m<sup>2</sup>); the observers had been trained to reliably estimate mat area, and their skill was subsequently tested using plastic mats of known (unknown to the observers) area. We assumed that observer performance was uniform across observers and over time.

Seaweed mats and their associated fish fauna were collected at haphazard intervals along the transects when steaming (nominally 5 m s<sup>-1</sup>) from station to station with the goal of collecting four to five mats between stations. Mat area was measured prior to collection using either a 1- or 0.5-m<sup>2</sup> frame that was lowered over the side to the surface of the mat. Mats were then collected using a scoop net (5 m wide by 2.5 m high) fitted with a 5 m (deep) 7.6 mm stretched mesh similar to that used by commercial fishermen for collecting yellowtail juveniles. Upon retrieval, the seaweed was thoroughly rinsed and examined using a series of 75-L tubs filled with clean seawater. Fish were separated from the seaweed, collected and preserved in a 5% formalin/seawater solution or kept frozen (-20°C) for later identification and measurement. All yellowtail were counted and measured ( $\pm 0.01$  mm fork length; FL) and weighed ( $\pm 0.01$  g) using a caliper and an electronic balance, respectively. The seaweed wet biomass (WB) was estimated using an onboard balance beam ( $\pm 10$  g). SST was recorded at the time of mat collection using a bucket and thermometer.

### Analyses

Sea surface temperature isotherms were constructed using conservative gridding and Kriging parameters (Surfer 7.04; Golden Software Inc., Golden, CO, USA). As the majority (93%) of the seaweed samples included mat area estimates only, we initially determined that the relation between measures of mat area and measures of WB were not significantly different

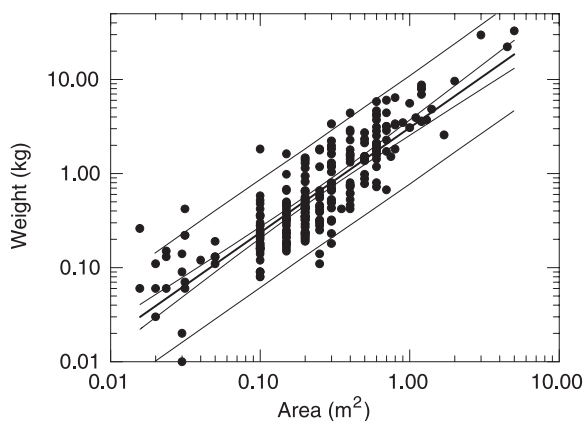
among the three surveys (ANCOVA, log transformed data;  $F = 0.85$ ,  $P = 0.43$ ). We then converted the visual estimates of mat area ( $A$ ,  $m^2$ ) to estimates of biomass (WB, kg) using the following log–log linear regression equation based on the measures provided among all cruises (Fig. 2):

$$WB = 3.078A^{1.115} \quad r^2 = 0.73, \quad n = 247. \quad (1)$$

To assess the relation between seaweed biomass concentration and regional hydrography, we first examined interval-specific biomass sums of seaweed (ISBS) as a function of SST classes resolved into  $1^\circ\text{C}$  temperature classes. Biomass estimates calculated as above were summed over each station-to-station interval, while the SST class for an interval was calculated using the average SST measured at the two adjacent stations. The geometric mean of the ISBS estimate was then calculated for each SST class. We also calculated  $\Delta\text{SST}$  using the interval differences in the SST and employed  $\Delta\text{SST}$  as an index of hydrographic heterogeneity among station intervals (e.g. fronts).

Our investigation of the influence of abiotic and biotic variables on the abundance of yellowtail juveniles associated with seaweed mats was exploratory and multivariate. We used only those data where the entire seaweed mat was collected with one successful sweep of the scoop net. Biotic variables (abundance of yellowtail per seaweed mat and WB) were  $\log(x + 1)$  transformed to reduce heteroscedacity, and the transformed data were used throughout the analyses.

**Figure 2.** Scattergram showing seaweed mat wet weight as a function of seaweed area as measured off the southeast coast of Japan during April and June 1996, and April 1997. The log-log linear regression ( $r^2 = 0.73$ ,  $P < 0.001$ ) is shown by the heavy line delimited by the upper and lower 95% confidence interval for the model (innermost) and for the predictions (outermost).



We selected the highest correlates among the biotic (abundance of yellowtail juveniles and WB) and abiotic (latitude, longitude, SST, and  $\Delta\text{SST}$ ) variables to assist in the selection of variables for multiple regression analysis of juvenile abundance among mats and to minimize the potential for multiple collinearity. Model selection was based on multivariate linear regression employing criteria to maximize the explained variance, reduce Mallows  $C_p$  statistic (as described in Hocking, 1976), and maintain significant ( $P \sim 0.05$ )  $F$ -values for the model and the contributing variables. The data in each of April 1997 and April 1996 were used independently to provide annually independent model parameters. The parameters from the two resulting models were then compared and the models were each tested using independent data (i.e., the April 1997 model was tested on the April and June 1996 data, and the April 1996 model was tested on the April 1997 and June 1996 data). The goodness of fit between the observed and predicted estimates of juvenile abundance was assessed using the Pearson correlation statistic. All statistical tests were conducted using Systat 10 (SPSS Inc., Chicago, IL, USA) and SAS (SAS Institute Inc., Cary, NC, USA).

## RESULTS

### Hydrography

Typical oceanographic features for the region were observed in the SST structure. From the relatively cool coastal waters, SST increased with distance offshore and decreasing latitude toward the northern and western boundary of the Kuroshio near the  $19\text{--}20^\circ\text{C}$  isotherms in April and near the  $24\text{--}25^\circ\text{C}$  isotherms in June (Fig. 1). SST gradients were stronger in April than in June. In April 1996, the warmest water was east of Kyushu where there was also weak evidence of a warm-core water mass derived from the Kuroshio (transect-8; Fig. 1a). In April 1997, warm-core water masses were to the southeast of Shikoku (transect-4) and east of Kyushu (transect-9 to -10), and a cold-core water mass was located to the east of Kyushu (transect-11; Fig. 1b). In June 1996, there was weak evidence of a warm-core water mass to the south of Shikoku (transect-5; Fig. 1c).

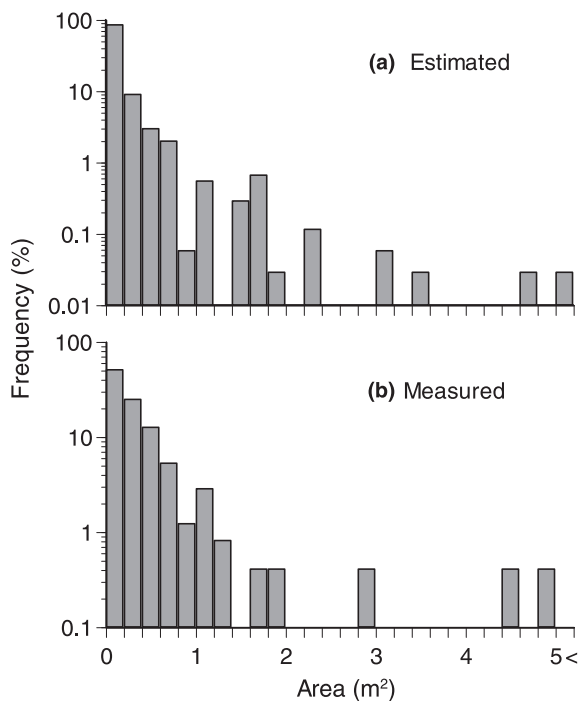
### Seaweed abundance, biomass, and hydrography

In April and June 1996 and April 1997, we counted a total of 174, 2586, and 731 seaweed mats, respectively, and their areas were estimated along combined survey transect lengths of 594, 831, and 742 km in each

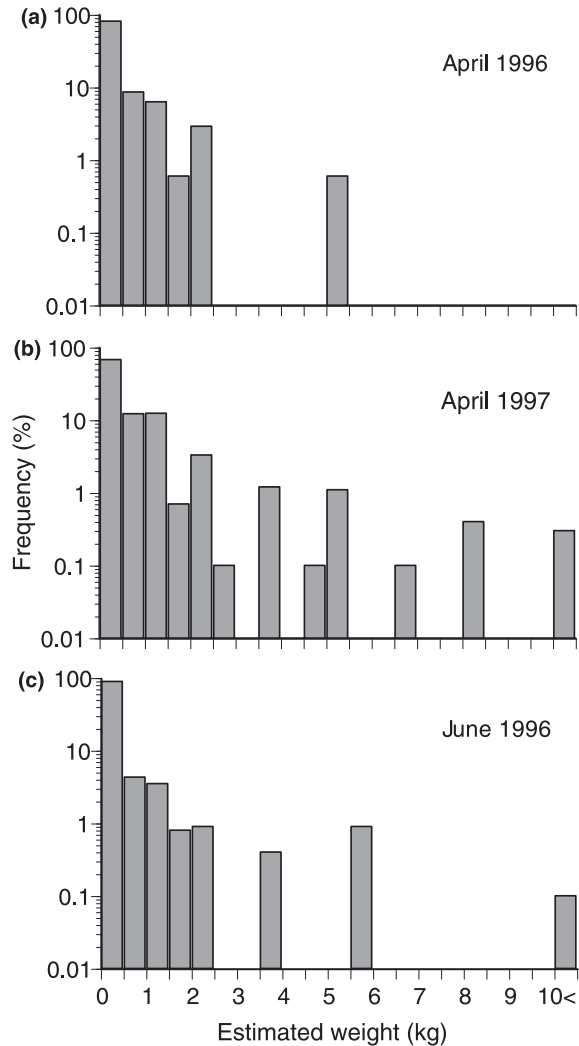
cruise, respectively (range average of 0.3–3 mats km<sup>-1</sup>). Of these, a total of 247 mats were used to derive biomass estimates from area measurements (Fig. 2). For the observer-based estimates of mat area, the frequency distributions were highly left skewed (skewness = 11.97) with >80% of the observations ≤0.2 m<sup>2</sup> and 2% ≥1 m<sup>2</sup> (Fig. 3a). For those mats where area was directly measured, the frequency distributions were also left skewed (skewness = 5.53) with >50% of the observations ≤0.2 m<sup>2</sup> and 7% ≥1 m<sup>2</sup> (Fig. 3b). Overall, the resultant seaweed biomass estimates were consequently left skewed with >60% of the mats having an estimated biomass of ≤0.5 kg (Fig. 4), although there was an order of magnitude or more uncertainty in the biomass estimate for a given measured area (Fig. 2).

The ISBS as a function of SST varied by 1–2 orders of magnitude within and among cruises (Fig. 5). In April, the highest ISBS was associated with the lowest SST class (16°C in 1996 and 14°C in 1997) and declined exponentially at a rate of 55% per °C increase in 1996 ( $r^2 = 0.86$ , d.f. = 1; log-linear fit) and at 79% per °C in 1997 ( $r^2 = 0.90$ , d.f. = 1) until reaching 17–18°C after which ISBS remained relatively low

**Figure 3.** Percentage frequency distribution of seaweed area (0.2 m<sup>2</sup> class intervals) across all cruises off the southeast coast of Japan, calculated from: (a) observer estimates of seaweed mat area along transects (N = 3491); and (b) measured mat area (N = 247).

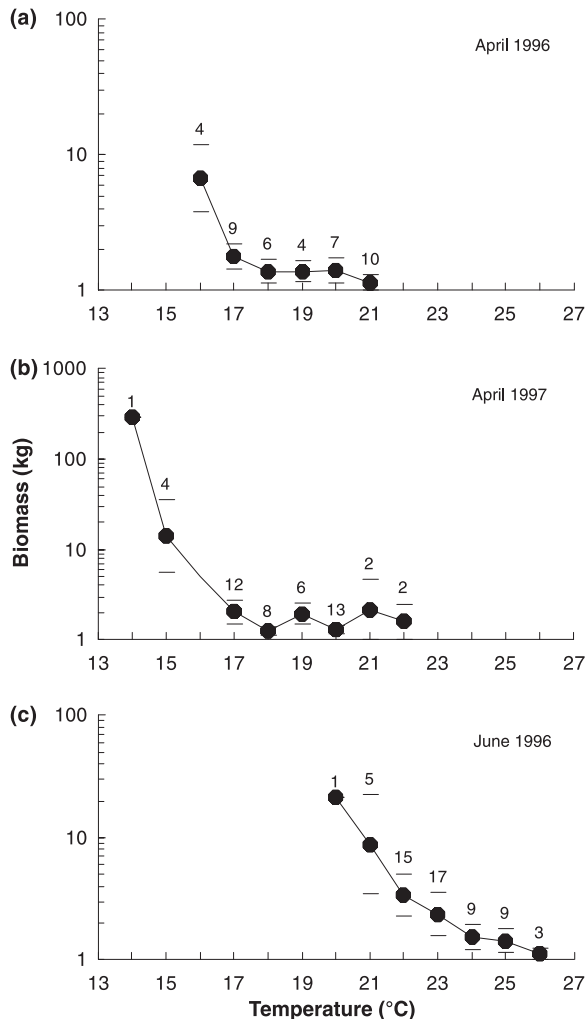


**Figure 4.** Percentage biomass frequency distribution (0.5 kg class intervals) of seaweed mats calculated from observer estimates of seaweed mat area along transects off the southeast coast of Japan during: (a) April 1996 (N = 174); (b) April 1997 (N = 731); and (c) June 1996 (N = 2586).



and invariant across the 17–22°C range. In June, the highest ISBS was also associated with the lowest SST class (20°C) and again declined exponentially at 48% per °C increase ( $r^2 = 0.96$ , d.f. = 3) until reaching ~24°C, after which it also remained relatively low and invariant toward higher SST. When ISBS was examined in relation to  $\Delta$ SST (an index of frontal structure) for each cruise, no clear pattern emerged, although there was weak evidence of modes in the ISBS distribution near 19 and 21°C in April 1997 (Fig. 5b). While our observations showed the seaweed mats were not concentrated near the boundary of the

**Figure 5.** Scattergram of the relationship between the geometric mean (solid symbol)  $\pm$ SE of interval-specific biomass sum of seaweed (ISBS, kg) calculated from interval-specific SST classes ( $1^{\circ}\text{C}$  class intervals) as observed off the south-east coast of Japan during: (a) April 1996; (b) April 1997; and (c) June 1996. Sample size is provided above each estimate.



Kuroshio (i.e., not consistently where the SST gradients were strong), they were consistently concentrated in water masses on the landward side of the current, and therefore the current appears to act as a large-scale boundary except where seaweed was associated with cold-core (Figs 1b and 6b) and warm-core (Figs 1a,c and 6a,c) water masses.

#### Yellowtail juveniles

We collected 1627, 575, and 2178 yellowtail juveniles from a total of 128, 181, and 209 seaweed mats in April and June 1996, and April 1997, respectively

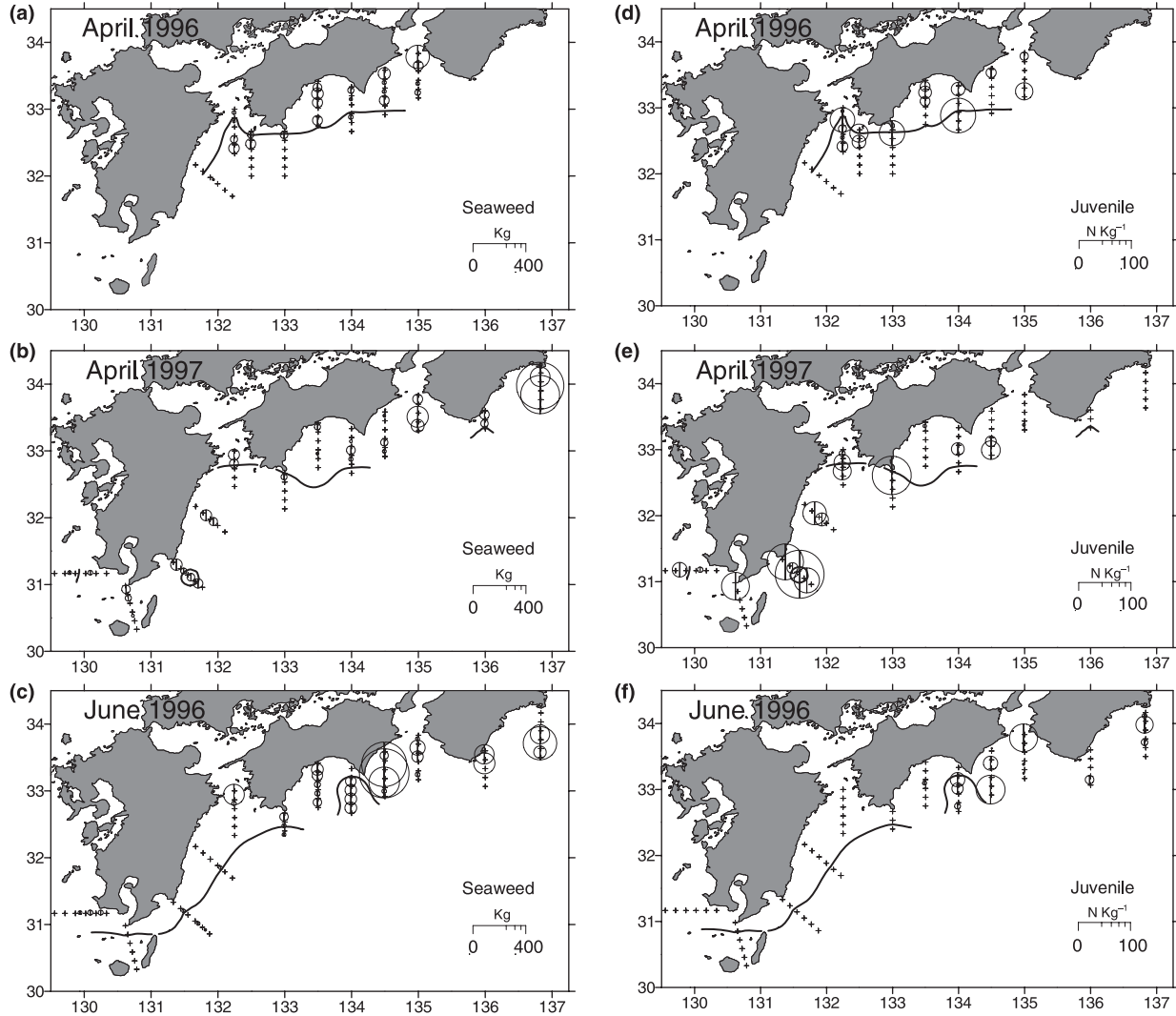
(range average of 3–13 juveniles per mat). From the individually measured, collected, and weighed mats, yellowtail was the most abundant fish species associated with mats in April 1996 and 1997, representing 62% and 51% of the total number of fish collected in each year, respectively. Yellowtail was the most abundant species in June 1996, though it constituted about a third (29%) of the total catch. The average number of yellowtail juveniles per unit seaweed biomass (juveniles  $\text{kg}^{-1}$ ) was 6.7, 4.0, and 18.5 in April and June 1996, and April 1997, respectively. Yellowtail juveniles were distributed throughout most of the survey area during April 1996 (Fig. 6d), though number per unit seaweed biomass tended to be greater in the southwest portion of the region during April 1997 (Fig. 6e) and in the northeast portion during June 1996 (Fig. 6f). In the waters around southern Shikoku in 1996, very few juveniles (0–1.3 juveniles  $\text{kg}^{-1}$ ) occurred in June (Fig. 6f), though they were relatively abundant (0–23.7 juveniles  $\text{kg}^{-1}$ ) in April (Fig. 6d).

Where the size frequency distribution of yellowtail was clearly unimodal (near 50 mm FL) in April 1996, it was bimodal in April 1997 with modes near 25 and 75 mm (Fig. 7). These distributions were used to classify ‘small’ yellowtail as those <50 mm and ‘large’ yellowtail as  $\geq 50$  mm FL as they are consistent with at least a single dominant (small-size) cohort in April 1996 and at least two dominant (small- and large-size) cohorts in April 1997. The June 1996 distribution appeared multimodal with small-size modes (near 45 and 55 mm) and large-size modes (near 70, 85, and 110 mm).

Correlation analyses of the abiotic and biotic variables revealed several to be strongly correlated (Table 1). There was a strong negative correlation between SST and geographic location (latitude and longitude), with SST generally decreasing from southwest to northeast. Only in June 1996 was WB significantly correlated with latitude ( $r = 0.25$ ) and longitude ( $r = 0.24$ ) and the positive nature reflects increases in WB from southwest to northeast at this time of year (Table 1). Despite the strong relation between SST and geographic location, there were no significant correlations between WB and either SST or  $\Delta\text{SST}$  in any survey.

The total number of yellowtail juveniles was significantly and positively correlated (though with considerable scatter) with WB in each survey (Fig. 8; Table 1). The correlation was strongest ( $r = 0.59$ ) in April 1996 when there was a single cohort dominated by small juveniles (Fig. 7a); therefore there was a significant correlation ( $r = 0.53$  and  $0.70$ , respectively)

**Figure 6.** Station-to-station interval (interval-specific) biomass sum of seaweed (ISBS, kg, expanding symbols) during: (a) April 1996; (b) April 1997; and (c) June 1996 and station-to-station interval (interval-specific) average number of yellowtail per unit seaweed biomass (individuals  $\text{kg}^{-1}$ , expanding symbols) during: (d) April 1996; (e) April 1997; and (f) June 1996 in relation to the sampling station locations (crosses) and the approximate western boundary of the Kuroshio ( $19.5^{\circ}\text{C}$  in April 1996, 1997, and  $24.5^{\circ}\text{C}$  in June 1996; bold line).

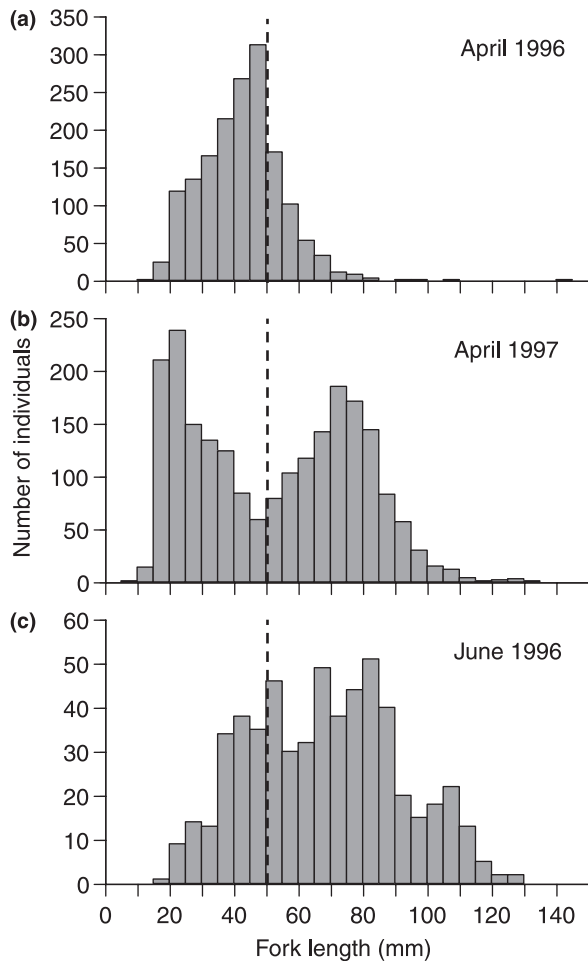


between small- and large-size juveniles with WB (Table 1). The correlation structure was similar, though weaker, in April 1997 ( $r = 0.36$  between total number of yellowtail and WB) when one small-size ( $r = 0.17$ ) and one large-size ( $r = 0.56$ ) cohort dominated (Fig. 7b). Correlation between the total number of juveniles and WB was weakest ( $r = 0.27$ ) in June 1996 when the juvenile size frequency was multimodal (Fig. 7c). We also examined the shape or density metrics for each mat by dividing the estimated hemispherical volume (derived from the mat area) by WB and found no significant correlation with

yellowtail abundance. Only in April 1997 were there significant correlations between the abundance of yellowtail juveniles (total number and both size classes) and SST, and there were no significant correlations between any of the juvenile abundance estimates and  $\Delta\text{SST}$  in any survey, which would have been indicative of frontal accumulation (Table 1).

Exploratory multiple regression models developed using the April 1996 data showed that WB alone explained 35% of the variation in the abundance of juvenile yellowtail (Table 2). A model incorporating WB ( $P < 0.001$ ), latitude ( $P = 0.02$ ), and longitude

**Figure 7.** Size (mm, fork length) frequency distribution (5-mm class intervals) of juvenile yellowtail collected from seaweed mats along transects off the southeast coast of Japan during: (a) April 1996 ( $N = 1627$ ); (b) April 1997 ( $N = 2178$ ); and (c) June 1996 ( $N = 575$ ). Dashed line indicates the arbitrary boundary between small and large juveniles.



( $P = 0.01$ ) explained 42% of the total variation ( $P < 0.001$ ) along with a significant reduction in Mallow's  $C_p$  statistic. Although useful for geographic positioning purposes, the high collinearity between latitude and longitude prevented (parsimonious) further use of this particular model. When the parameters from the April 1996 univariate model were used to 'predict' the total abundance of yellowtail in April 1997 and in June 1996, the model was able to explain 13% and 7% of the variation, respectively.

Similar to April 1996, multiple regression models showed that latitude and WB explained 43% of the variation in the total number of yellowtail juveniles in April 1997 (Table 2). In contrast to the April 1996 model, latitude alone explained 31% of the variation

( $P < 0.001$ ). However, none of the other variables examined (longitude, SST, and  $\Delta$ SST) provided significant improvements to explained variation. Separate analyses of the abundance of small and large size classes of juvenile showed only latitude to be of significance in explaining variation in the number of small yellowtail ( $r^2 = 0.32$ ;  $P < 0.001$ ). For large yellowtail abundance, latitude and WB explained 41% of the variation and seaweed biomass explained more of the variation (32%) than did latitude. When the parameters from this exploratory model were used to 'predict' the total abundance of yellowtail in April 1996 the model was able to explain 28% of the observed variation and none of the variation in June 1996.

Finally, the only exploratory model to explain juvenile abundance variation in June 1996 was one that also incorporated WB ( $P = 0.02$ ). Though the model explained only 7% of the variation in abundance, it is consistent with the April 1996 model, where juvenile abundance is positively correlated with WB.

## DISCUSSION

We observed 0.3 and 1.0 seaweed mats  $\text{km}^{-1}$  in April 1996 and 1997, respectively, but threefold more per km later in spring (June 1996). This is consistent with the pattern observed off the Pacific coast of western Japan, when most mats occur in May and June (Yoshida, 1963). *Sargassum* is typically deciduous, shedding most of the thallus in late spring during the latter stages of reproduction (Yoshida, 1963; Ohno, 1984). Most (70–90%) of the mats we observed were  $<0.5$  kg, considerably smaller than the 24-kg average reported from Sendai Bay ( $6^\circ$  north of our study area), but approaching the 9-kg average reported near the Kuroshio Extension at  $38^\circ\text{N}$  (Safran and Omori, 1990). Previous studies showed that small mats were abundant in the Bungo Channel and Tosa Bay ( $32\text{--}33.5^\circ\text{N}$   $132\text{--}134^\circ\text{E}$ , Ohno, 1984), both located in our study area, and thus, small mat-size may be typical for the study area.

Our results show that off the southeast coast of Japan the amount of drifting seaweed increases in a northeastward manner into the cooler coastal waters (Fig. 6a–c). Further, during all our three cruises, ISBS decreased in a near-exponential manner with increasing SST toward some low asymptotic value at higher SSTs (Fig. 5). This implies that the origin of the drifting mats is the neighboring coastal and vegetated areas that are cooler than the offshore area near the Kuroshio. Frontal structure, as indexed by our station-to-station  $\Delta$ SST, was not useful in explaining the

**Table 1.** Pearson correlation coefficients for: (a) WB, seaweed wet biomass; (b) TYn, total number of yellowtail juveniles; (c) TYSn, total number of small juveniles (<50 mm FL); and (d) TYLn, large juveniles ( $\geq 50$  mm; FL) among sampling station latitude (Lat) and longitude (Lon), sea surface temperature (SST), and the station-to-station SST gradient ( $\Delta$ SST) in April 1996 and 1997, and June 1996. Biological variables were  $\log(x + 1)$  transformed, and correlation coefficients considered significant at  $P \leq 0.05$  are indicated in bold type.

Date	TYn	TYSn	TYLn	Lat	Lon	SST	$\Delta$ SST
(a) WB							
April 1996	<b>0.59</b>	<b>0.53</b>	<b>0.70</b>	-0.12	-0.09	0.17	-0.04
April 1997	<b>0.36</b>	0.17	<b>0.56</b>	-0.04	0.01	0.14	-0.03
June 1996	<b>0.27</b>	0.16	<b>0.25</b>	<b>0.25</b>	<b>0.24</b>	-0.19	0.10
(b) TYn							
April 1996		<b>0.99</b>	<b>0.73</b>	-0.06	0.08	0.16	0.06
April 1997		<b>0.91</b>	<b>0.77</b>	<b>-0.56</b>	<b>-0.47</b>	<b>0.48</b>	-0.11
June 1996		<b>0.77</b>	<b>0.91</b>	0.20	<b>0.23</b>	-0.00	0.10
(c) TYSn							
April 1996			<b>0.64</b>	-0.01	0.13	0.14	0.03
April 1997			<b>0.48</b>	<b>-0.57</b>	<b>-0.50</b>	<b>0.51</b>	-0.10
June 1996			<b>0.49</b>	<b>0.27</b>	<b>0.31</b>	-0.21	0.04
(d) TYLn							
April 1996				-0.23	-0.12	0.23	0.08
April 1997				<b>-0.32</b>	<b>-0.23</b>	<b>0.23</b>	-0.04
June 1996				0.09	0.11	0.11	0.13

spatial variation in ISBS, and this is consistent with earlier studies on drifting seaweed distribution that have similarly documented seaweed mats being more frequently encountered near the coast than in offshore frontal regions (Hanaoka *et al.*, 1984; Sugimura, 1984). Thus, it appears that drifting seaweed is typically more prevalent in coastal water masses.

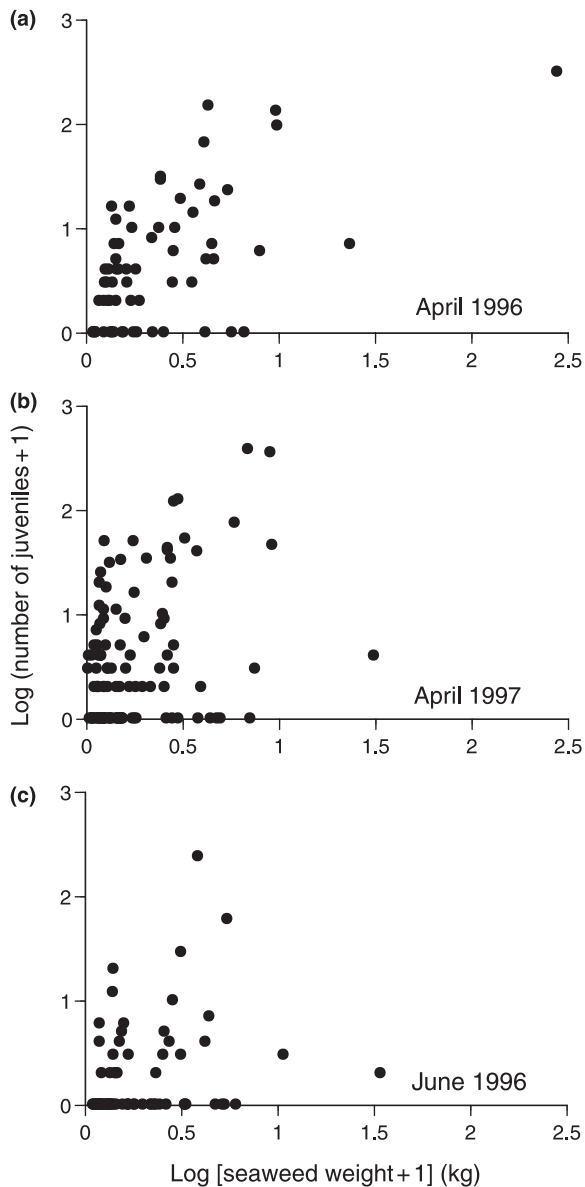
At the scale of our study, we reject our initial working hypothesis, although we must acknowledge that frontal structures, which typically vary at spatial and temporal scales below the resolution provided by sampling design (e.g. 15-km station intervals), may be too small for us to detect relative to the larger scales associated with the coastal waters.

As with the mats, the distribution patterns of juvenile yellowtail per kg of seaweed varied considerably among oceanographic surveys. The geographic distribution patterns were different among months; i.e., more easterly in June than in April in 1996 around the southern Shikoku, and more southwesterly in April 1997 versus more northeasterly in June 1996. This was readily apparent despite the occurrence of some seaweed in the southern transects in June 1996, where there were no associated juveniles. It is known that yellowtail shift their spawning northeastward with seasonally increasing ocean temperature from the East China Sea to coastal waters around Japan (Mitani, 1960; Murayama, 1991; Uehara *et al.*, 1998), a phenomenon that may explain some of the distributional variation in the association of juveniles with seaweed.

The median length of yellowtail juveniles in 1996 increased from 43 mm in April to 68 mm in June (approximately  $0.4 \text{ mm day}^{-1}$  population growth rate). However, at a growth rate of  $2.4 \text{ mm day}^{-1}$  (based on age cohorts, Sakakura and Tsukamoto, 1997), the mode of the April 1996 cohort would be expected to appear in the 186–190 mm size class in June 1996, which is beyond the size of juveniles typically associated with seaweed mats. It is thus most likely that most of the April 1996 cohort had departed the seaweed mats and new cohorts had sequentially recruited to the mats by June. The size frequencies in 1996 as well as the two conspicuous cohorts in 1997 show that yellowtail juveniles associated with seaweed mats were composed of multiple cohorts.

The abundance of yellowtail was positively correlated with the WB, although this relationship was not significant in two periods for the smaller size class of yellowtail (Table 1). We infer that large yellowtail juveniles ( $\geq 50$  mm FL) are strongly associated with the mats until approximately 150 mm FL, whereas smaller individuals may recruit to the mats at a range of sizes and exhibit less mat fidelity. It is known that as they grow, the food habit of yellowtail juveniles changes from small copepods to large ones, and then to fish (Anraku and Azeta, 1965), though our criterion of 50 mm FL (based on modal characteristics in length frequency distributions) was used simply to separate the relatively large from the relatively small juveniles. As the association of food items with seaweed mats is

**Figure 8.** Scattergram of the total abundance of yellowtail [ $\log(x + 1)$  transformed] as a function of seaweed biomass [ $\log(x + 1)$  transformed] during: (a) April 1996 ( $r = 0.59$ ); (b) April 1997 ( $r = 0.36$ ); and (c) June 1996 ( $r = 0.27$ ).



very weak (Anraku and Azeta, 1965), differences in mat fidelity among the juvenile yellowtail size classes may be independent of their food habit.

The multiple regression model derived from our largest data set (April 1997) employed only latitude and WB and explained 43% of the variation in total yellowtail abundance (Table 2). Our interpretation is that the negative latitudinal effect incorporates the positive SST effect, as well as the effect of the general geographic location of the Kuroshio Current. This same model could account for 28% of the variance in April 1996 (Table 2) where there was no latitudinal effect, and virtually none of the variance in June 1996 when the fish were too few and the correlation with mat size was the weakest. The results presented here suggest that, off the southeast coast of Japan, during April, yellowtail juveniles are most abundant when seaweed biomass is high and occurs offshore on the landward side of the Kuroshio Current near the 19–20°C SST isotherm. It is important to note that the abundance of yellowtail juveniles associated with inshore seaweed mats (individuals  $\text{kg}^{-1}$ ) was lower than that associated with offshore mats despite the abundant inshore seaweed mats. This implies a process by which larvae of yellowtail are transported to the study area from southwestern spawning grounds by the Kuroshio where they encounter seaweed mats near the landward side of the Kuroshio. Although the nature of our surveys could not capture the synoptic variation in hydrographic conditions, our simple model demonstrates that significant proportion of the variation in yellowtail juvenile abundance is a function of latitude, itself a proxy for the geographic location of seaweed biomass within coastal water masses bounded by the Kuroshio Current. In other words, juvenile abundance is a function of the habitat domain (seaweeds in coastal water masses) and the amount of the habitat (the number of mats) within the domain. It is uncertain as to how seaweed mats are associated with the regional oceanography, and how the yellowtail juveniles become associated with the seaweed mats. We have provided some quantitative

**Table 2.** Multivariate linear regression models describing the total abundance of juvenile yellowtail (TYn) off the south coast of western Japan during April 1996 and 1997 as a function of latitude (Lat) and seaweed biomass (WB) where abundance and biomass are the  $\log(x + 1)$  transformed estimates. The coefficient of determination ( $r^2$ ) and total degrees of freedom (d.f.) and the significance level of the model and contribution of each variable is shown. No meaningful model was determined for June 1996.

Multivariate regression models	$r^2$	d.f.	Model	Lat	WB
April 1997; $\text{TYn} = -0.3646 \text{ Lat} + 0.8489 \text{ WB} + 12.1947$	0.43	116	0.0001	0.0001	0.0001
April 1996; $\text{TYn} = 0.9442 \text{ WB} + 0.3110$	0.35	63	0.0001	–	0.0001

insights into those associations and have identified some of the important variables that appear to influence them. Further, the simple model that we developed appears to provide some basic information useful for improving estimates of total yellowtail juvenile abundance and for improving the management of aquaculture seed-stock fisheries that rely on the mats and the associated fish.

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