Catchability and retention of larval European anchovy, Engraulis encrasicolus, with bongo nets

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Whenever data on larval abundance are used in producing estimates or indices of stock size or recruitment, accurate length distributions are required. Factors that might bias sample distributions must be taken into account and, in broadscale ichthyoplankton surveys, the effect of environmental and behavioral factors on the content of the samples or collections must be considered (Zweifel and Smith, 1981). The objective is to standardize sampling gear by applying correction factors to make samples comparable (Smith and Richardson, 1977).

A factor contributing to a possibly serious source of bias in larval fish collections is net avoidance. Larvae may be agile and capable of avoiding nets, with the general effect of inaccurate abundance and mortality estimates (Clutter and Anraku, 1968). Catchability varies mainly with light regime and larval length. The visual stimulus of the sampling device is believed to be of crucial importance. This is indicated by numerous investigations showing diel variation in avoidance, catches being significantly smaller during daylight than at night (Morse, 1989, and references therein).

A second factor affecting larval fish collections is extrusion of captured material through the net mesh. According to the "diagonal rule" (Saville, 1958; Smith et al., 1968), the maximum cross-sectional diameter of an organism must be greater than the mesh diagonal if it is to be fully retained. However, the "diagonal rule" is often too conservative (Lenarz, 1972; Colton et al., 1980).

We examined the effects of time of day (day-night-twilight), fish length, and ontogeny on the catchability of European anchovy (Engraulis encrasicolus), by using a 60-cm bongo net. We also investigated biases resulting from differential retention of larvae of different lengths, and, further, we examined the effect of correction of catch for net avoidance on estimation of mortality.

Information on catchability and retention of anchovy with plankton nets is very limited and results are often contrasting. Catchability of European anchovy with bongo nets is unknown. Regarding retention, there is just a single study indicating full retention of European anchovy larvae with the 0.333-mm net (Aldebert et al., 1975), whose data are contradictory to Lo (1983) who has estimated a 0.63 retention rate for northern anchovy, Engraulis mordax, larvae <4.0-mm with a 0.333-mm net.

Materials and methods

From 1992 through 1995, five ichthyoplankton surveys were carried out in the Aegean Sea. A total of 474 stations were occupied in continental shelf and slope waters and areas characteristic of larval anchovy habitat (Fig. 1). Plankton and hydrographic sampling were performed at each station and cruise information is given in Table 1. Most stations were positive (i.e. at least one larva was captured).

A 60-cm bongo net sampler (Hydrobios) was used during all cruises. Mesh sizes on the sampler were 0.250-mm, and 0.500- or 0.335-mm, depending on the cruise (Table 1). The 0.250-mm mesh net is considered to retain clupeoid eggs and larvae completely (Aldebert et al., 1975; Colton et al., 1980; Leslie and Timmins, 1989).

Tows at two knots were double-oblique, within 5 m of the bottom to the surface, or from 120 m depth to the surface at deep stations. All tows consisted of a wire released to the desired depth and retrieved to the surface at standard speeds. The depth of the sampler could be monitored onboard at any time during the tow by means of a recording depthmeter attached to the sampler. Plastic codend buckets, with side windows of 155 cm^2 covered with net gauze, were used in an effort to minimize damage to larvae. Volumes filtered were calculated from a calibrated flowmeter in the mouth of each net.

All samples were sorted in the laboratory and larvae were identified to the lowest possible taxonomic level. Larval anchovies were counted and measured (notochord

or standard length to the nearest 0.1 mm). If more than 100 specimens of anchovy were captured in a tow, 100 randomly selected larvae were measured, and subsequent length frequencies were raised to the total number of larvae. Lengths were rounded to 1-mm length groups (e.g. 2–2.99: 2.5 mm).

Each station was assigned to day, night, or twilight hours according to the recorded time at the beginning of the tow. Twilight was designated as one hour before or after sunrise and sunset (Morse, 1989).

The analysis of retention and catchability was made after pooling all available data and, subsequently, estimating mean catch per length group. For example, mean catch per m^2 in each length category was calculated for 227 day, 146 night, and 84 twilight positive stations (Table 1). Pooling data over large temporal and spatial regimes integrates areal and temporal heterogeneity in distribution and abundance, and results of the analyses represent average conditions (Hewitt, 1981; Morse, 1989).

Negative stations (where no anchovy larvae were caught by either of two nets) were not included in our analysis (sensu Hewitt, 1981); we assumed that they represent samples drawn from outside larval habitat. Given that the number of negative stations was very low in our data set (17 out of 474, of which 10 were from one cruise, 92ANC2, Table 1), inclusion or exclusion of such negative stations was not expected to affect results.

Catches were standardized to numbers per m^3. This standardization is sufficient for comparing larval retention in paired different mesh-size nets but, in comparing daytime or twilight and nighttime catches, data had to be standardized to numbers per m^2, by using maximum tow depth and volume of water filtered (Houde, 1977). Mean standardized catches per length group were used to calculate the following ratios: day:night and twilight:night as well as 0.500-:0.250-mm mesh and 0.335-:0.250- mm mesh. Variances of ratios were approximated as in Somerton and Kobayashi (1989).

The calculation of mean catch and its variance followed the methods of Pennington (1983) for the delta-distribution of catch frequencies (see also Morse (1989)). The estimators based on the lognormal model (delta distribution) are more efficient for marine data than the usual sample estimators (Lo et al., 1992; Pennington, 1996). In particular, they provide rea-
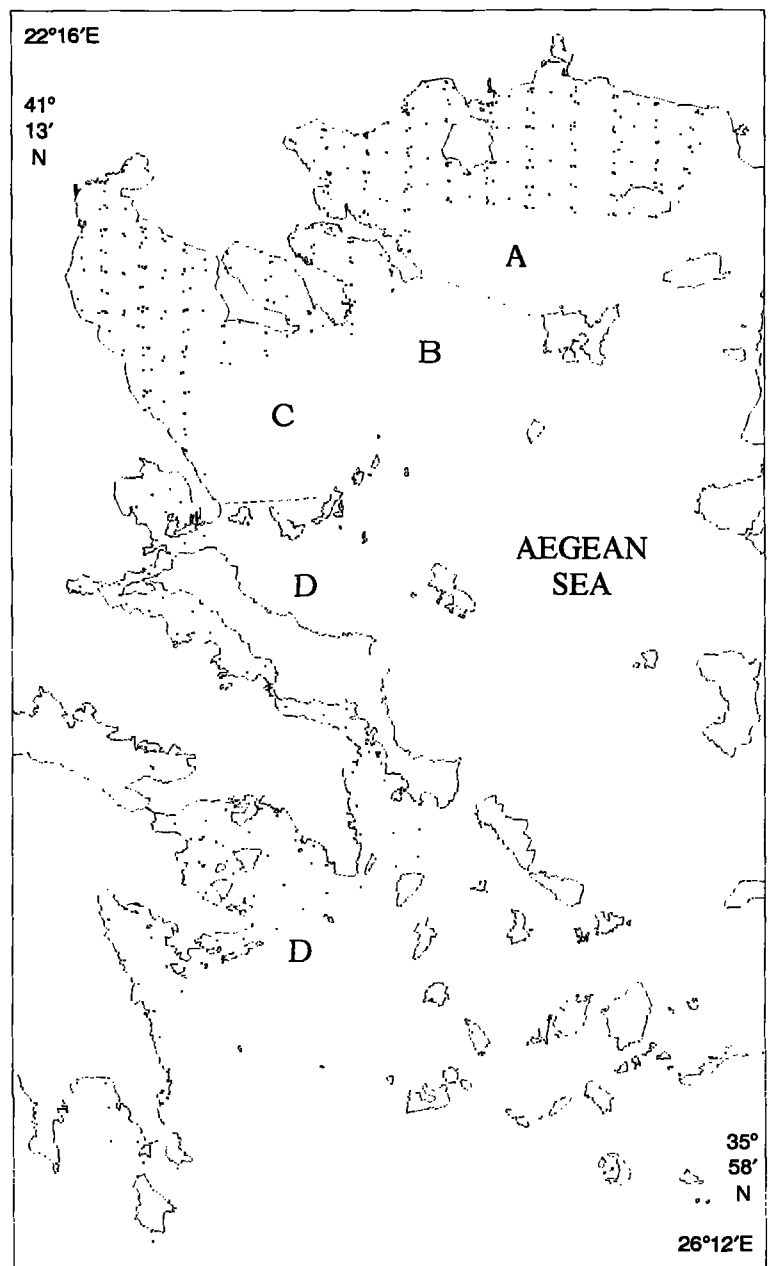
Figure 1

Map of the study area showing the location of sampling stations (black dots). A = Thracian Sea; B = Chalkidiki gulfs; C = Thermaikos Gulf; D = Gulfs of central and southeastern Greece.

sonable estimates for data sets that contain isolated large catches.

Anchovies collected during 1995 were further sorted into yolksac, preflexion, flexion, and postflexion larvae. Eye pigmentation, functional mouth, and the formation of intestine (Regner, 1985; Palomera et al., 1988; Clarke, 1989) were used to distinguish yolksac from preflexion larvae. The flexion stage begins at initial notochord flexion and ends (postflexion stage starts)

Table 1

Cruise data. Subregions A, B, C (northern Aegean Sea), and D (central-southern Aegean Sea) are indicated in Figure 1. n = number of stations. n_p = number of positive stations. D = daytime stations. N = nighttime stations. T = twilight stations.

Cruise	Date	Subregion	n	n_p	D	N	T	Mesh size (mm)	Larval abundance/m^2
92ANC1	16 Jul–3 Aug 1992	A-B-C	117	117	54	44	19	0.250, 0.500	97.25
92ANC2	3–9 Sep 1992	D	80	70	30	26	14	0.250, 0.500	21.02
93ANC3	7–14 Jul 1993	A-B-C	110	110	62	30	18	0.250, 0.500	233.91
94ANC4	19–24 Jan 1994	A-C	46	43	16	18	9	0.250, 0.335	114.55
95EP1	15–30 Jun 1995	A-B-C	121	117	65	28	24	0.250, 0.335	69.17
Total			474	457	227	146	84		

when the posterior margin of the upper hypural plate is at 90° from the notochord axis (Moser, 1996).

Additionally, to determine whether the inferences drawn regarding retention rates were plausible in terms of the "diagonal rule," we plotted maximum head width values against standard length based on measurements of 74 staged anchovy larvae (for a justification of using head width, see Colton et al., 1980). In postyolksac larvae, maximum head width was the maximum body width and was greater than any body-depth measurement (Somarakis, unpubl. data). This is not the case for yolksac larvae because of the bulk of the yolk sac. Yolk sacs, however, may be easily compressed or crushed, hence, we considered head width to be the significant dimension.

Correction for net avoidance and mortality estimates

In studies on mortality of European anchovy the usual practice has been to correct catches for net avoidance by using day:night catch ratios and the methods available for northern anchovy (e.g. Palomera and Lleonart, 1989) because catchability of European anchovy has been unknown. As a final step of this study we estimated mortality during 1994 and 1995 cruises without correcting catches for net avoidance, as well as after correction using three different methods:

Method 1   The correction for avoidance of the net during day-light was calculated by the sinusoidal function (Hewitt and Methot, 1982):

$$f1 = \frac{(1 + DN_L)}{2} + \frac{(1 - DN_L)}{2} \cos\left(\frac{2\pi t}{24}\right),$$

where DN_L = the midday-to-midnight catch ratio of L-length larvae; and
t = the hour of the tow.

DN_L data used were those available for *E. mordax*.[1]

Method 2   The same as method 1, DN_L data used were those calculated for *E. encrasicolus* in the present study.

Method 3   The sinusoidal function was not used. Length-specific ratios of day:night and twilight:night catches calculated in the present study were used to correct catches of day and twilight stations.

The correction for duration of each size class (Hewitt and Methot, 1982; Lo et al., 1989) was calculated from growth of postyolksac larvae in the sea measured by daily increments in otoliths (see also Somarakis et al., 1997a). Age-(micro-increment count)-at-length data and respective growth curves were available from 336 postyolksac larvae collected during the 1994 cruise, and 294 postyolksac larvae from the 1995 cruise. Significant spatial or interannual differences in growth of the European anchovy larvae in the Aegean Sea can be found, which cannot be explained by temperature differences (Somarakis et al., 1997a; Somarakis et al., 1997b). Thus, we estimated mortality for only the 1994 and 1995 cruises for which otolith data were available.

Mean corrected catches at length (i.e. length-specific daily production of larvae per m^2) were calculated based on the lognormal model (delta distribution—see above). Mortality was estimated for larvae >4-mm and <10-mm. The 3–3.99 size class was not used because it includes both yolksac and feeding larvae (the yolksac stage is characterized by different mortality rates than the feeding stage [Lo, 1985a; Lo, 1985b]). Mean length-specific daily production of larvae per m^2 with its age (calculated from the

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[1] Lo, N. C. H. 1996. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038. Personal commun.

respective growth curve) constituted the database for nonlinear regression estimation of instantaneous mortality rate of postyolksac larvae in a simple exponential model,

$$P_t = P_0 \exp(-zt),$$

where P_t = the daily production of larvae at age t;
t = the age in days from the end of the yolksac stage;
P_0 = the daily larval production at $t = 0$; and
z = the daily instantaneous mortality rate.

The simple exponential mortality model fitted the data very well (Watanabe and Lo, 1988).

Mortality models resulting from the application of different methods of correcting (or not correcting) catches for light-induced net avoidance were compared by an analysis of the residual sum of squares (Chen et al., 1992).
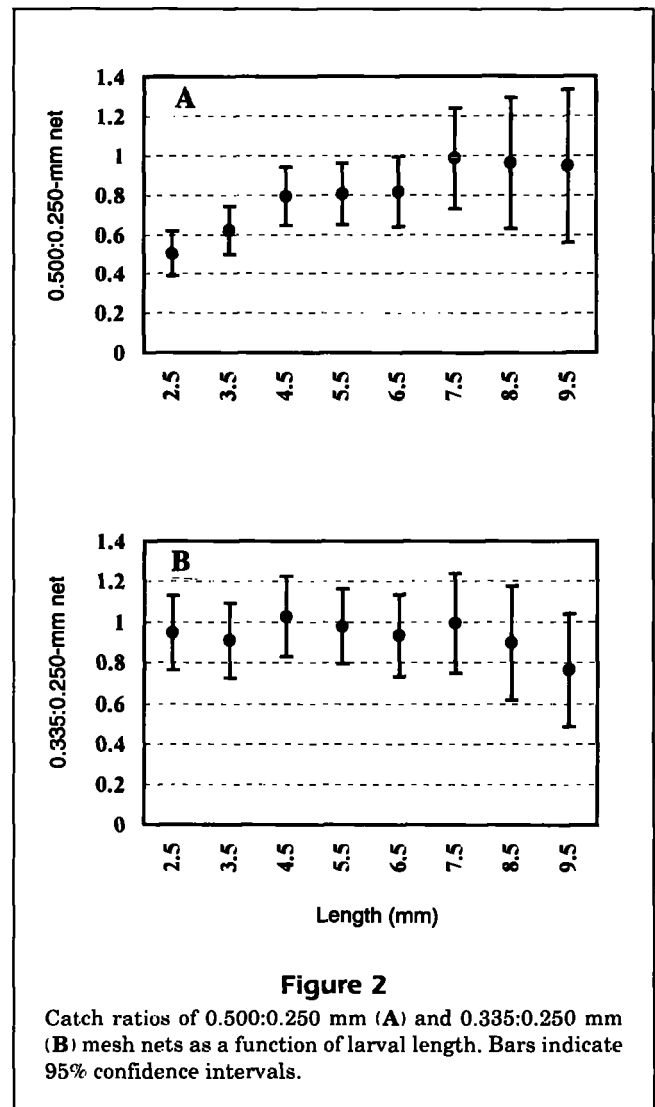
Results

Estimates of mean catch

No larvae >12-mm were caught in any of the 227 day-time tows. Estimates of mean catch per length group (Table 2) indicated that catches of >10-mm larvae were very low and their coefficients of variation too great (generally >20%) to be useful in this study. Thus, our analysis was restricted to larvae <10-mm (see also Lenarz, 1972).

Retention of anchovy larvae in the 0.335- and 0.500-mm mesh nets

Results of the catch analysis indicate that the 0.500: 0.250-mm mesh catch ratio was less than one for larvae <7 mm but the 0.335:0.250-mm mesh ratio was not significantly different from one, at any length (Fig. 2).

Data of maximum head width against standard length of the 74 anchovy larvae, along with the mesh diagonals of 0.500-, 0.335-, and 0.250-mm, are presented in Figure 3. A comparison of head-width measurements with mesh diagonals indicates that the minimum lengths for complete retention in the 0.500- and 0.335-mm mesh nets were approximately 7.5 and 3.5 mm, respectively. The head-width measurements further suggest that to ensure full retention of larvae, it would be necessary to use netting with a mesh aperture of 0.250 mm or less. In terms of ontogenetic stages, the 0.335-mm mesh net is expected to retain all except the yolksac larvae, whereas the 0.500-mm mesh net seems to be inefficient for yolksac and

Figure 2

Catch ratios of 0.500:0.250 mm (A) and 0.335:0.250 mm (B) mesh nets as a function of larval length. Bars indicate 95% confidence intervals.

preflexion larvae. It therefore appears that the "diagonal rule" is conservative for yolksac larvae of the European anchovy, when head width is used as the maximum cross-sectional diameter of the larva.

Differences in day versus night and twilight versus night catches

Results of the catch analysis show a change in the day:night and twilight:night catch ratios at $L = 6.5$ mm (Fig. 4). In general, both ratios are practically one for larvae <6 mm, at which point they drop substantially, continuing to decrease more or less linearly thereafter. This decrease is stronger for the day:night than for the twilight:night catch ratio, the day:night ratio being significantly less than one from 6 mm onwards and greater than the corresponding twilight:night ratio. Thus, for larvae >6 mm, it seems

Table 2

Estimates of mean catch and their coefficients of variation (in parentheses), by length class.

	Length (mm)									
	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5
0.500:0.250										
0.500	0.419	0.378	0.323	0.264	0.187	0.136	0.078	0.054	0.020	0.012
	(0.079)	(0.067)	(0.062)	(0.064)	(0.072)	(0.082)	(0.115)	(0.131)	(0.200)	(0.248)
0.250	0.836	0.607	0.408	0.329	0.230	0.139	0.080	0.056	0.021	0.012
	(0.084)	(0.071)	(0.069)	(0.072)	(0.080)	(0.101)	(0.128)	(0.156)	(0.233)	(0.306)
0.335:0.250										
0.335	0.581	0.453	0.438	0.325	0.225	0.182	0.098	0.062	0.023	0.013
	(0.067)	(0.067)	(0.068)	(0.064)	(0.077)	(0.089)	(0.109)	(0.132)	(0.201)	(0.249)
0.250	0.614	0.498	0.427	0.332	0.241	0.184	0.109	0.082	0.024	0.015
	(0.068)	(0.076)	(0.068)	(0.069)	(0.074)	(0.085)	(0.110)	(0.124)	(0.232)	(0.287)
day:night and twilight:night										
day	4.008	2.900	2.047	1.582	0.890	0.587	0.326	0.201	0.059	0.043
	(0.067)	(0.072)	(0.075)	(0.082)	(0.093)	(0.107)	(0.132)	(0.167)	(0.297)	(0.335)
night	4.002	2.775	2.090	1.512	1.352	1.003	0.623	0.496	0.221	0.099
	(0.085)	(0.087)	(0.088)	(0.102)	(0.101)	(0.111)	(0.129)	(0.145)	(0.191)	(0.280)
twilight	3.864	3.098	2.322	1.683	1.146	0.748	0.454	0.319	0.161	0.101
	(0.115)	(0.113)	(0.114)	(0.114)	(0.129)	(0.156)	(0.186)	(0.217)	(0.319)	(0.397)

that catchability changes with varying light conditions and length. On the other hand, the "sudden" change in catchability at 6.5 mm coincides with the onset of the development of the tail, i.e. the flexion stage (Fig. 5).

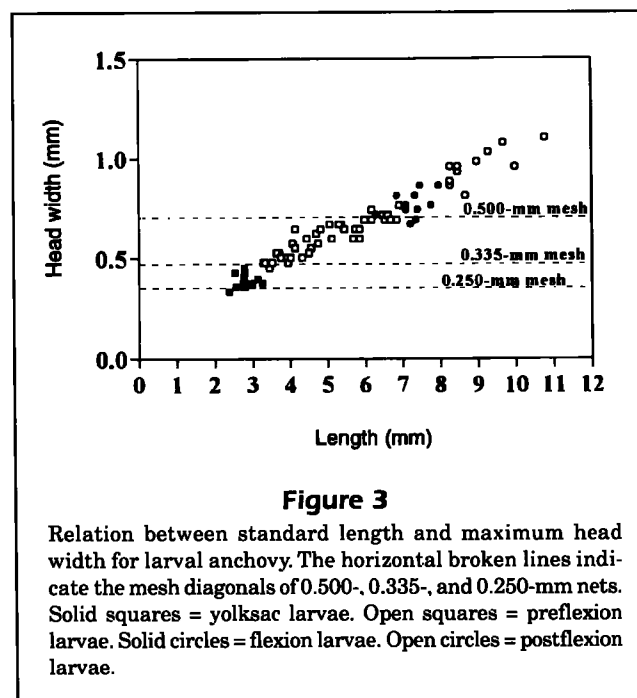## Correction for avoidance and its effect on mortality estimates

Estimates of length-specific larval production for the 1994 and 1995 cruises obtained by using the three different methods of adjusting data for net avoidance, or without any correction, were very similar (Table 3). Method 1, which was based on length-specific day:night catch ratio values calculated for *Engraulis mordax*, gave slightly greater values for larvae 4–6 mm, although differences were not statistically significant (overlapping confidence intervals).

Consequently, analyses of the residual sum of squares showed that the resulting mortality curves (Table 4) were not statistically different (1994: $F=$ 0.361, $P>0.5$; 1995: $F=0.780$, $P>0.5$).
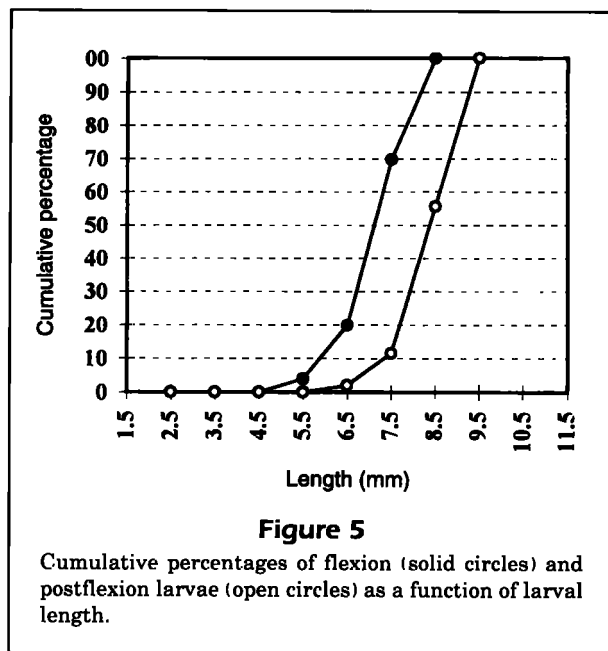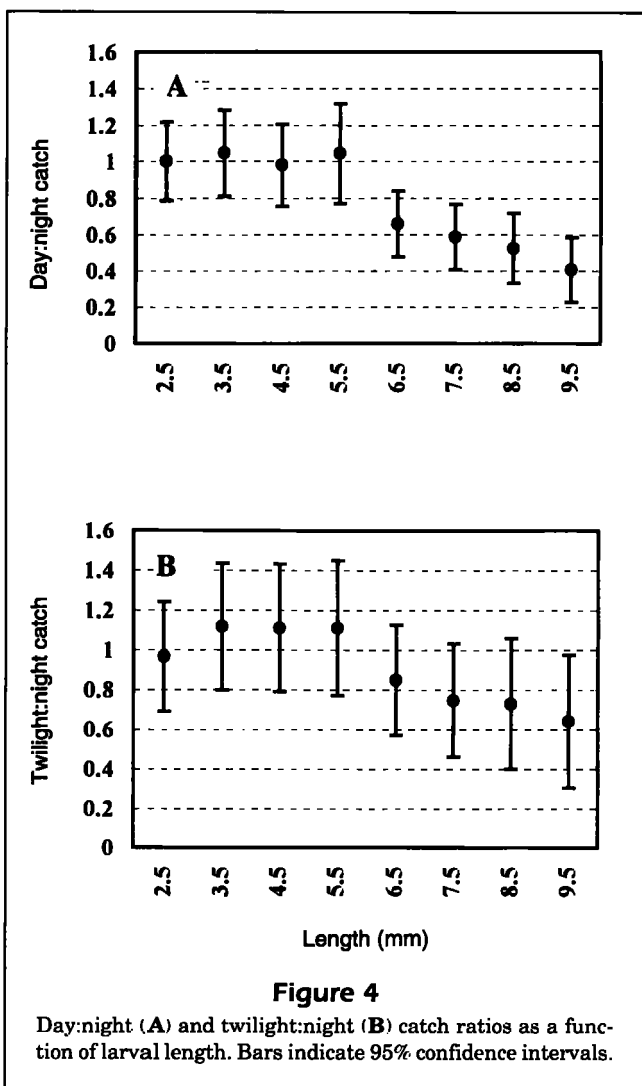

Figure 3

Relation between standard length and maximum head width for larval anchovy. The horizontal broken lines indicate the mesh diagonals of 0.500-, 0.335-, and 0.250-mm nets. Solid squares = yolksac larvae. Open squares = preflexion larvae. Solid circles = flexion larvae. Open circles = postflexion larvae.

Discussion

Retention of larvae

The results of this study indicate that the "diagonal rule" (maximum head width being considered as the

maximum cross-sectional diameter of the larva) may adequately "predict" retention of anchovy larvae in the 0.500-mm mesh net but appears to be conservative in the case of the 0.335-mm mesh net. Specifically, yolksac larvae have a smaller head width than the diagonal of the 0.335-mm mesh net, but the latter seems to fully

Figure 4

Day:night (A) and twilight:night (B) catch ratios as a function of larval length. Bars indicate 95% confidence intervals.

Figure 5

Cumulative percentages of flexion (solid circles) and postflexion larvae (open circles) as a function of larval length.

retain them. This is attributable to the fact that maximum head width is not the maximum cross-sectional diameter of the larva, because of the bulk of the yolk sac. Our method of towing (at low speed, with plastic codend buckets) did not seem to cause damage to yolk sacs and resulted in full retention of yolksac larvae by the 0.335-mm mesh. However, the degree of extrusion strongly depends on filtration velocity (Smith and Richardson, 1977; Colton et al., 1980). Thus, at high towing speeds yolk sacs may easily be crushed.

In his study on anchovy, Lenarz (1972) used depth of body at the insertion of the pectoral fin as the critical dimension to compare with mesh diagonal and concluded that the mesh "diagonal rule" was too conservative in the case of slowly towed nylon nets. However, body depth is not the critical dimension for clupeoids (Colton et al., 1980). The latter found no differences related to mesh size (0.253- and 0.333-mm mesh nets) in the length frequency distributions and

abundances of larval herring in their collections at 1.5-knot towing speed. The mesh "diagonal rule" (with skull width as the critical dimension) was also conservative in their case, but for the length interval including only yolksac larvae. They found that most yolksac larvae caught in their slowly towed bongo nets, which were also equipped with plastic codend buckets, were undamaged.

We feel that at a low, constant towing speed (1.5–2.0 knots), bongo nets equipped with a 0.335-mm mesh net and plastic codend buckets are very efficient in retaining larvae of clupeoids.

Net avoidance

Changes in catchability with varying light conditions and larval length are demonstrated in this study. These changes begin at notochord flexion. If visual detection of the net is the primary cue for net avoidance, flexion and postflexion European anchovy larvae show the expected relationship of night>twilight>day catches (Morse, 1989).

In another study, Murphy and Clutter (1972) compared catches of larval Hawaiian anchovy (*Stolephorus purpureus*) taken by conventional towed conical nets with catches taken by a miniature purse seine constructed of the same netting. The latter was considered to be a more effective sampler of the full size range of anchovy larvae than towed nets. In a way similar to the present study, larvae <6 mm long were captured with approximately equal efficiency by both the towed net and the seine (i.e. these larvae did not seem to avoid the towed net). For larger lar-

Table 3

Estimates of length-specific larval production for the 1994 and 1995 cruises (and their standard errors in parentheses) with different methods of adjusting data for net avoidance. Method 1 is based on day:night catch ratio values available for *Engraulis mordax*, and methods 2 and 3 are based on day:night and twilight:night values calculated in the present study (see text for details).

Cruise	Correction	Length (mm)					
		4.5	5.5	6.5	7.5	8.5	9.5
1994	none	1.984	1.655	1.169	0.893	0.518	0.413
		(0.198)	(0.198)	(0.139)	(0.127)	(0.110)	(0.093)
	method 1	2.142	1.793	1.281	0.972	0.569	0.450
		(0.214)	(0.212)	(0.152)	(0.138)	(0.121)	(0.102)
	method 2	1.984	1.655	1.231	0.944	0.553	0.445
		(0.198)	(0.198)	(0.146)	(0.134)	(0.118)	(0.101)
	method 3	1.984	1.655	1.258	0.979	0.573	0.475
		(0.198)	(0.198)	(0.150)	(0.140)	(0.122)	(0.109)
1995	none	1.537	1.235	0.928	0.690	0.472	0.341
		(0.111)	(0.090)	(0.080)	(0.071)	(0.052)	(0.046)
	method 1	1.721	1.409	1.076	0.722	0.559	0.399
		(0.029)	(0.015)	(0.058)	(0.045)	(0.046)	(0.047)
	method 2	1.537	1.235	1.009	0.681	0.531	0.390
		(0.111)	(0.090)	(0.086)	(0.062)	(0.057)	(0.051)
	method 3	1.537	1.235	1.026	0.706	0.549	0.412
		(0.111)	(0.090)	(0.087)	(0.064)	(0.059)	(0.054)

vae, the efficiency of the towed net decreased with larval length relative to the seine.

The change in catchability at flexion, observed in our study, can be attributed to a change in the swimming ability of larvae, which is associated with flexion. Batty (1984) found that Atlantic herring larvae, as they grow, change from an anguilliform mode of swimming to a subcarangiform mode of swimming. This change of swimming mode occurs as the caudal fin develops (at a body length of about 22 mm). Subsequently, Heath and Dunn (1990) using the large (5 m²), high-speed LOCHNESS sampler, found that the day:night catch differential increased with body length for larval herring in the North Sea, with a maximum fivefold difference between day and night catches for larvae >25mm. In another study, Osse and van den Boogaart (1995) reported results similar to those of Batty (1984) for common carp (*Cyprinus carpio*). The morphological differentiation of the caudal fin, which begins at flexion and is accompanied by ossification of the caudal-fin rays and the caudal part of the notochord, closely parallels a change in the swimming mode from anguilliform to carangiform. Burst-speed capability, which is believed to determine, in part, the ability of a larva to avoid plankton nets (Hunter, 1976), might also change with the development of the tail.

Table 4

Estimated parameters of the exponential mortality models $(P_t = P_0 \exp(-zt))$ for the 1994 and 1995 cruises. A different model was fitted for each different method of adjusting data for net avoidance (see text for details). r^2 = coefficient of determination.

Cruise	Correction	P_0	z	r^2
1994	none	2.931	0.143	0.980
	method 1	3.156	0.142	0.979
	method 2	2.872	0.135	0.979
	method 3	2.832	0.131	0.978
1995	none	2.195	0.136	0.992
	method 1	2.463	0.135	0.989
	method 2	2.139	0.126	0.989
	method 3	2.109	0.121	0.989

Alternatively, changes in catchability may have a behavioral component. A substantial change in day:night catches of northern anchovy (*Engraulis mordax*) with bongo nets occurs at approximately 11 mm (Fig. 2 in Hewitt and Methot, 1982). Flexion in this species occurs at around 11 mm (Watson and Sandknop, 1996). Laboratory and field studies (Hunter and Sanchez, 1976; Hewitt, 1981; Hunter

and Coyne, 1982) have shown that, at about 11 mm, swimbladder inflation and schooling begins, whereupon patchiness increases rapidly. Our field observations of European anchovy indicate initiation of swimbladder inflation at flexion. It is therefore possible that schooling behavior also begins during this stage in *E. encrasicolus.*

School formation during the day and dispersion of schools during the night could result in low day:night catches for two main reasons: 1) larvae are less vulnerable to plankton nets when in a school than when reacting individually, owing to the reduction in the reaction distance of the organisms in the school to the approaching net; and 2) increased patchiness resulting from schooling during the day produces a larger number of negative tows.

In summary, field data on the European anchovy suggest the existence of an ontogenetic change in catchability with slowly towed plankton nets, which can be attributed to a respective change in the swimming ability, or a change in behavior (i.e. onset of schooling), or both.

To our knowledge, the present study is the first to examine retention and catchability in a larval fish not only in terms of length but also of ontogeny. Surprisingly, this study also shows that, when sampling is undertaken on a 24-h basis, bias that results from light-induced avoidance of the net may not be great enough to affect significantly estimates of daily larval production or larval mortality. However, when only daytime sampling is undertaken, mean catches of postflexion larvae may well be biased and correction factors may have to be applied.

Size selectivity due to net avoidance by larvae is expected to lead to an overestimation of mortality rate, because older larvae are underrepresented in relation to younger larvae. In a recent simulation study, Somerton and Kobayashi (1992) have shown that approaches usually taken to eliminate the selection bias from sampled length frequencies (i.e. division of sampled length frequencies by length-specific estimates of capture probability or elimination of the biased portion of the length distribution) may be only partially effective in reducing the bias in estimated mortality rates. The latter, as well as the present paper, suggests that the effectiveness of methods that attempt to correct for net avoidance is largely unknown. Their effectiveness has to be fully addressed.

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