Influence of release season on size-dependent survival of cultured striped mullet, *Mugil cephalus*, in a Hawaiian estuary

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Abstract.–The concept that depleted populations of marine fishes can be revitalized by releasing cultured fish is being tested in Hawaii. In this study we evaluated effects of interaction between release season and size-at-release on recapture rates of cultured striped mullet, *Mugil cephalus*, released into Kaneohe Bay, Hawaii. Over 90,000 cultured *M. cephalus* fingerlings, ranging in size from 45 to 130 mm total length, were tagged with binary coded-wire tags. Half were released in spring, the remainder in summer. In both seasons, releases were made in three replicate lots. In each replicate, five size intervals of fish were released at two nursery habitats in Kaneohe Bay. Monthly cast-net collections were made in 6 nursery habitats over a 45-week period to monitor recapture rates, growth, and dispersal of cultured fish.

Recapture rate was directly affected by the seasonal timing of releases. Greatest recovery of the smallest fish released (individuals <60 mm) occurred following spring releases and coincided with peak recruitment of similar-size wild *M. cephalus* juveniles. In contrast, recovery of fish that were <60 mm at release was very poor after summer releases. Overall survival was similar at both release sites. We hypothesize that survival of released cultured fish will be greater when releases are timed so that fish size-at-release coincides with modes in the size structure of wild stocks. To optimize effectiveness of stock enhancement as a fishery-management tool, pilot release-recapture experiments should be conducted to evaluate effects of release season on size-dependent recovery of released animals.

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With world fisheries yields in steady decline (FAO, 1992, 1994; WRI, 1996), renewed interest in stock enhancement based on marine hatchery-releases is growing worldwide. This interest follows the demonstrated impact of stock enhancement in freshwater systems (e.g. Foerster, 1936; Solazzi et al., 1991) and is coupled with rapidly expanding marine aquaculture technology (Colura et al., 1976; Roberts et al., 1978; Øiestad et al., 1985; Lee and Tamaru, 1988; Eda et al., 1990; Forés et al., 1990; Tilseth and Blom, 1992; Honma, 1993; Main and Rosenfeld, 1994; Ostrowski et al., 1996).

An experimental and careful approach is needed to ensure that hatchery releases in marine systems result, at best, in successful supplementation or replenishment of marine fish populations, or, at least, in a better understanding of system uncertainty (Peterman, 1991; Blankenship and Leber, 1995). This approach should involve an initial research phase with pilot releases to explore the effectiveness of release strategies. Before initiating a test release to evaluate stock-enhancement potential in Hawaiian coastal environments, initial research was focused on a series of release experiments to determine which release strategies yielded greater survival of hatchery fish in the wild. This approach provided a more powerful field test of the marine stock-enhancement concept by using prior knowledge about the effects of 1) fish size-at-release, 2) release habitat, and 3) release season on growth and survival (Cowx, 1994; Blankenship and Leber, 1995; Leber et al., 1996).

Evidence is mounting that release habitat, season, and size-at-release, can substantially affect success of marine hatchery releases (e.g. Tsukamoto et al., 1989; Svasand

and Kristiansen, 1990; Stoner, 1994; Leber, 1995; Willis et al., 1995). Pilot releases have shown that survival rates following hatchery releases of striped mullet, *Mugil cephalus*, in Hawaii (Leber and Arce, 1996; Leber et al.[1]) and of queen conch, *Strombus gigas*, in the Caribbean (Stoner, 1994) were strongly affected by release habitat. Pilot releases with *M. cephalus* have also shown differential survival based on size-at-release. Pilot releases conducted during summer and fall in Maunalua Bay, Hawaii, (southern exposure) and during summer in Kaneohe Bay (eastern, windward exposure) have shown poor survival of cultured *M. cephalus* smaller than 70 mm total length (TL) at the time of release, compared with survival of larger-size individuals (e.g. 70 to 130 mm TL, Leber, 1995). In this study, we document a substantial effect of the seasonal timing of releases upon size-at-release–dependent recapture rates (number recaptured/number released) of cultured *M. cephalus*.

Materials and methods

Hatchery releases

Striped mullet were spawned at The Oceanic Institute in 1991 and reared to fingerling size. Batches of striped mullet eggs were hatched approximately every 5–6 weeks over a 5-month period and reared through three stages in cylindrical tanks. Larvae from each batch were hatched and cultured in 5,000-L conical-bottom tanks for 45 days. Stage-1 juveniles (i.e. postlarvae 45 days old, 20 mm total length [TL]) were transferred to 8,000-L tanks and reared for 40 days to stage-2 juveniles (i.e. the age and size at which we typically transfer fish out of nursery tanks into larger growout tanks, 85 days old, around 40 mm TL). Stage-2 juveniles were transferred to 30,000-L tanks and reared to tagging size (45 to 130 mm TL).

A factorial-design release-recapture experiment was performed to compare interactive effects of release season and fish size-at-release upon growth and survival of about 90,000 cultured striped mullet in the wild. During the period 5 May through 17 May 1991, and again from 12 July through 26 July 1991, juvenile striped mullet, ranging in size from 45 to 130 mm TL, were harvested from culture tanks and transferred to 40,000-L holding tanks. These fish were graded into five size groups, tagged, then released into Kaneohe Bay; half were released in May, the other half in July.

To identify experimental treatment conditions, all released fish were tagged with binary coded-wire tags (Jefferts et al., 1963). Tags identified release season, release site, size-at-release (SAR), release lot (date), and number of fish per treatment condition. Fish were tagged in batches, with a different code for each season-site and SAR-lot combination (2×2×5×3=60 batch codes). The five size groups released were 45–60 mm; 60–70 mm; 70–85 mm; 85–110 mm; and 110–130 mm TL.

Tags were implanted in the snout area with an automatic injector with head molds designed specifically for striped mullet. Previous studies have shown a coded-wire tag retention rate of 97% for striped mullet over a 6-month period (Leber, 1995). To verify tag-retention rates in this study, at least 5% of the fish tagged for each release lot were randomly subsampled prior to each release. The subsamples were retained in tanks for up to 6 months to check tag retention. Subsampled fish were not released.

Release statistics

During May and July 1991, 90,817 juvenile striped mullet were tagged and released into Kaneohe Bay. Numbers of fish released varied among size groups but were held nearly constant among release lots and between release sites and seasons (Table 1). At least 7,500 tagged fish were released in each of 12 release lots. There was size variation in all batches of mullet reared for this study. However, the primary difference among size-at-release groups was fish age.

For each season and SAR treatment combination, the experiment was replicated at two sites in Kaneohe Bay, and within each site, three replicate release lots were made (Table 1). The release lots were introduced into the bay over a 3-week period during both seasons (spring and summer). In each season, releases were made simultaneously at the inlets of two primary striped mullet nursery habitats, Kahaluu Stream and Kaneohe Stream. Kahaluu Stream is located in the north end of Kaneohe Bay (Fig. 1). This tributary is fed by several stream systems that originate in the Ko'olau mountain range. Kahaluu Stream expands into a lagoon about 300 m upstream. The mouth of Kaneohe Stream is 11.6 km southeast of Kahaluu Stream. Kaneohe Stream is also a Ko'olau mountain drainage system. Selection of release habitats in the vicinity of fresh-water tribu-

[1] Leber, K. M., D. A. Sterritt, R. N. Cantrell, and R. T. Nishimoto. In press. Contribution of hatchery-released striped mullet, *Mugil cephalus*, to the recreational fishery in Hilo Bay, Hawaii. *In* K. Lowe (ed.), Proceedings of the first biennial symposium for the Main Hawaiian Islands Marine Resources Investigation. Technical Rep. 96-01. Hawaii Department of Land and Natural Resources, Division of Aquatic Resources, Honolulu, HI.

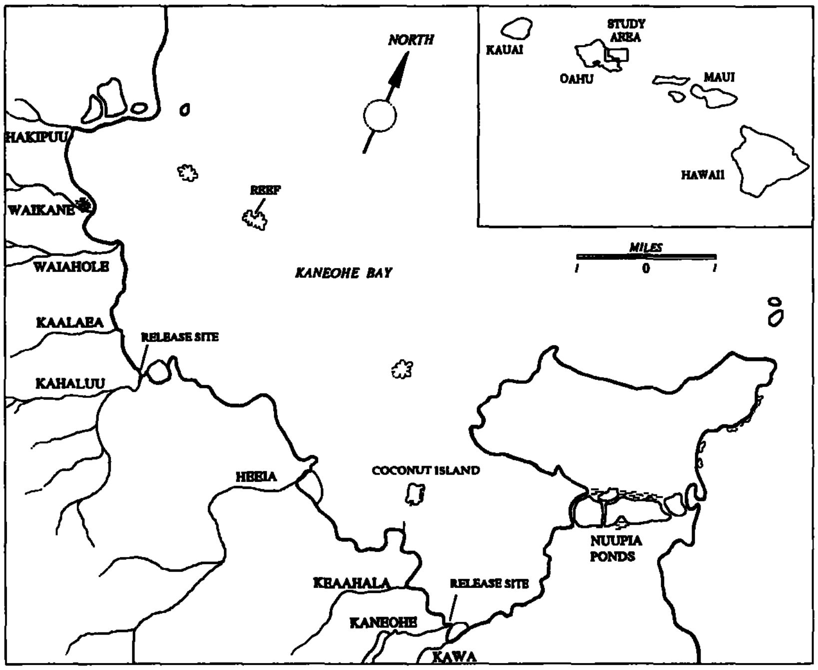

Figure 1

Map of the study area in Kaneohe Bay. Releases were conducted near the mouths of Kahaluu Stream and Kaneohe Stream. Recapture collections were conducted in streams throughout the Bay and on reef flats in the vicinity of stream mouths.

Table 1

Summary statistics for 90,817 striped mullet, *Mugil cephalus*, tagged and released in the 1991 pilot experiment to evaluate release-season effects on hatchery releases in Kaneohe Bay. Unique batch codes were used to identify fish from each cell in the matrix. Spring release lot 1 occurred on 3 May, lot 2 on 10 May, and lot 3 on 17 May. Summer release lot 1 occurred on 12 July, lot 2 on 19 July, and lot 3 on 26 July.

		Release season							
		Spring				Summer			
		Release lot				Release lot			
Release site	Size at release	1	2	3	Total	1	2	3	Total
Kahaluu Stream	45–60 mm	2,090	2,090	2,088	6,268	2,081	2,058	2,084	6,223
	60–70 mm	2,090	2,089	2,087	6,266	2,082	2,090	2,085	6,257
	70–85 mm	2,054	2,090	2,090	6,234	2,084	2,088	2,085	6,257
	85–110 mm	1,119	959	990	3,068	1,128	956	1,296	3,380
	110–130 mm	150	323	386	859	151	323	76	550
	Subtotal	7,503	7,551	7,641	22,695	7,526	7,515	7,626	22,667
Kaneohe Stream	45–60 mm	2,065	2,087	2,089	6,241	2,281	2,088	2,001	6,370
	60–70 mm	2,070	2,089	2,088	6,247	2,044	2,086	2,086	6,216
	70–85 mm	2,088	2,090	2,088	6,266	2,047	2,088	2,090	6,225
	85–110 mm	1,127	958	990	3,075	1,152	959	1,298	3,409
	110–130 mm	147	323	386	856	151	323	76	550
	Subtotal	7,497	7,547	7,641	22,685	7,675	7,544	7,551	22,770
Grand total		15,000	15,098	15,282	45,380	15,201	15,059	15,177	45,437

taries was based upon results from earlier releases (Leber, 1995; Leber and Arce, 1996; Leber et al.[1]) where release habitat appeared to be critical to survival.

All releases were conducted at about noon or early afternoon. The successive weekly release lots spanned the rising tide (lot 1 on a low tide; lot 2 on a rising tide; lot 3 on a low tide in both seasons). Releases were made near the shoreline in water from 0.5 to 1.5 m deep. There was a wider range of salinities at the southernmost site (Kaneohe Stream; Table 2).

Monitoring

Beginning 21 May 1991, we monitored abundances of hatchery-released and wild *Mugil cephalus* in Kaneohe Bay monthly for 11 months by sampling with cast nets. Recaptured tagged fish were removed from collections and returned to the laboratory for tag analysis. The first field collection after spring and summer releases began 2 weeks after the middle release lot (lot 2) was planted.

Each monthly collection was conducted over approximately a 2-week period. Collections were made at six nursery sites (sampling stations) within Kaneohe Bay. Collections were made for about an 8-hr period during the day at each sampling station. Stations were established in the vicinity of documented striped mullet nursery habitats at various tributaries located throughout the bay (Leber, 1995; six streams in Fig. 1: Waiahole, Kaalaea, Kahaluu, Heeia, Keaahala, and Kaneohe Streams).

To standardize collection effort, at each station two substations were sampled—one substation was established upstream, the other near the mouth of the tributary. Within substations, 15 cast net throws were made. To broaden the range of microhabitats and fish size-ranges sampled, two sizes of cast nets were employed. Ten of the 15 casts per substation were made with a 5-m diameter, 10-mm mesh net, and 5 casts were made with a 3-m diameter, 6-mm mesh net. Thus, a total of 180 casts were made each month.

Placement of net samples was stratified over observed schools of striped mullet juveniles. Completely random sampling in preliminary collections yielded few wild striped mullet and very few tagged individuals. Striped mullet schooled in fairly low densities within these clear-water nursery habitats, and our stratified-random collections targeted those schools. Nevertheless, the sample data used to determine proportions of tagged versus untagged mullet were randomly distributed because we had no a-priori indication that schools, once sighted, contained tagged individuals.

All striped mullet sampled were measured and checked for tag presence with a field-sampling detector (Northwest Marine Technology, Inc., Shaw Island, WA). Tagged fish were placed on ice and returned to the laboratory where the tags were recovered, and each fish was weighed and measured. Untagged fish were held at the field site in oxygenated water and then released after the 30 cast-net samples were completed.

Treatment identifications were made on the basis of the tags retrieved from recaptured fish. In the labora-

Table 2

Physical data recorded at the two release sites in Kaneohe Bay, Kahaluu Stream and Kaneohe Stream, for each release lot (release date) of striped mullet, *Mugil cephalus*. IN = incoming.

Season and release site (stream)	Release date	Tide stage	Secchi (cm)	Depth (cm)	Temperature (°C)		Salinity (‰)	
					Top	Bottom	Top	Bottom
Spring								
Kahaluu	5/03/91	IN 0.2'	51	59	33	32	11	12
Kaneohe	5/03/91	IN 0.5'	110	120	27	27	6	32
Kahaluu	5/10/91	IN 0.8'	70	75	29	26.5	15	27
Kaneohe	5/10/91	IN 1.6'	92	92	26	27	4	35
Kahaluu	5/17/91	IN 0.0'	25	40	29	29	24	26
Kaneohe	5/17/91	IN 0.0'	55	80	28	28.2	3	15
Summer								
Kahaluu	7/12/91	IN 0.8'	57	57	27.5	28	11	28
Kaneohe	7/12/91	IN 0.8'	75	122	27	27	11	35
Kahaluu	7/19/91	IN 1.6'	85	100	25.3	27	10	19
Kaneohe	7/19/91	IN 1.7'	115	115	26	27	4	35
Kahaluu	7/26/91	IN 0.7'	40	70	27.6	28	12	20
Kaneohe	7/26/91	IN 0.9'	65	90	26.2	26.5	6	34

tory, tags were located and extracted with a field-sampling detector. Tags were decoded by using a binocular microscope (at 40×). To verify tag codes, each tag was read twice (once each by two different research assistants).

Data were analyzed with Systat (Wilkinson, 1990). A randomized-block factorial analysis of variance (ANOVA) was used to compare means. Systat Basic was used to write tag decoding algorithms. For each recaptured fish, the algorithms identified batch size, release date (lot), release site, size-at-release, and release season from the tag codes identified in the laboratory. An error-check algorithm was also written to help identify errors that may have been made in reading tag codes. Variance estimates are expressed throughout as standard errors (with n=number of release lots).

Results

Tag retention

Tag retention in 4,799 individuals subsampled and held in tanks for six months averaged 98.6% (0.4% SE). With one exception (92.4%), all retention rates within release lots exceeded 97%. No significant tag loss was observed in any group later than 1 month after tagging. This is a normal tag loss rate for coded-wire tags (Blankenship, 1990).

Recapture summary

Of the fish released, 2,511 cultured striped mullet were recaptured in monthly cast-net samples at nursery habitats. Based on the 98.6% average tag retention rate, the number of cultured fish recaptured can be extrapolated to 2,546, or 2.8% of the fish released. About 6.6% (166) of the tags taken from the 2,511 recaptured fish were lost during extraction.

Total number of tagged fish in samples decreased over the 11-month monitoring (Table 3) but was fairly constant during the last 7 months of the study (when numbers of tagged fish ranged from 49 to 134 individuals). Total number of tagged fish collected was greater at Kaneohe Stream. However, this pattern varied considerably from month to month, and most of those fish were collected within 1 month after the May and July releases.

Tagged fish represented between 8% and 48% of the striped mullet captured in monthly samples (from all stations combined; Table 3). Percentage of cultured fish in samples was greatest at Kaneohe Stream, where contribution rates declined from 76% following the May release to 41% by the end of the study. Although numbers of tagged fish collected at Kahaluu Stream were often similar to those for Kaneohe Stream, there were always greater numbers of wild fish in collections at Kahaluu Stream (Table 3).

Impact of release season

Recapture rates and contribution rates When size-at-release was not considered, the contribution of cultured fish to recruitment appeared to be unaffected by release season. Release season had no significant effect on mean recapture rates over time (ANOVA, P>0.54, data from all size-at-release intervals combined). After 3 months in the wild, mean numbers of cultured fish in samples varied between

Table 3

Numbers of wild and hatchery-released striped mullet, *Mugil cephalus*, recovered in cast-net samples made in Kaneohe Bay. Proportions of hatchery fish were determined by the presence of a coded wire tag.

		1991								1992					
Collection site	Source	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Total	Mean	Standard Error
All stations in Kaneohe Bay	Wild	985	1,099	1,439	453	659	722	952	550	824	864	310	8,857	805.2	95.7
	Hatchery	912	194	551	184	101	117	134	76	116	77	49	2,511	228.3	79.9
	% Hatchery	48.1	15.0	27.7	28.9	13.3	14.0	12.3	12.1	12.3	8.2	13.6		18.7	3.5
Kahaluu Stream (Release site in N. Kaneohe Bay)	Wild	265	201	303	137	260	318	331	158	350	184	134	2,641	240.1	24.3
	Hatchery	184	122	237	25	20	56	91	25	46	15	18	839	76.3	22.7
	% Hatchery	41.0	37.8	43.9	15.4	7.1	15.0	21.6	13.7	11.6	7.5	11.8		20.6	4.1
Kaneohe Stream (Release site in S. Kaneohe Bay)	Wild	207	87	264	88	44	85	115	52	85	87	41	1,155	105.0	20.9
	Hatchery	653	64	270	135	43	52	35	45	55	45	28	1,425	129.5	56.5
	% Hatchery	75.9	42.4	50.6	60.5	49.4	38.0	23.3	46.4	39.3	34.1	40.6		45.5	4.2

about 10 and 27 individuals per release lot throughout 36 weeks (Fig.2). However, as shown below, recapture rate was in fact dependent upon the interactive effect of release season and size-at-release. (Note: for evaluating the effect of release-season, data can be compared only through weeks 35 or 36 following releases, the length of time fish were monitored after summer releases; by the end of the study, fish released in the spring had been in the wild for an average of 45 weeks, 10 weeks longer than those released in summer.)

Dispersal patterns There were no clear seasonal trends in dispersal patterns. Cultured striped mullet showed a strong tendency to remain in the vicinity of release sites, regardless of release season or size-at-release. Few of the 2,511 tagged fish recovered in samples had moved into other nursery habitats in the bay. The only significant movements observed were from release habitats into the streams located immediately to the north of each release site (Table 4). This pattern was repeated after spring and summer releases. There were isolated cases of fish moving from one release habitat to the other, as well as movement from release habitats into other nursery habitats in the bay. But the magnitude of dispersal out of release habitats and beyond the streams immediately north of those sites was negligible. Overall, 90.8% ± 3.1% (SE) of the cultured fish collected through 36 weeks in the wild were recovered at the nursery habitats into which they had been released.

Growth Growth after spring releases was similar to growth following summer releases. Length increase following releases is plotted in Figure 3 for fish from the 70–85 mm treatment group, which was representative of all 5 size-at-release groups. There was little change in mean length during winter months (from September 1991 through February 1992; weeks 20–45 following spring releases in Fig. 3).

Release season effect on recapture frequencies among size-at-release groups Recapture frequencies ([number recaptured / number released] × 100%) within size-at-release intervals revealed an obvious

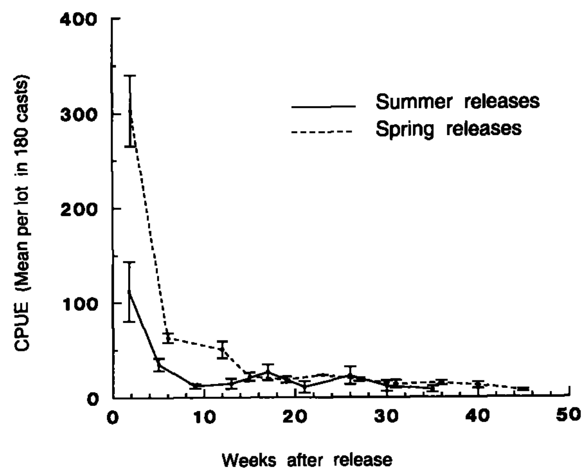

Figure 2

Mean number of tagged cultured fish in samples following spring and summer releases into Kaneohe Bay. Data are means per release lot (± standard error [SE]; n = 6 lots per season [3 at each release site]).

Table 4

Movement patterns following 1991 releases in Kaneohe Bay. Release season and release site are identified for tagged fish recovered at the various collection (recapture) sites throughout the Bay. Recapture sites (and distances travelled) are ordered geographically within collection dates, from the northernmost site (Waiahole Stream) to the southernmost site (Kaneohe Stream) at which tagged fish were collected (see Fig. 1). Totals for spring releases represent those through week 36; totals for summer releases are those through week 35. To compare results between release seasons over a similar time frame, data are excluded for weeks 40 and 45 after spring releases.

Release season and recapture site	Kahaluu Stream n	Kahaluu Stream Distance (km)	Kaneohe Stream n	Kaneohe Stream Distance (km)	Release season and recapture site	Kahaluu Stream n	Kahaluu Stream Distance (km)	Kaneohe Stream n	Kaneohe Stream Distance (km)
Spring release					**Summer release**				
Waiahole	1	3.05	0	15.00	Waiahole	0	3.05	0	15.00
Kaalaea	92	0.98	0	12.59	Kaalaea	14	0.98	0	12.59
Kahaluu	509	0	1	12.04	Kahaluu	298	0	0	12.04
Heeia	0	5.55	1	5.88	Heeia	0	5.55	0	5.88
Keaahala	0	10.61	31	1.08	Keaahala	1	10.61	57	1.08
Kaneohe	1	11.58	947	0	Kaneohe	0	11.58	392	0
Total	603		980		Total	313		449	

and direct relationship between size-at-release and recapture rate (Fig. 4)—when fish were released in summer, recapture frequency was almost directly proportional to size-at-release within 1 month after release. This pattern was evident throughout the rest of the study. In contrast, size-at-release had much less effect on recapture frequencies for fish released 10 weeks earlier, in the spring (Fig. 5).

Recapture frequencies of small tagged fish (<70 mm TL) were clearly greater throughout collections made following spring releases than in those after summer releases. After 45 weeks in the wild, fish from the smallest size classes released in spring remained abundant in net samples. The relative impact derived from the smallest fish released in spring (45–60 mm) corresponded to impacts of some of the larger sizes released. In contrast, on the majority of collection dates following summer releases, not a single individual (released in summer) was collected from the 45-mm to 60-mm size-at-release group. After a few months in the wild, the larger fish released (>85 mm) generally were more abundant in samples when they were liberated in summer rather than in spring.

To compare recapture frequencies statistically among size-at-release intervals, values per release lot were summed across weeks for the period between 16 and 36 weeks after releases. After summer releases, mean recapture frequencies of fish <70 mm when released were substantially less than frequencies for fish > 85 mm when released (Fig. 6; ANOVA, $P < 0.001$ in a posteriori orthogonal contrasts [Sokal and Rohlf, 1981] of intervals 1 and 2 combined versus intervals 4 and 5 combined).

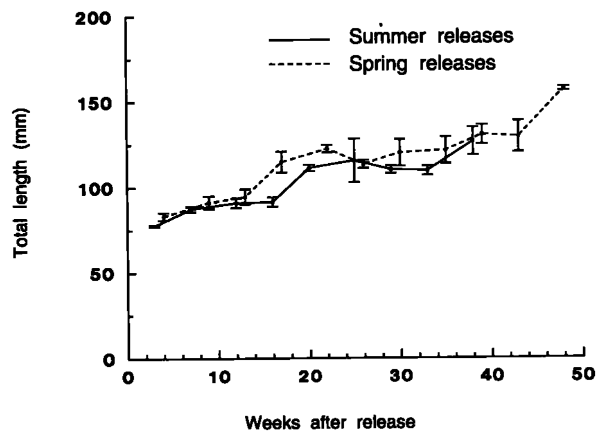

Figure 3

Mean total length (± SE) of cultured fish recaptured in collections made following spring and summer releases into Kaneohe Bay. Data are for the 70–85 mm size-at-release interval. Length was averaged within replicate release lots. Standard errors were based on replication established by release lots (n=6 lots per season [3 at each release site], not total number of individuals recaptured).

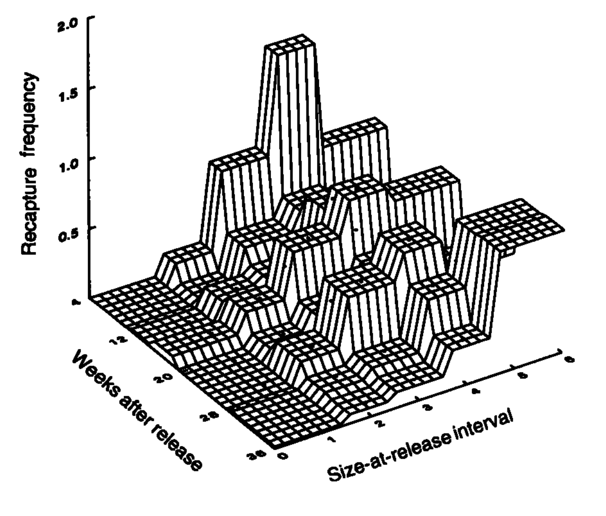

Figure 4

Recapture frequencies of tagged cultured *Mugil cephalus* recaptured in cast-net samples after summer releases into Kaneohe Bay. Data are presented for each of the five size intervals released (size-at-release: 1=40–60 mm total length, 2=60–70 mm, 3=70–85 mm, 4=85–110 mm, and 5=110–130 mm). Data are given as percent recaptured fish of the total fish released per size-at-release interval.

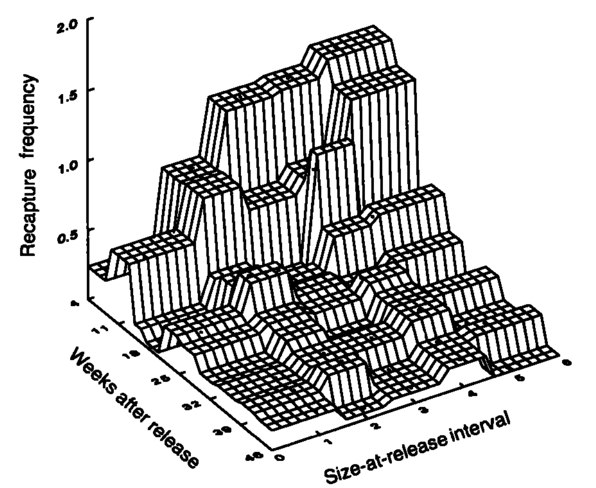

Figure 5

Recapture frequencies of tagged cultured *Mugil cephalus* recaptured in cast net samples after spring releases into Kaneohe Bay. See Figure 4 for description of fish size-at-release. Data are given as percent recaptured fish of the total fish released per size-at-release interval.

However, with the data from spring releases, mean recapture frequency of the smallest fish released (45 to 60 mm) was statistically similar to frequencies of some of the larger fish released (70 to 85 mm and those >110 mm) (Fig. 7; P=0.33). Fish from groups 2 and 4 (60 to 70 mm and 85 to 110 mm when released) had marginally greater recapture frequencies than those for small fish (P <0.03; spring releases). Fish from the two largest size intervals (fish >85 mm) released in summer exhibited mean recapture frequencies about twice as high as those for any size fish from spring releases (P<0.02).

Interaction between size-at-release effects and release season effects was statistically significant (P=0.01, season × size interaction term, Table 5). A significant interaction term indicates dependence of one factor upon the other; in this case, size-at-release affected recapture rate (P<0.001), but the degree of that effect depended upon release season.

Size structures of released cultured *Mugil cephalus* and wild recruits A comparison of the sizes of fish in cast-net scamples revealed that similar-size individuals schooled together. One month after spring releases, most of the smaller tagged striped mullet collected were schooling with relatively large numbers of wild *M. cephalus* similar in size to the tagged individuals. However, the larger cultured fish released found relatively few counterparts in size among wild individuals at that time (Fig. 8). The size structure of cultured fish released in spring was clearly out of phase with the wild recruitment pulse at that time. Whereas we had timed spring releases

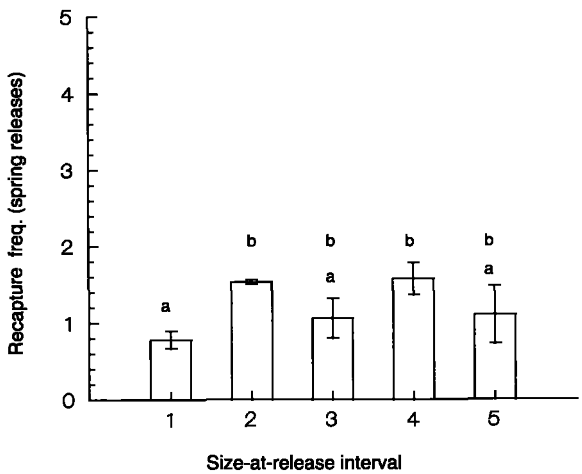

Figure 7

Recapture frequencies (± SE, n=6 lots) for the five sizes of fish released into Kaneohe Bay during spring releases (see Fig. 4 for description of fish size-at-release). Data are mean recapture frequencies per release lot ([number recaptured/number released] × 100%) summed over collections made between 16 and 36 weeks after release. Letters above bars indicate results of multiple comparisons of means; size-at-release intervals that share the same letter were not significantly different.

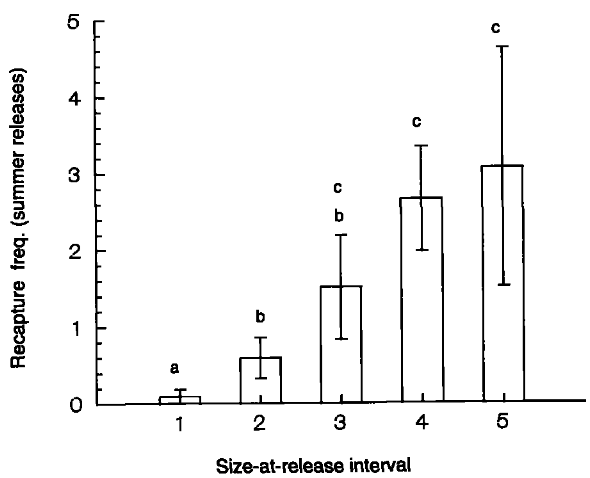

Figure 6

Mean recapture frequencies (± SE, n=6 lots) for the five sizes of fish released into Kaneohe Bay during summer releases (see Fig. 4 for description of fish size-at-release). Data are mean recapture frequencies per release lot ([number recaptured/number released] × 100%) summed over collections made between 16 and 36 weeks after release. See Figure 4 for description of fish size-at-release codes. Letters above bars indicate results of multiple comparisons of means; size-at-release intervals that share the same letter were not significantly different.

Table 5

ANOVA table (randomized-block design, lots=blocking variable) for evaluation of release season and size-at-release effects on recapture frequencies after 4 months in the wild. Data (means per release lot) were combined here over the 20-week period following 4 months in the wild (weeks 16 to 36). Recapture frequencies are percent of the total number of fish released that were recovered during this period; these proportions were arc-sin square-root transformed prior to analysis.

Source of variation	Sum of squares	df	Mean square	F-ratio	P
Release lot	0.009	2	0.004	4.309	0.030
Release season	0.000	1	0.000	0.021	0.886
Size-at-release	0.030	4	0.007	7.173	0.001
Season × size	0.019	4	0.005	4.577	0.010
Error	0.019	18	0.001		

to coincide with peak abundances of young-of-the-year recruits in these nursery habitats, the modal size of cultured fish led that of the wild recruitment pulse by around 30 mm at one month after spring releases. In contrast, the size structures of wild young-of-the-year and cultured fish were nearly identical 1 month after summer releases (Fig. 9).

Discussion

Recapture rates and release impact

Release impact on striped mullet abundance was comparable to contributions from experimental releases of cod in Norway (e.g. Kristiansen and Svasand, 1990; Nordeide et al., 1994), red drum in Florida (Willis et al., 1995), and to proportions of cultured flounder in commercial landings in Japan (Kitada et al., 1992). Cultured striped mullet amounted to no less than 7% of the fish in monthly samples throughout the 11-month study period at both release sites. By the end of this study, cultured fish represented about 12% of the striped mullet sampled at Kahaluu Stream, over 40% of those sampled in Kaneohe Stream, and 13.6% of the total collected in Kaneohe Bay.

There was clearly an improvement in this study in recapture frequencies compared with initial releases into the Bay in 1990 (Leber, 1995). The improvement was largely due to adjusting release strategy in this study to avoid releases outside of streams, the nursery habitats preferred by striped mullet. Recovery rates (number recaptured/number released) × 100%) of fish released at Kahaluu Stream in 1991 (this study) were similar to rates following a release of 10,000 fish at the same site in 1990; whereas, considerably fewer striped mullet were recovered following 1990 releases of 30,000 fish into more marine conditions near Coconut Island in the southern portion of the bay (authors' unpubl. data for juveniles; and see Leber and Arce, 1996, for data on adults).

Temporal changes in abundance of released fish

Reduction in abundance of cultured fish over time at release sites was likely a result of 1) mortality, 2) emigration from nursery habitats into adjacent reef habitats in the bay, and 3) sampling bias as fish grew to larger sizes and moved out of shallow water. Mortality appeared to be more important than emigration as the cause for reduction over time in recapture rates.

Juvenile striped mullet have a relatively strong affinity for brackish water during the nursery stage of their life cycle (Major, 1978; Blaber, 1987). After earlier pilot releases, when cultured striped mullet were released into more marine conditions (surface salinities >25 ppt), they schooled in both directions along the shore and rapidly occupied nearly all striped mullet nursery habitats (streams and tributaries) in those bay systems (Leber, 1995). In contrast, when striped mullet were released into habitats with lower surface salinities, as in this study, the majority of individuals recaptured were caught at or near the release site (Leber et al., 1995, 1996).

Had emigration out of release habitats remained high in this study after fish had had time to accli-

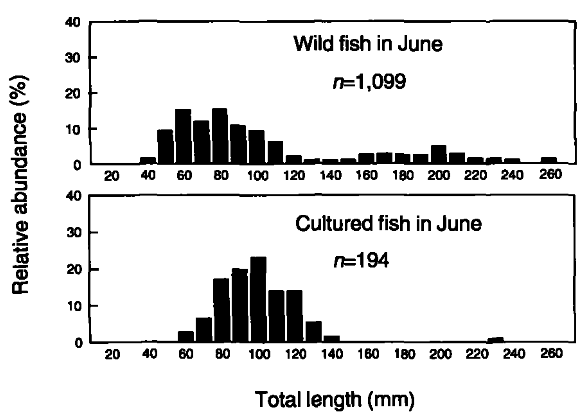

Figure 8
Size structures of wild and cultured *Mugil cephalus* collected in samples made about 1 month following spring releases into Kaneohe Bay.

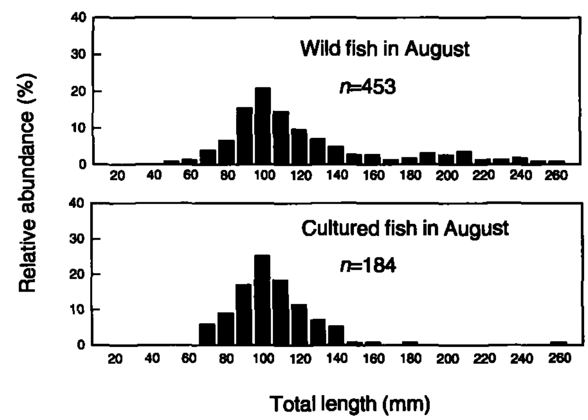

Figure 9
Size structures of wild and cultured *Mugil cephalus* collected in samples made about 1 month following summer releases into Kaneohe Bay.

mate in the wild, then cultured individuals should have occupied several of the other tributaries sampled. However, few tagged fish were collected farther than 1 km away from either release site, and the difference in proportions of cultured fish retrieved outside of release sites, compared with proportions collected at release sites, did not increase over time. These data (Table 4) provide circumstantial evidence that, following 2 weeks of acclimation in the wild, cultured striped mullet then tended to stay at or near the stream they occupied for the duration of the study. Strong site fidelity (during the juvenile stage) has also been documented in marine nursery habitats following hatchery releases of lobster (Bannister and Howard, 1991; Latrouite and Lorec, 1991) and cod (e.g. Nordeide et al., 1994).

Impact of release season

Fish size-at-release is clearly an important mediator of the effect of hatchery releases on stock abundance (Hager and Noble, 1976; Bilton et al., 1982; Tsukamoto et al., 1989; Liu, 1990; Svasand and Kristiansen, 1990; Ray et al., 1994; Leber, 1995; Wahl et al., 1995; Willis et al., 1995). At all of the release sites tested in Hawaii, size-at-release has been an important factor affecting recapture probability of cultured striped mullet (Leber, 1995; Leber et al.[1]). In previous studies with striped mullet, where releases were conducted in summer and fall, recapture rate was directly related to size of fish at the time of release.

As expected (Leber, 1995), in this study recapture rates after summer releases of small fish (individuals <60 mm long) approached zero and were an order of magnitude less than recapture rates of the larger fish released. Thus, when releases are made in summer in Kaneohe Bay, small (<60 mm) cultured striped mullet do not significantly affect juvenile recruitment in Kaneohe Bay. It is important to note that the fish in the different size intervals released were produced from multiple rearings and that the smallest fish released in summer were not merely the slowest growing individuals; rather, size-at-release was related primarily to age.

A new finding revealed by this study was that the seasonal timing of striped mullet releases can substantially alter size-at-release effect on recapture rate. Compared with recapture rates after summer releases, recovery of the smallest individuals released was significantly greater when releases were timed to coincide with peak recruitment of small wild individuals (in the spring). This was the first evidence that releases of relatively small (45 to 60 mm TL) individuals could make any lasting contribution to striped mullet abundances in nursery habitats on Oahu. Subsequently, Leber and Arce (1996) showed that some of the small fish released in spring did survive to adult size and contribute to the commercial fishery catch in Kaneohe Bay. The latter study also revealed that the smallest individuals in summer releases from this study apparently suffered total mortality. Because of the obvious economic importance of our findings, we replicated part of this study in a follow up study, with spring releases of the same size groups studied here; the results were identical— small fish (<60 mm) did contribute to juvenile recruitment when releases were made in spring (Leber et al., 1996).

It is not clear how one is to interpret the lack of a strong correlation between size-at-release and recapture rates following the spring releases. On the basis of cast-net samples alone, we cannot rule out the possibility that a direct relation existed between size-at-release and survival after spring releases. Cast nets are biased in favor of collecting small individuals (Leber et al.[1]). Thus, a weak size-at-release effect following spring releases could be masked by sampling bias. Indeed, for fish from the spring releases, data from subsequent samples of adult cultured fish caught in the Kaneohe Bay mullet fishery revealed a (nonsignificant) trend towards a direct size-at-release effect (Leber and Arce, 1996). As in this study of juveniles, the data for adults revealed a highly significant effect of size-at-release on recovery rates when releases were made in summer.

On the basis of this study and on subsequent data on adult recruitment to the commercial fishery (Leber and Arce, 1996), striped mullet < 60 mm should not be released during summer in Kaneohe Bay. However, early (spring) releases of 45–60 mm striped mullet can make a contribution both to juvenile recruitment (this study) and to adult recruitment (Leber and Arce, 1996). Maximum recovery from summer releases will occur when individuals are >85 mm at the time of release. To determine optimal size-at-release, an economic analysis is needed to evaluate benefits and costs of releasing larger individuals.

Bilton et al. (1982) showed an interaction between release timing and size of juvenile coho salmon, *Oncorhynchus kisutch*, released in British Columbia. In that study, returns would be maximized from early release of large juveniles. The effect of the seasonal timing of releases on size-dependent recapture rates may not be universal (e.g. Willis et al., 1995); nevertheless, release season could be a key factor in successful enhancement of many marine species.

What processes could account for the seasonal change in size-at-release dependent recapture rates? Size structures of cultured and wild fish suggest that schooling behavior of striped mullet may partly control the release-season effect. Schools of juvenile striped mullet are usually aggregated according to size (Leber, 1995). Because of the difference in size structures between wild and cultured fish in the spring, schools of larger striped mullet, after spring releases, contained mostly cultured fish and few wild fish. We hypothesize that at the time of spring releases, the large individuals were more susceptible than smaller ones to mortality from predation. We reason that, because the smallest fish released in spring had merged with relatively large numbers of small wild striped mullet, the smallest fish should have been afforded greater refuge from predators than that provided the large fish in our spring releases, because there were more small wild fish than large ones (i.e. refuge effect from schooling behavior; e.g. Parrish, 1989, 1992; deVries, 1990; Ranta et al., 1994).

This pattern was reversed following summer releases, when size structures of the larger cultured and wild individuals were equivalent. By summer, most wild juveniles had grown larger than the size range of the smallest cultured individuals released. Thus, few small wild juveniles were available to form schools with small cultured fish and thus the advantage of refuge that such schooling behavior would provide to small cultured fish was reduced.

The results of this study are consistent with the hypothesis that size-selective predation is a primary mechanism controlling recapture rates following hatchery releases in Kaneohe Bay (Leber, 1995). Although, after summer releases, large wild fish were not as abundant as small wild fish in the spring (thus reducing the advantage gained by cultured fish from schooling with large wild fish), larger cultured fish would have the added advantage of size in escape from predators. Whatever the cause(s) of size-at-release impact on recovery rates, it was clear from this study that release season can influence the underlying mechanism.

Conclusions

The importance of conducting test releases to evaluate release strategies prior to conducting full-scale hatchery releases cannot be overemphasized. This study documented that release season can have a significant effect upon recovery of cultured striped mullet in the wild by affecting size-at-release dependent recapture rates. To optimize the impact of full-scale releases, marine stock-enhancement programs should perform test releases to evaluate interaction of release season with size-at-release effects.

We hypothesize that survival of cultured fish will be greater when releases are timed so that size-at-release coincides with modes in population size structures of wild stocks. A corollary to this is that the fewer cultured fish there are in a particular size interval at the time of release, the lower survival will be for wild fish in that interval.

These results need to be related to the hatchery costs of rearing fingerlings to various sizes and also to the increased production allowed by releasing small fingerlings in the spring, because spring releases would make nursery tanks or ponds available to grow more fish for summer releases.

Although the mechanism underlying the direct relationship between survival and size-at-release is not well understood, it is clear that in Hawaii, fish size-at-release can determine release success following summer releases of striped mullet. Based on this study, critical release size (CSAR, the size-at-release below which probability of survival approaches zero; Leber, 1995) for enhancing striped mullet in Kaneohe Bay appears to be lower when releases are made in spring (CSAR <45 mm) than when releases are made in summer (CSAR <60 mm).

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Literature cited

Bannister, R. C. A., and A. E. Howard.
1991. A large-scale experiment to enhance a stock of lobster (*Homarus gammarus* L.) on the English east coast. ICES Mar. Sci. Symp. 192:99–107

Bilton, H. T., D. F. Alderdice, and J. T. Schnute.
1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Can. J. Fish. Aquat. Sci. 39:426–447.

Blaber, S. J. M.
1987. Factors affecting recruitment and survival of mugilids in estuaries and coastal waters of Southeastern Africa. Am. Fish. Soc. Symp. 1:507–518.

Blankenship, H. L.
1990. Effects of time and fish size on coded wire tag loss from chinook and coho salmon. Am. Fish. Soc. Symp. 7:237–243.

Blankenship, H. L., and K. M. Leber.
1995. A responsible approach to marine stock enhancement. *In* H. L. Schramm Jr. and R. G. Piper (eds.), Uses and effects of cultured fishes in aquatic ecosystems, p. 165–175. Am. Fish. Soc. Symp. 15.

Colura, R. L., B. T. Hysmith, and R. E. Stevens.
1976. Fingerling production of striped bass (*Morone saxatilis*), spotted seatrout (*Cynoscion nebulosus*), and red drum (*Sciaenops ocellatus*) in saltwater ponds. Proceedings of the World Mariculture Society 7:79–92.

Cowx, I. G.
1994. Stocking strategies. Fish. Manage. Ecol. 1:15–30.

deVries, D. R.
1990. Habitat use by bluegill in laboratory pools: Where is the refuge when macrophytes are sparse and alternative prey are present? Environ. Biol. Fish. 29(1):27–34.

Eda, H., R. Murashige, Y. Oozeki, A. Hagiwara, B. Eastham, P. Bass, C. S. Tamaru, and C.-S. Lee.
1990. Factors affecting intensive larval rearing of striped mullet, *Mugil cephalus.* Aquaculture 91:281–294.

FAO (Food and Agriculture Organization of the United Nations).
1992. Food and Agriculture Organization of the United Nations yearbook: fishery statistics 70 (1990). FAO, Rome.
1994. Marine Resources Service, Fishery Resources and Environmental Division, FAO Fisheries Department. Review of the state of world marine fishery resources. FAO Fish. Tech. Pap. 335. Rome, 136 p.

Foerster, R. E.
1936. The return from the sea of sockeye salmon, *Oncorhynchus nerka*, with special reference to percentage survival, sex proportions and progress of migration. J. Biol. Board Can. 3:26–42.

Forés, R., J. Iglesias, M. Olmedo, F. J. Sánchez, and J. B. Peleteiro.
1990. Induction of spawning in turbot (*Scophthalmus maximus* L.) by a sudden change in the photoperiod. Aquacult. Eng. 9:357–366.

Jefferts, K. B., P. K. Bergman, and H. F. Fiscus.
1963. A coded-wire identification system for macroorganisms. Nature (Lon.) 198:460–462.

Kitada, S., Y. Taga, and H. Kishino.
1992. Effectiveness of a stock enhancement program evaluated by a two-stage sampling survey of commercial landings. Can. J. Fish. Aquat. Sci. 49:1573–1582.

Hager, R. C., and R. E. Noble.
1976. Relation of size at release of hatchery-reared coho salmon to age, size, and sex composition of returning adults. Prog. Fish-Cult. 38:144–147.

Honma, A.
1993. Aquaculture in Japan. Japan FAO Assoc., Tokyo, 98 p.

Kristiansen, T. S., and T. Svåsand.
1990. Enhancement studies of coastal cod in western Norway. Part III: Interrelationships between reared and indigenous cod in a nearly land-locked fjord. J. Int. Counc. Explor. Sea 47:23–29.

Latrouite, D., and J. Lorec.
1991. L'expérience française de forçage du recrutement du homard européen (*Homarus gammarus*): résultats préliminaires. ICES Mar. Sci. Symp. 192:93–98.

Leber, K. M.
1995. Significance of fish size-at-release on enhancement of striped mullet fisheries in Hawaii. J. World Aquacult. Soc. 26:143–153.

Leber, K. M., and S. M. Arce.
1996. Stock enhancement effect in a commercial mullet (*Mugil cephalus* L.) fishery in Hawaii. Fish. Manage. Ecol. 3:261–278.

Leber, K. M., S. M. Arce, D. A. Sterritt, and N. P. Brennan.
1996. Marine stock enhancement potential in nursery habitats of striped mullet, *Mugil cephalus*, in Hawaii. Fish. Bull. 94(3):452–471.

Leber, K. M., N. P. Brennan, and S. M. Arce.
1995. Marine enhancement with striped mullet: Are hatchery releases replenishing or displacing wild stocks? *In* H. L. Schramm Jr. and R. G. Piper (eds.), Uses and effects of cultured fishes in aquatic ecosystems, p. 376–387. Am. Fish. Soc. Symp. 15.

Lee, C.-S., and C. S. Tamaru.
1988. Advances and future prospects in controlled maturation and spawning of grey mullet (*Mugil cephalus*) L. in captivity. Aquaculture 74 (1 and 2):63–73.

Liu, J. Y.
1990. Resource enhancement of Chinese shrimp, *Penaeus orientalis*. Bull. Mar. Sci. 47:124–133

Main and Rosenfeld.
1994. Culture of high-value marine fishes in Asia and the United States. The Oceanic Institute. Honolulu, HI, 319 p.

Major, P. F.
1978. Aspects of estuarine intertidal ecology of juvenile striped mullet, *Mugil cephalus*, in Hawaii. Fish. Bull. 76(2): 299–314.

Nordeide, J. T., J. H. Fosså, A. G. V. Salvanes, and O. M. Smedstad.
1994. Testing if year-class strength of coastal cod, *Gadus morhua* L., can be determined at the juvenile stage. Aquacult. Fish. Manage. 25 (suppl. 1):101–116.

Øiestad, V., P. G. Kvenseth, and A. Folkvord.
1985. Mass production of Atlantic cod juveniles (*Gaddus morhua* L.) in a Norwegian saltwater pond. Trans. Am. Fish. Soc. 114:590–595.

Ostrowski, A. C., T. Iwai, S. Monahan, S. Unger, D. Dagdagan, P. Murakawa, A. Schivell, and C. Pigao.
1996. Nursery production technology for Pacific threadfin (*Polydactylus sexfilis*). Aquaculture 139:19–29.

Parrish, J. K.
1989. Re-examining the selfish herd: are central fish safer? Anim. Behav. 38(6):1048–1053.
1992. Do predators "shape" fish schools: Interactions between predators and their schooling prey. Neth. J. Zool. 42:358–370.

Peterman, R. M.
1991. Density-dependent marine processes in North Pacific salmonids: lessons for experimental design of large-scale manipulations of fish stocks. ICES Mar. Sci. Symp. 192:69–77.

Ranta, E., N. Peuhkuri, and A. Laurila.
1994. A theoretical exploration of antipredatory and foraging factors promoting phenotype-assorted fish schools. Ecoscience 1(2):99–106.

Ray, M., A. W. Stoner, and S. M. O'Connell.
1994. Size-specific predation of juvenile queen conch *Strombus gigas*: implications for stock enhancement. Aquaculture 128:79–88.

Roberts, D. E., Jr., B. V. Harpster, and G. E. Henderson.
1978. Conditioning and induced spawning of the red drum (*Sciaenops ocellatus*) under varied conditions of photoperiod and temperature. Proceedings of the World Mariculture Society 9:311–332.

Sokal, R. R., and F. J. Rohlf.
1981. Biometry. W.H. Freeman, San Francisco, CA.
Solazzi, M. F., T. E. Nickelson, and S. L. Johnson.
1991. Survival, contribution, and return of hatchery coho salmon (*Oncorhynchus kisutch*) released into freshwater, estuarine, and marine environments. Can. J. Fish. Aquat. Sci. 48:248–253.
Stoner, A. W.
1994. Significance of habitat and stock pre-testing for enhancement of natural fisheries: experimental analysis with queen conch *Strombus gigas*. J. World Aquacult. Soc. 25:155–165.
Svåsand, T., and T. S. Kristiansen.
1990. Enhancement studies of coastal cod in western Norway. Part IV: Mortality of reared cod after release. J. Cons. Cons. Int. Explor. Mer 47:30–39.
Tilseth, S., and G. Blom.
1992. Recent progress in research and development of marine cold water species for aquaculture production in Norway. J. World Aquacult. Soc. 23(4):277–285.
Tsukamoto, K., H. Kuwada, J Hirokawa, M. Oya, S. Sekiya, H. Fugimoto, and K. Imaizumi.
1989. Size-dependent mortality of red sea bream, *Pagrus major,* juveniles released with fluorescent otolith tags in News Bay. J. Fish Biol. 35(suppl. A):56–69.
Wahl, D. H., R. A. Stein, and D. R. DeVries.
1995. An ecological framework for evaluating the success and effects of stocked fishes. Am. Fish. Soc. Symp.15:176–189.
Wilkinson, L.
1990. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL, 676 p.
Willis, S. A., W. W. Falls, C. W. Dennis, D. E. Roberts, and P. G. Whitchurch.
1995. Assessment of season-of-release and size-at-release on recapture rates of hatchery-reared red drum (*Sciaenops ocellatus*) in a marine stock enhancement program in Florida. Am. Fish. Soc. Symp.15:354–365.
WRI (World Resources Institute).
1996. World resources 1996–1997. Oxford Univ. Press, New York, NY, 400 p.